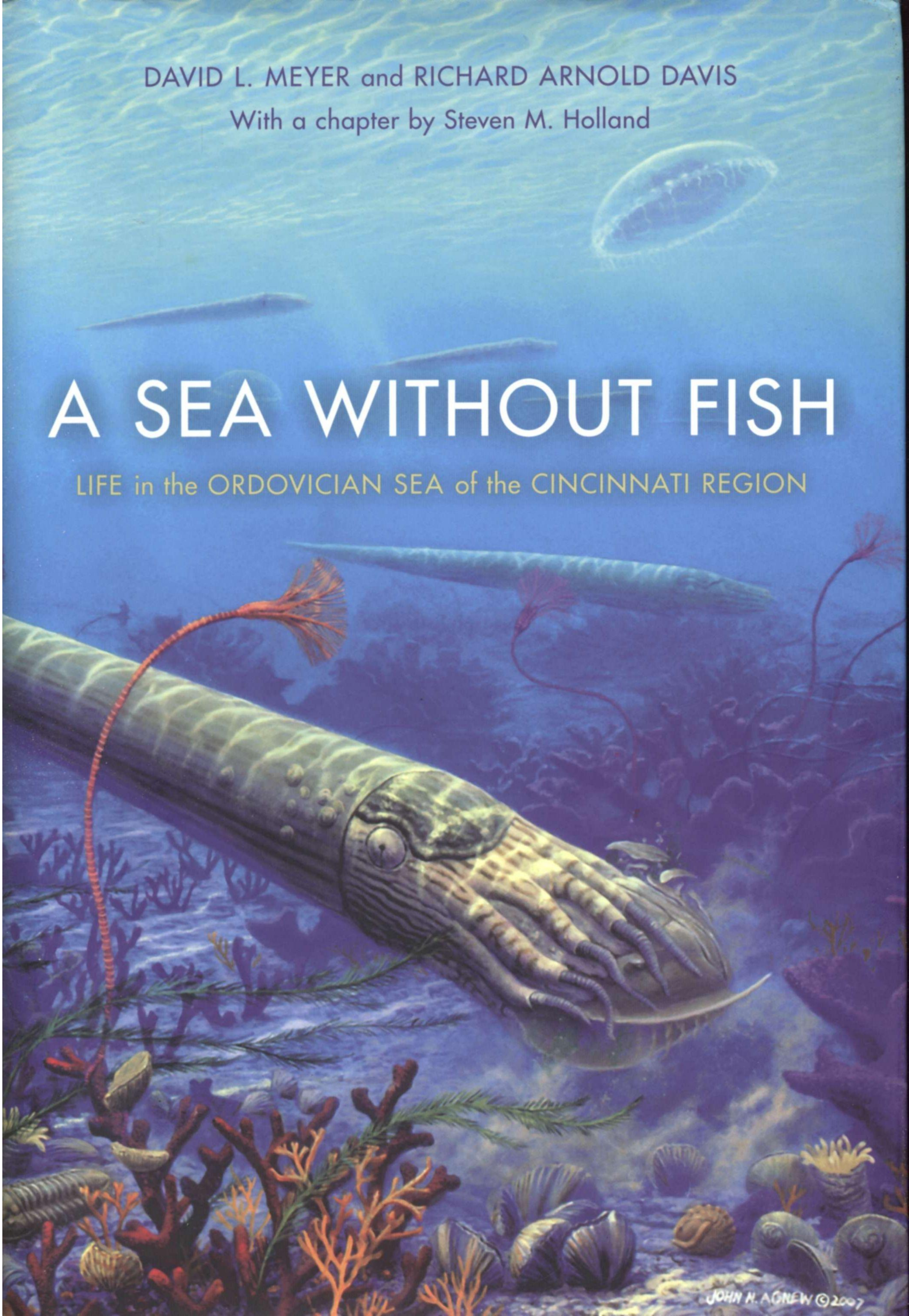
DAVID L. MEYER and RICHARD ARNOLD DAVIS

With a chapter by Steven M. Holland

A SEA WITHOUT FISH

LIFE in the ORDOVICIAN SEA of the CINCINNATI REGION



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The worldwide fame of the fossils and rocks of the Cincinnati, Ohio, region grew out of the labors of myriad amateur fossil collectors. The current embodiment of those folk is the "Dry Dredgers, " a group founded in Cincinnati in 1942 and, to this day, dedicated to collecting and understanding those fossils.

We dedicate this volume to the "Dry Dredgers" and to the host of fossil collectors they represent. *Vos salukimus!*

CONTENTS

PREFACE

Two principal goals motivated us to write this book. First, knowledge of the Earth's ancient history from geology provides a powerful lesson about the ever-changing nature of the planet, and the ancient history of one's home region can be particularly meaningful. The present nature of the landscape in the Cincinnati region (southwestern Ohio, northern Kentucky, and southeastern Indiana) is the product of its most recent geologic history, the Pleistocene ice Age, when continental ice sheets repeatedly forced their way as far south as the Ohio River. As recently as 20,000 years ago, much of southwestern Ohio was covered with an ice sheet much as Greenland is today. As the glaciers receded, melt waters carved the present valleys and left a mantle of debris that determined the topography, drainage, soils, and vegetation of the region. A magnificent Ice Age exhibit at the Cincinnati Museum Center enhances public awareness of the profound environmental changes that took place across the region in the short time span in which humans inhabited the ice-free land. Three works also provide a concise history of the environmental changes during the Ice Age: Richard H. Durrell's A *Recycled Landscape* (1977), Richard Arnold Davis's "Land Fit for a Queen: The Geology of Cincinnati" (1981), and the recently published *Natural History of the Cincinnati Region,* by Stanley Hedeen (2006).

As impressive as the Ice Age history of the region is as evidence of geologic and climatic change, the story that can be told from the ancient bedrock underlying the Pleistocene cover extends the record of global change into deep time. The bedrock exposed at the surface across southwestern Ohio, northern Kentucky, and southeastern Indiana is the record of the Ordovician sea of some 450,000,000 years ago, one of the most extensive marine flooding intervals of the North American continent during Earth history. In stark contrast to the barren ice sheet of the Pleistocene, the Cincinnati seascape of the Ordovician was water from horizon to horizon—not a deep ocean blue, but perhaps shades of aquamarine like the waters over the present-day shallow Great Bahama Bank. No landmasses broke the horizon, and no birds crossed the skies. All the action was beneath the sea surface, where life thrived in abundance. This profusion of life left a fossil record in the rocks that formed from the bottom sediments of the Cincinnatian sea that is among the world's richest treasure troves of the past. For present-day Cincinnatians, fossils in their backyards are a commonplace, and many natives grow up not realizing that most of the rest of the world has nothing to rival the fossil riches of their home! We seek to recount the history of the Cincinnati region in deep time, its vastly different environment and marine life, for the general public and for amateur geologists.

Many local residents who have been fascinated by the fossils underfoot collected and studied them almost since the earliest settlements of the eighteenth and nineteenth centuries. Generations of geologists and paleontologists from abroad have visited the region and written of the abundant fossils and the strata, including the pioneering British geologist Charles Lyell in 1842. Because the Cincinnati region has been a focus for geological research by so many scientists over so main years, there exists today a vast amount of information about the fossils and rocks of the region. This information is scattered in many sources, including the latest issues of some of the world's leading international geological journals, Internet websites, and numerous types of publications, some widely available, some obscure. Much of the early work describing new species of Cincinnati fossils dates to the second half of the nineteenth century, and is found in periodicals no longer published, such as the *Cincinnati Quarterly journal of Science, The Paleontologist,* and the *Journal of the Cincinnati Society of Natural History.* No single library houses all of the geological information published about the Cincinnati region. Moreover, most studies deal with only a small fraction of the total fossil richness of the region, and, most importantly for us, there has never been a synthesis of the vast range of fossil diversity and its geological context. In this book we present a synthesis that will reconstruct the life of the Ordovician sea in order to show not only what organisms inhabited this sea but also how they lived and interacted with each other to constitute the variety of ecosystems of the Ordovician sea in the Cincinnati region. The book is not intended as a textbook of geology or paleontology, but we present sufficient background information on each fossil group and the geological context for readers unfamiliar with fossils and geology. We explain what kind of animal each fossil represents and how it lived and interacted with other organisms, thereby defining the role of each group of animals in its ancient ecosystem. We hope that this approach will benefit readers with a background in geology as well as those seeking an introduction to the fossils and rocks of the Cincinnati region.

Conventions

In scientific publications, certain conventions are used to save time and trouble. These are understood by the scientists who generally write and read such publications. Because this is a scientific work, we have used some of these conventions. However, this book is also intended for the general reader who might not be familiar with such conventions. IHere are some explanations:

Literature Citations in the Text

Footnotes or endnotes are not ordinarily used in scientific publications. Instead, literature citations are inserted in the text. This commonly is done where it is appropriate in the context. At other times, especially in instances in which the reader is being referred to a number of publications, the literature citation may be at the end of the appropriate sentence or paragraph. Those enamored of footnotes or endnotes might find this peculiar, but the idea is for the reader to be referred to other publications immediately, and not have to search at the bottom of the page or the end of the chapter, or, even, volume, for the pertinent reference.

Thus, when we refer you to a publication, the literature citation will be in the following format: "(S. A. Miller 1875). " This means that you are being referred to a publication authored by S. A. Miller and published in 1875; hence, you know who said what is being cited and when. If you need the complete bibliographic information about that publication, it is provided in the bibliography toward the end of the volume. In cases in which it is important for you to know the page number within that publication where the information or quotation is found, the literature citation will be in the form "(S. A. Miller 1875, 87). "

Names of Organisms and Groups of Organisms

By international agreement of zoologists, the *International Code of Zoological Nomenclature* is the document that specifies how the names of species, genera, and other groups of animals are stated and used in scientific works (International Commission on Zoological Nomenclature 1999). General recommendation Bio of the Code encourages that the author and date of every taxon in the species group, genus group, or family group mentioned in a publication be cited at least once in that publication, and recommendation 51G encourages the full citation of original authors and dates as well as revisers and their dates. However, such citation of authors, dates, revisers, and dates of revisions does detract from the flow of the words. Because of the intended audience of this volume, we have decided not to do such detailed citations on a routine basis, but, rather, only when clarity demands it. If you want to know the nomenclatorial history of a particular group of organisms, we recommend that you consult the scientific literature about the larger group of organisms to which those organisms belong. The bibliography of this volume is a good place to start.

We debated at some length as to whether to give a complete list of all the subdivisions for each major group of organisms discussed. We recognize that such listings might be genuinely useful for the really serious fossil-collector. However, we decided that, for the intended audience of this volume, the number of pages necessary would have made the book too long, and, hence, inordinately expensive. Up-to-date classifications can be found in the following references: the many volumes of the *Treatise on Invertebrate Paleontology* (a multi-authored, multi-edited series of volumes published by the Geological Society of America and the University Press of Kansas), the textbook *Fossil Invertebrates* (Boardman et al. 1987), or *Fossils of Ohio* (Feldmann and Hackathorn 1996).

Photographs, Drawings, Maps

Many of the illustrations in this volume were made specifically for this work: however, some were made by others and are used here with permission, in some instances, after modification (for example, to remove labels not pertinent to the present context). Unless otherwise indicated, a given photograph in this volume was prepared especially for this work, primarily by one of us (DLM).

Technical Terms and the Glossary

Science is replete with technical terms that do not appear commonly in non-scientific contexts. To make matters worse, scientists often use common, everyday terms in ways that are not their common, everyday usages. Thus, we felt it important to include a glossary; this is found near the end of the volume. In the interests of space, however, we have not included every technical term in this book in the glossary. For its first use, each technical term is defined and is in boldface type. Those technical terms that are used in more than one chapter are listed in the glossary. A technical term that is used in only one chapter, such as the name of an anatomical feature that occurs in only one major group of organisms, is defined the first time it is used in the volume; however, we have not listed such terms in the glossary—again, in the interests of space. Such words are listed in the index to the volume.

So what do you do if you find a technical term that is unfamiliar to you and the definition is not right there where you encounter the word? First, go to the glossary. If the technical term is not in the glossary, or if, God forbid!, the coverage of that term in the glossary is insufficient, then go to the index and then to the text of the book to which you are referred. (College professors, like us, sometimes are accused of stating the obvious. Generally, this is done in an attempt to answer the questions of some students in a given class before they are asked. There is, of course, a danger of offending other students in the same class who are more adept at recognizing the obvious. And so it is with readers as well!)

In the glossary, and elsewhere, we have included advice on how to pronounce terms. As you know, lexicographers have developed a scheme of symbols to indicate how they feel particular letters, syllables, and words should be pronounced. We have tried to keep the use of such symbols to a minimum. We hope that, in so doing, we still have managed to help you pronounce words in a way useful to you.

ACKNOWLEDGMENTS

We are very grateful to the following colleagues who read preliminary drafts of various chapters: Loren E. Babcock (The Ohio State University), Richard Bambach (Virginia Polytechnic Institute and State University), Steven H. Felton (Cincinnati), Robert J. Elias (University of Manitoba), J. Mark Erickson (St. Lawrence University), Steven M. Holland (University of Georgia), Steven Leslie (University of Arkansas, Little Rock), James Sprinkle (University of Texas), and Colin Sumrall (University of Tennessee). In particular, we thank Professor Holland for contributing the chapter on the Cincinnatian paleoenvironment.

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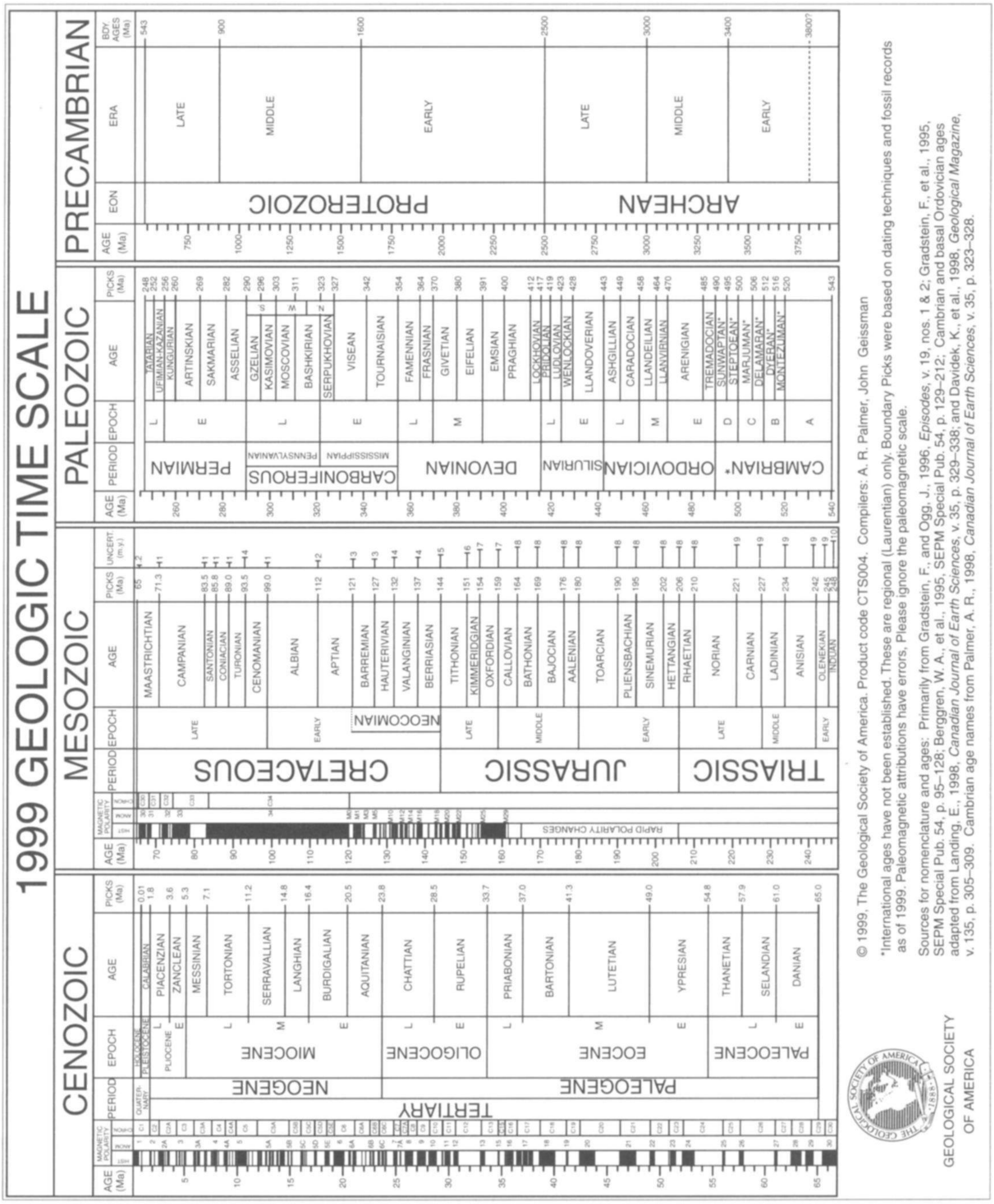
REPOSITORIES OF FOSSILS ILLUSTRATED IN THIS BOOK

BMNH	Natural History Museum, London
CMC IP	Cincinnati Museum Center, Invertebrate Paleontology Collections
FMNH	Field Museum of Natural History, Chicago, Illinois
MCZ	Harvard University, Museum of Comparative Zoology
MUGM	Miami University, Carl F. Limper Geological Museum, Oxford, Ohio
OSU	Orion Geological Museum, The Ohio State University, Columbus, Ohio
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

A SEA WITHOUT FISH



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*International ages have not been established. These are regional (Laurentian) only. Boundary Picks were based on dating techniques and fossil records as of 1999. Paleomagnetic attributions have errors, Please ignore the paleomagnetic scale.

Sources for nomenclature and ages: Primarily from Gradstein, F., and Ogg, J., 1996, *Episodes*, v. 19, nos. 1 & 2; Gradstein, F., et al., 1995, SEPM Special Pub. 54, p. 95–128; Berggren, W. A., et al., 1995, SEPM Special Pub. 54, p. 129–212; Cambrian and basal Ordovician ages adapted from Landing, E., 1998, *Canadian Journal of Earth Sciences*, v. 35, p. 329–338; and Davidek, K., et al., 1998, *Geological Magazine*, v. 135, p. 305–309. Cambrian age names from Palmer, A. R., 1998, *Canadian Journal of Earth Sciences*, v. 35, p. 323–328.

Figure 1.1. 7999 *Geologic Time Scale. Reprinted by permission of the Geological Society of America. In order to read this chart in stratigraphic order, read the columns from bottom to top, starting at the bottom of the Precambrian column, adding the bottom of the Paleozoic column to the top of the Precambrian column, the bottom of the Mesozoic column to the top of the Paleozoic column, and the bottom of the Cenozoic column to the top of the Mesozoic column.*

INTRODUCTION

1

> *Of the many prolific collecting grounds in the continental interior, none excels the Ohio river bluffs at Cincinnati, Ohio. Here the Upper Ordovician rocks are almost literally made of fossils; many are as perfectly preserved as fossils can be. The river banks, road cuts, and even the soil in the gardens are replete with fossils more common than pebbles. Almost every museum in the world has specimens from this locality.*
>
> **William Lee Stokes**
> **1960, 188-189**

The vicinity of Cincinnati, in the Ohio River Valley of southwestern Ohio, including adjacent northern Kentucky and southeastern Indiana, is among the most fossil-rich regions in North America, if not the entire world. The profusion of fossils in the local limestone and shale attracted many pioneering geologists and paleontologists of the nineteenth century, and much fundamental work in American paleontology and stratigraphy was accomplished here. Hundreds of fossil species were first discovered and named from these rocks. Early geologists gave the entire series of strata exposed here the name "Cincinnatian," and this name was applied to strata of similar age throughout North America. Cincinnatian fossils are displayed in museums all over the world. Researchers, students, and amateur fossil collectors regularly visit the Cincinnati region to collect fossils. Many of those who have grown up in the region are aware of the abundance of fossils, yet few appreciate the uniqueness of this richness and its broader significance to our understanding of the Earth's past. The purpose of this book is to explore the richness of Cincinnatian fossils and the stories they tell about life over 450 million years ago, when shallow seas inundated North America and the site of Cincinnati was in the Southern Hemisphere.

Why are fossils so abundant in the rocks of Cincinnati's hills? Beyond sheer abundance, what is their significance for our knowledge of the history of life, evolution, and ancient environments? There is no single answer to these questions, but rather several answers can be given which collectively reveal the significance of Cincinnatian fossils. These answers can be found under four categories: *organic evolution, environment, preservation,* and *history.*

Organic Evolution

> *[The Ordovician radiation] represents one of the largest major turnovers in the history of life and marks the appearance of groups that came to dominate marine ecosystems for the next 250 million years.*
>
> **Droser, Fortey, and Li 1996, 122**

Fossils found in Cincinnati's limestones and shales are the remains of animals that lived during an interval of Earth history called the Ordovician Period. The Ordovician is the second oldest period of the larger time interval known as the Paleozoic Era (Figure 1. 1). The beginning of the Paleozoic Era (meaning "time of ancient animals") is marked by the oldest rocks containing abundant fossils of multi-celled animals (metazoans). Radiometric dating of volcanic ash beds interbedded with these fossiliferous rocks places the beginning of the Paleozoic at about 543 million years ago. Similar methods date the beginning of the Ordovician Period at about 490 million years ago and its end at about 443 million years ago. The span of Ordovician time represented by the Cincinnatian strata amounted to less than 10 million years, and tell approximately during the latter part of the Ordovician, termed the Late Ordovician. In the Cincinnati region, a total thickness of over 250 me-

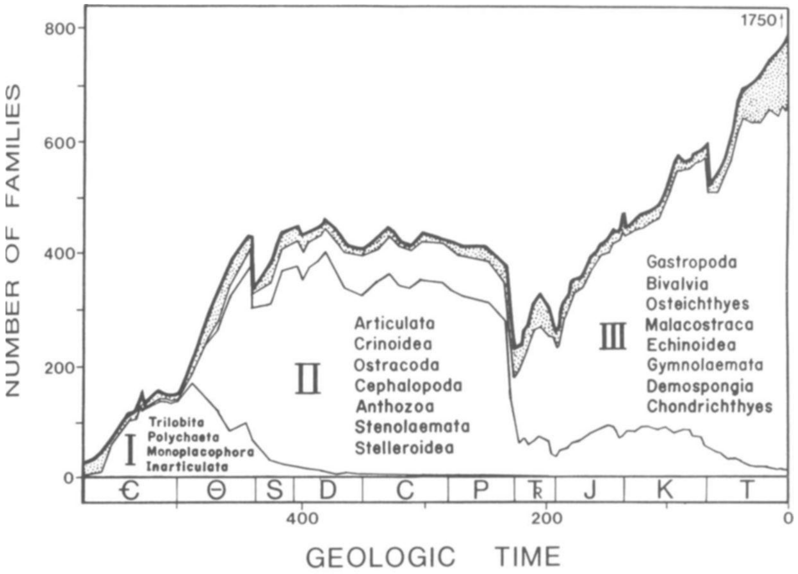


Figure 1. 2. *Diversity of marine fossil metazoan families through the Phanerozoic. The heavy uppermost curve depicts the sum of the three "evolutionary faunas," each shaded differently, while the stippled portion below the total curve represents residual diversity not accounted for by the three component faunas. Taxa listed for each evolutionary fauna are those taxa that contribute most heavily to the diversity of that fauna. I = Cambrian Fauna, II = Paleozoic Fauna, and III = Modern Fauna. From Sepkoski (1981) and reprinted by permission of The Paleontological Society.*

ters (820 feet) of interbedded limestone and shale was deposited during the Late Ordovician, constituting the Cincinnatian and containing fossils throughout. Further discussion of the nature and subdivisions of Cincinnatian rocks, and estimates of their age, are the subject of chapter 4.

Professor Stig M. Bergstrom of the Ohio State University is among the world's most knowledgeable and widely-traveled specialists on Ordovician fossils and stratigraphy. He indicated to us that "there is nothing that can be compared elsewhere in the world" to the diversity of shelly fossils in the Cincinnatian (Bergstrom, pers. comm.). Metazoan marine life first began to diversify during the so-called Cambrian explosion that marked the onset of the Paleozoic, but accelerated during the Cambrian and Ordovician Periods to reach a peak late in the Ordovician when the Cincinnatian strata were deposited. In fact the Ordovician Period is recognized as a unique time of evolutionary diversification, termed the Ordovician Radiation (Droser et al. 1996) or the Ordovician Biodiversification Event (Webby, Paris, Droser, and Percival 2004). The Ordovician marked a convergence of what Sepkoski (1981) called three "evolutionary faunas": metazoan groups that first appeared during the Cambrian but persisted into the Ordovician ("Cambrian Fauna"), groups that began to diversify during the Ordovician ("Paleozoic Fauna"), and groups that first appeared in the Ordovician that diversified after the end of the Paleozoic ("Modern Fauna") (Figure 1.2). At the end of the Ordovician there occurred a global mass extinction that eliminated species on a large scale. Thus the Cincinnatian time was significant in the history of life as a Golden Age of evolutionary diversification just before a major crisis of mass extinction. In many ways the Fate Ordovician is comparable to the Late Cretaceous Period, another Golden Age preceding a crisis (Figure 1. 2; Seilacher 1998). Few if any fossil species found in the Cincinnatian strata survived into the succeeding Silurian Period. Chapters 5-14 introduce each of the major groups of organisms found as fossils in the Cincinnatian.

Environment

*We are accustomed to thinking of North America as terra firma, one of the large high and dry segments of the earth's crust, and it is difficult for us to imagine a time in the past when our continent was so submerged beneath the sea that fish could have swum directly from the Atlantic Ocean to the Pacific Ocean, from Hudson Bay to the Gulf of Mexico. Yet such a time did exist 450 million years ago when the epeiric sea spread from Arctic to Gulf, from Atlantic to Pacific**

Clark and Stearn
1960, 68

The environment of Late Ordovician time in the Cincinnati region contributed to the abundance and richness of fossils in several fundamental ways. Cincinnatian fossils and rocks bear profound testimony to the existence of widespread shallow seas (called epicontinental or epeiric seas) over most of the North American continent at this time (Plate 1). Using many sources of evidence, geologists have compiled a record of the rise and fall of sea level during the past half billion years of Earth history (figure 1. 3). The Late Ordovician was one of the times of maximum rise of sea level over the entire globe, rivaled only by the Late Cretaceous (according to the reconstruction by Hallam [1984]). The cause of this flooding has been attributed to high rates of sea floor spreading which swelled the mid-ocean ridges, displacing immense volumes of seawater from the deep ocean basins onto the continental plates. The Atlantic Ocean as we know it did not exist, but instead, a narrower ocean called the Iapetus Ocean separated North America from continental plates later to constitute Europe and Africa (Plate 1). The nearest landmasses to the Cincinnati region were the rising Appalachian mountain chain, about 300 miles to the east, and the low-lying Canadian Shield to the north. Just before and during the Late Ordovician, a phase of major tectonic (mountain-building) activity, the Taconic Orogeny, resulted in severe crustal deformation and uplift along the region bordering New York and New England. Islands were raised high above sea level as lofty and jagged mountain chains resembling the modern Alps or Himalayas. Weathering and erosion attacked these ranges, and rivers carried huge loads of fresh water, sediments, and nutrients into the shallow sea.

Great volumes of sediment, consisting of coarse gravels, sands, silts, and muds (termed siliciclastics) were deposited as river deltas and redistributed by oceanic currents near the coastline in the Appalachian Basin. The total thickness of the Late Ordovician strata in the Appalachian Basin in Virginia reaches about 1000 meters (over 3000 feet) whereas the same time interval is represented in the Cincinnati region by strata less than 300 meters (less than 1000 feet) thick (Figure 1. 4; Kay 1951). Offshore, only the muddy components of this heavy sediment input remained suspended as clay particles, and were carried by currents to reach the Cincinnati area. These muds were thus imports to the region that eventually lithified (turned to stone) to form shales. In the Cincinnati area, shales are interbedded with limestones, which are composed of calcareous shells and skeletons of "native" marine invertebrates. In the western United States and Canada, the Late Ordovician contains mostly limestones secondarily converted to dolomites. Thus, the Cincinnati region represents an intermediate zone of mixed shales and limestones between the great thickness of siliciclastics to the east and pure limestones farther west. Both sediments intermingled in the Cincinnati region, producing a varied and patchy sea floor that was muddy in places and shelly in others. Such a variegated bottom environment offered more potential types of living spaces for bottom-dwelling organisms (the benthos), and provides a further reason why high diversity developed in the region. Because there was very little vegetation on land during the Late Ordovician, erosion may have carried a heavier load of dissolved inorganic nutrients into the sea. These nutrients may have

"Of course, true bony fish had not yet evolved in Late Ordovician time, and as we will see, Cincinnatian rocks contain no fossil evidence of the early, jawless fish that are known from the Late Ordovician elsewhere.

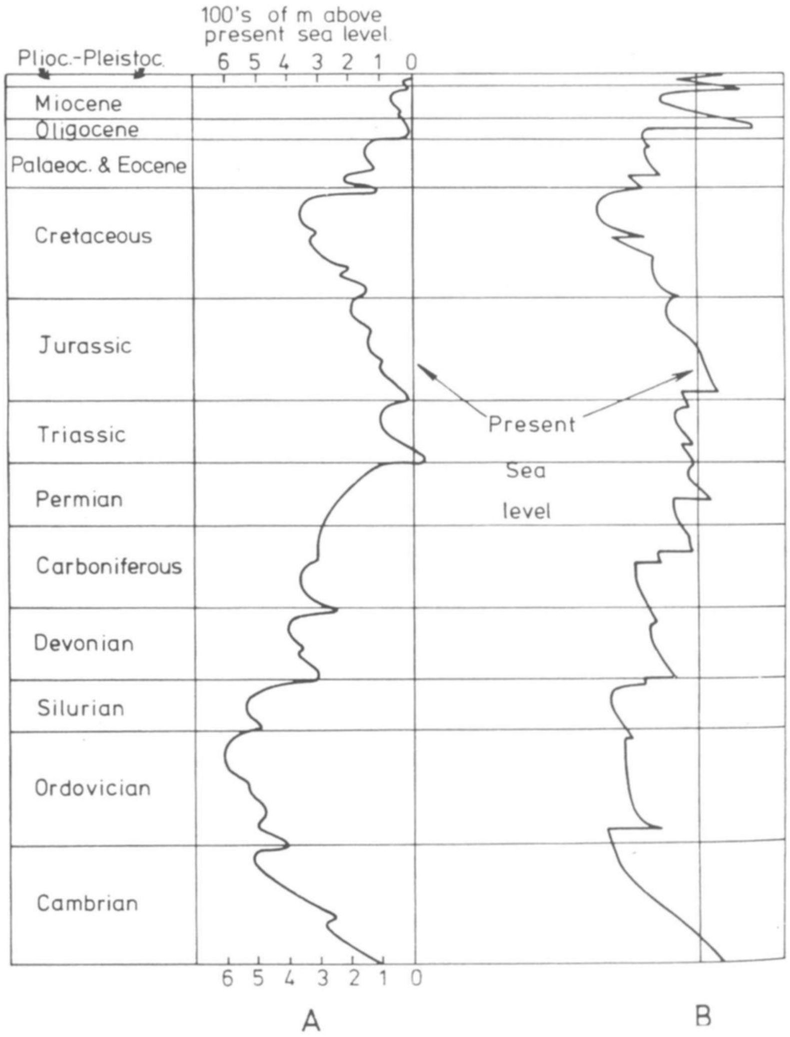


Figure 1.3. *Global sea level curves for the Phanerozoic.* A. *Hallam curve,* B. *Vall et al. curve (1977). From Hallam (1984) and reprinted by permission of Annual Reviews. According to more recent studies (Miller et al. 2006), maximum rise of sea level in the Cretaceous was lower than these estimates, reaching 100 m ± 50 m above present sea level, but this does not contradict the evidence that Ordovician sea level was also very high and extensive over North America.*

acted as a fertilizer to stimulate the production of benthic biomass. In addition, climate, oceanographic conditions, and available food supply must have been crucial to support prolific marine life in the Cincinnatian sea; these factors are explored in detail in chapter 15.

Preservation

When we look at rock layers as crowded with well-preserved fossils as those of the Cincinnatian, we tend to think we are looking at a complete picture of life on the Ordovician sea floor—a snapshot—in terms of both the diversity of species present and their abundance. Unfortunately, the correspondence between this fossil assemblage and the original living community from which it was derived is rarely that simple and direct. The fossil record provides a mere glimpse of ancient life, one that is heavily biased by many factors. In order to assess the impact of these factors on the quality of the fossil sample, paleontologists have devoted an entire subdiscipline, called taphonomy, to the investigation of processes affecting organic remains

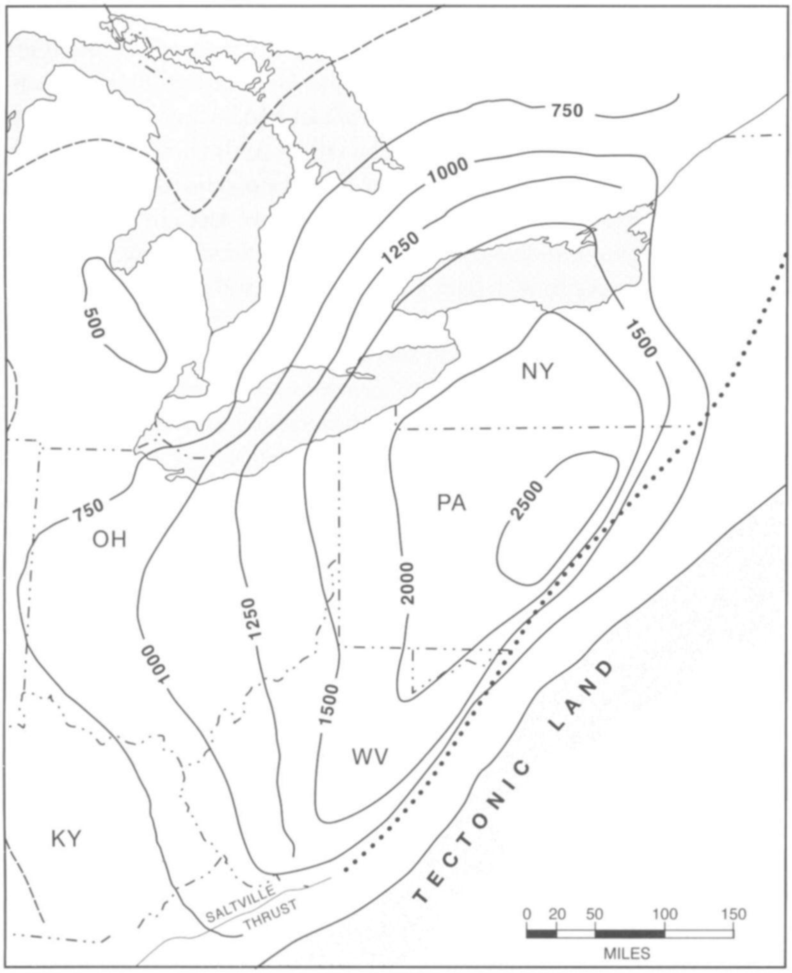


Figure 1.4. *Thickness of Upper Ordovician strata in relation to the ancestral Appalachian Mountains (tectonic land) that was uplifted during the Late Ordovician Taconic Orogeny. Contours are lines of equal rock thickness (isopachs). From Kay (1951, figure 4) and reprinted by permission of the Geological Society of America.*

from death to ultimate fossilization. Taphonomy emphasizes the wide variation in the preservation potential of organisms. An appreciation of the significance of variable preservation can be gained by considering aspects of life, death, and post-mortem history that entered into the complex equation that determined the ultimate fossil record of the Ordovician sea.

> *The organic remains here are remarkably well preserved for so ancient a rock, especially those occurring in a compact argillaceous blue limestone, not unlike the lias of Europe. Its deposition appears to have gone on very tranquilly, as the Lingula has been met with in its natural and erect position, as if enclosed in mud when alive, or still standing on its peduncle.*
>
> **Charles Lyell 1845, 49**

Nature of the laving Organism

Biological factors affecting preservation potential include presence of "hard parts," their chemistry, mineralogy, and construction, and the mode of life of the organism. By far the most important requirement for fossilization is possession of mineralized hard parts such as shells or skeletons. Soft body parts including skin, muscle, hair, and internal organs almost always decay rapidly following death. Many common marine invertebrates like worms lack hard parts altogether or have only hardened jaw structures. In some marine environments, animal communities are dominated in numbers of species or individuals by such soft-bodied species with little or no fossilization potential. One of the best-known exceptions to the dominant preservation of hard parts is the Cambrian Burgess Shale of British Columbia, with its amazing wealth of soft-bodied worms, arthropods, and other invertebrates, along with shell-bearing forms (Could 1989). In the Cincinnatian, there is virtually no preservation of soft-bodied species or soft parts of shell- or skeleton-bearing species. The only records known to us of soft-body preservation in the Cincinnatian are a worm described by Ulrich (1878) and the recent discovery of fossilized "tube feet" in a brittle star (Glass 2006). Our knowledge of the Cincinnatian biota is thus heavily biased in favor of species with hard parts, the shells and skeletons, complete or partial, known as body fossils. Fortunately, this is offset to some degree by evidence of the activity of soft-bodied species from trace fossils (burrows, tracks, and trails—the subject of chapter 14). However, it must be kept in mind that potentially great numbers of species in the biota will never be known because they left no fossil record whatsoever.

Shells and skeletons preserved in Cincinnatian strata are predominantly composed of calcium carbonate ($CaCO_3$) in the mineral form calcite. Some shells of brachiopods (see chapter 8) and the microfossils known as conodonts (see chapter 13) are preserved as calcium phosphate. Despite the abundance of calcium carbonate in Cincinnatian fossils, not all shells having this chemical composition are equally well preserved. The reason for this is that some organisms form calcium carbonate shells or skeletons not as calcite but as a different mineral called aragonite. Aragonite, with a different crystallographic structure than calcite, becomes unstable in seawater after death of the organism and recrystallizes as calcite. In some cases this transformation occurs as a solid-state replacement of aragonite by calcite, altering the microstructure but retaining the macroscopic structure of a shell. Aragonitic shells can also be lost entirely by dissolution even before burial in sediment. In other cases, a shell may become buried, and as the internal soft parts decay, sediment seeps into the shells, replacing the soft parts and forming a perfect mold of the interior. After the aragonitic shell dissolves, the sediment infilling remains and can be lithified by calcific cement. In this manner an internal mold or steinkern is formed which perfectly preserves the internal spaces of a shell, often molding features of the inner shell surface like muscle scars, even though the actual original aragonitic shell disappears. In other cases the shell may not be infilled, and once the shell dissolves, a void remains as an external mold of the outer surface of the shell, or the external mold can be infilled with sediment to form a cast. These arc often the only ways a record of an aragonitic shell is preserved, and we have no way of gauging how many aragonitic shells dissolved leaving no trace whatsoever. Thus it is very difficult to estimate the original abundance of species forming aragonitic shells.

Even among species forming calcitic shells, preservation can be highly selective. Thinner, more delicate shells are more likely to be destroyed before they can be buried. In groups like trilobites (see chapter 11), the exoskeleton is composed of the protein chitin, with varying amounts of calcium carbonate. Juvenile, or newly molted, trilobites had weakly calcified exoskeletons, and were thus less preservable than more heavily calcified individuals. Thus, within a single species, preservational potential is unequal. Species having shells formed of one or two valves (snails, clams, or brachiopods) have a higher preservation potential than species with multi-parted skeletons such as crinoids or trilobites. Multi-parted skeletons are held together with connective tissue, which is susceptible to scavenging and decay, causing the skeleton to become disarticulated and scattered by currents. The consequence of all these variable factors of shell composition and structure is that all organisms producing a calcitic shell capable of preservation do not have an equal potential for actual preservation. Preservation is highly selective even among shells chemically and mineralogically stable enough to survive post mortem.

The mode of life of organisms determines preservation potential even before animals die. For aquatic species, bottom-dwellers (benthos) have a higher likelihood of preservation than swimming (nektonic) or floating (planktonic) species. Among the benthos, species that burrow into the sediment for a living (infauna) obviously have a much higher potential for preservation than do surface dwellers (epifauna). Among the epifauna, species living permanently attached to the bottom often have a higher potential for preservation than free-living, mobile species, simply because they are unable to escape sudden burial by sediment.

Processes of Mortality

Fossilization is a rare event, not a process happening even day. Most animals that survive through old age and die of "natural causes" such as predation or disease will not become fossilized. Unburied carcasses are torn apart by predators and scavengers or destroyed by decay and exposure to the elements. Fossilization very often depends on a rare, catastrophic event that buries an entire assemblage of living organisms, much in way the eruption of Mt. Vesuvius buried Pompeii in AD 79, preserving incredible details of Roman life. Thus, processes of mortality are of fundamental importance in determining how organisms are preserved. When we see a fossil, the first question should be: "What happened?" The answer may tell us more about the nature of rare events, such as storms, earthquakes, or volcanic eruptions than about day-to-day processes.

The paleoecologist must never forget that he is studying not the living inhabitants of the village but only the bodies in the churchyard, and then only after many visits by grave robbers.

Derek V. Ager
1963, 184

In the Cincinnatian, the best-preserved fossils, such as complete trilobites or crinoids, probably resulted from sudden burial of a sea floor population by muddy sediment. Great storms are capable of shifting masses of sediment around on the sea floor or stirring it into suspension, only to settle-out as a blanket over the bottom when the storm subsides (see chapter 4). Organisms were smothered by these events and protected from the normal cycle of scavenging, decay, and destruction. These cases offer the best opportunity to see a snapshot of Ordovician marine life. But even here we should be cautious, because such smothering events can preserve not only organisms living at the tunc, but also remains long dead and accumulated over time. Indeed, many highly fossiliferous limestone beds in the Cincinnatian represent long-term (time-averaged) accumulations of shelly material along with better-preserved specimens that were buried alive in an instantaneous event. With care, these components can be recognized, so that we can assess what species made up the life assemblage. The death assemblage of remains already dead at the time of burial is also informative, because, like a graveyard, it can record multiple generations and occurrence of rare species. Table 1 lists some of the most useful characteristics to look for in distinguishing fossils buried while living from those accumulated gradually as dead remains.

Table 1. *Characteristics of Life Assemblages and Death Assemblages*

	Life assemblage	Death assemblage
Articulation	*good*	*disarticulated*
Breakage	*rare*	*common*
Abrasion	*rare*	*common*
Preserved in life position	*maybe*	*not often*
Size-sorting	*uncommon*	*possible*

History

... our search for a mechanism forces us to range far beyond the Cincinnati region and consider the geologic history of much of eastern North America, especially the continental collisions ... referred to as the Taconic, Acadian, and Alleghenian orogenies.

Paul E. Potter 1996, 71

If, in light of the foregoing discussion, the reader is not fully convinced of the extreme rarity of fossilization and the uniqueness of the fossil richness of the Cincinnatian strata, the following section should provide additional food for thought. Subsequent to life and death during the Late Ordovician Period, 450 million years ago, the remains of marine animals were buried in sediment. Worldwide, a great many fossils from very ancient Paleozoic strata are poorly preserved because they have suffered greatly from the ravages of time—chemical and physical modifications occurring during and alter burial. These changes, technically known as diagenesis, include dissolution of original shell material, with or without replacement by other minerals, pervasive recrystallization of the rock, with partial or complete obliteration of fossil contents, or crushing and deformation of fossils during compaction of the enclosing sediments, fossils that survive diagenetic damage at low temperatures may be later destroyed by actual metamorphism, in which deeply buried strata are heated, recrystallized, and deformed to varying degrees. Metamorphic processes transform primary sedimentary rocks such as shales into slates, limestones into marble, and sandstones into quartzite, accompanied by nearly total obliteration of fossils and other primary features of the sediment. Metamorphism is associated with deep burial by overlying strata, or mountain-building processes of tectonics, including folding, faulting, shearing, and volcanic activity.

The pristine quality of many Cincinnatian fossils is clear evidence that they have undergone very little diagenetic alteration and no metamorphic change over their long burial since the Ordovician. How could these fossils have survived with so little alteration over such a vast span of time? The answer is "location-location-location" and the history of the Cincinnati Arch.

Because the Cincinnati region is located inland from the continental margins, it is far distant from regions that have undergone intense deformation and metamorphism over the course of time. The closest deformed strata of the Appalachian tectonic zone lie about 200 miles to the southeast (Pine Mountain, Tennessee), and metamorphosed rocks are even farther (the

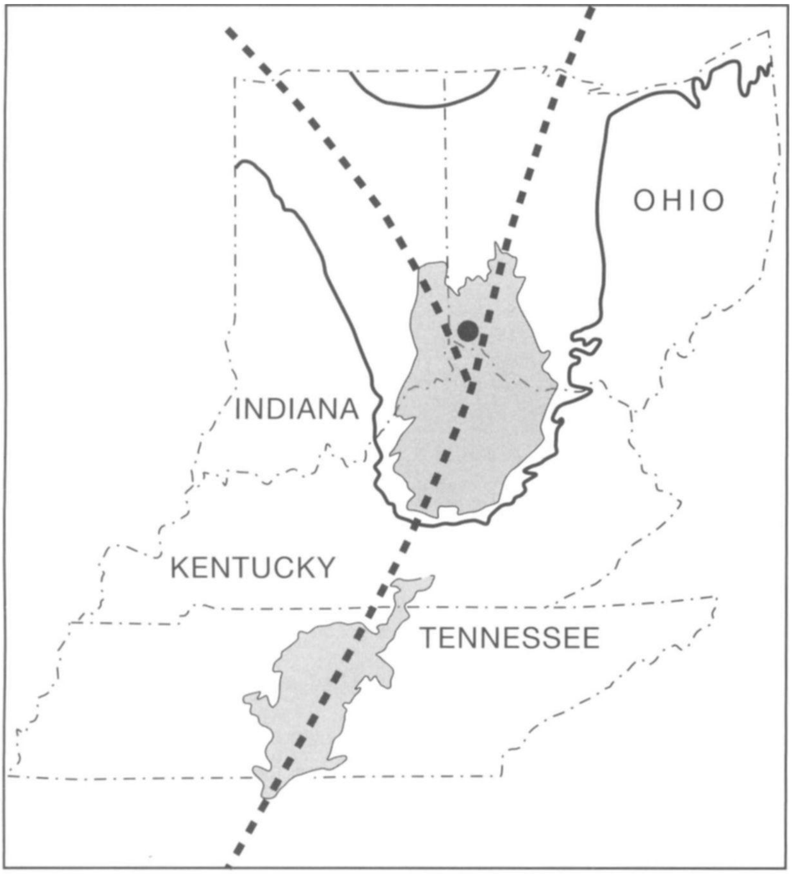


Figure 1.5. *Axis of the Cincinnati Arch and its branches, the Findlay Arch (through Ohio) and the Kankakee Arch (through Indiana). Shaded areas depict outcrop of Ordovician bedrock; heavy lines indicate Silurian-Devonian contact that defines the Findlay and Kankakee branches.*

Great Smokies and Blue Ridge of Tennessee). Furthermore, the Upper Ordovician strata of the Cincinnati region were never buried deeply beneath younger sedimentary strata. At the close of Ordovician time in the region, there is evidence that the seas became very shallow, the sea floor perhaps exposed subacrially (above sea level), producing a gap in the stratal record known as an unconformity. Subsequent sedimentation from the Silurian through Pennsvlvanian Periods (a span of 150 million years) was again submarine, but mostly of very shallow water origins. After the Pennsylvanian Period (about 290 million years ago), there is no record of further marine sedimentation in all of Ohio. Altogether, the total thickness of strata deposited over the Ordovician may have been 300-600 meters (1000-2000 feet) at most (Potter 2007). Indications of shallowing, retreating seas suggest that the Cincinnati region was undergoing regional uplift, because marine deposits are thicker to the east and west than those closer to Cincinnati. On the continental scale as well, epicontinental seas retreated by the end of the Paleozoic, only to return during the Mesozoic, but farther west than Ohio.

The regional uplilt that affected the Cincinnati region was part of a broad zone called the Cincinnati Arch, trending north-south and splitting just north of Cincinnati into the northeasterly-trending Findlay Arch and the northwesterly-trending Kankakee Arch (Figure 1.5). The term "arch" implies an upwarping of the Earth's crust, but anyone who has noticed the

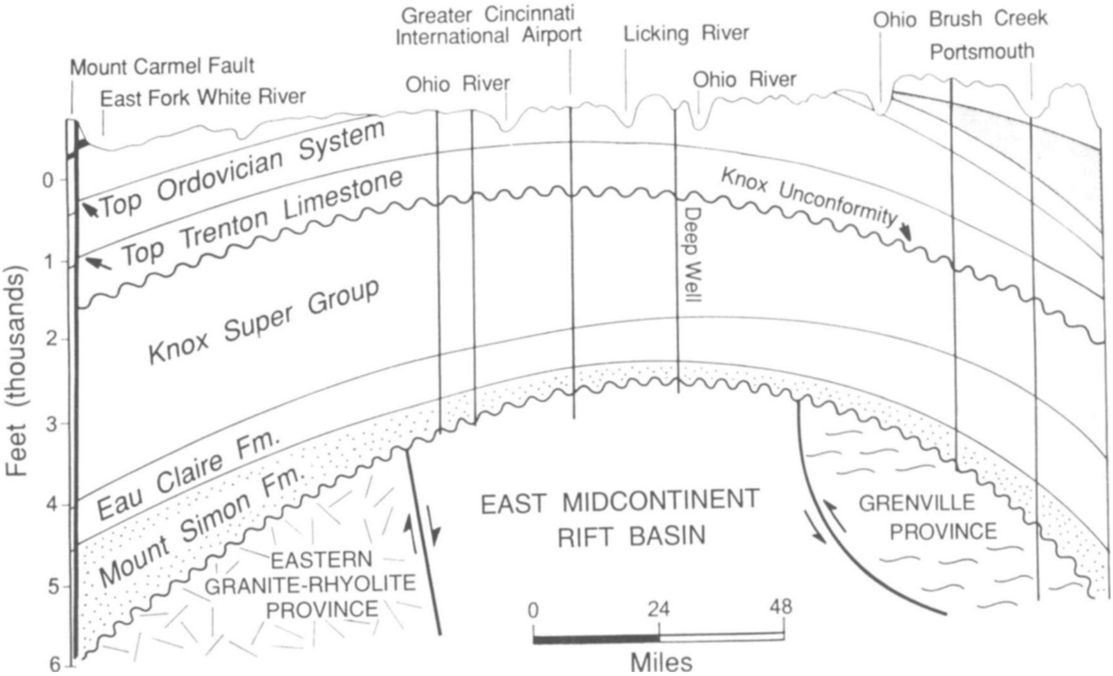


Figure 1. **6.** *Diagrammatic east-west cross section from near Bedford in south-central Indiana across the Cincinnati Arch to near Portsmouth, Ohio. From Potter (1996) and reprinted by permission of the Kentucky Geological Survey.*

strata of limestone and shale exposed in roadcuts around Cincinnati has seen essentially horizontal layers. It is only when we travel eastward or westward from Cincinnati that we encounter geologically younger strata overlying the Ordovician strata along the axis of the Arch, and the character of the Arch as a very gentle, broad upwarping becomes apparent. The tilt or dip of the strata across the Arch is usually less than one degree, or four to seven feet per mile, in Hamilton County (Potter 1996). Over a distance of about 80 km (50 miles) cast and west of Cincinnati, a cross-section through the bedrock shows the structure of the Arch clearly (figure 1.6). Even though the Cincinnati region is distant from the deformed rocks of the Appalachian mountain belt, the Cincinnati Arch may have resulted from the same large-scale tectonic processes that uplifted the Appalachians, beginning in Ordovician time. The reader is referred to Potter (2007) for further discussion of the origin of the Cincinnati Arch.

Because uplift continued along the axis of the Cincinnati Arch, it was continually eroded, stripping away strata lying above the Ordovician, preventing their deep burial. During the past two million years, the glaciers of the Pleistocene Epoch covered most of Ohio and the ice sheet scraped away remaining overburden or washed it away- as the ice melted, completing the exposure of Ordovician strata at the surface. By these processes, begun virtually at the same time the Ordovician seas covered the Cincinnati region, sediments and fossils deposited then were never deeply buried and deformed, and became exposed over a broad belt through the region. The significant consequence is that the entire Cincinnati Arch region has one of the most extensive surface exposures of Upper Ordovician strata in North America, if not the entire world. Natural exposures (outcrops) in streambeds and the sides of valleys (Figure 1. 7A) and human-made exposures, mainly as roadcuts

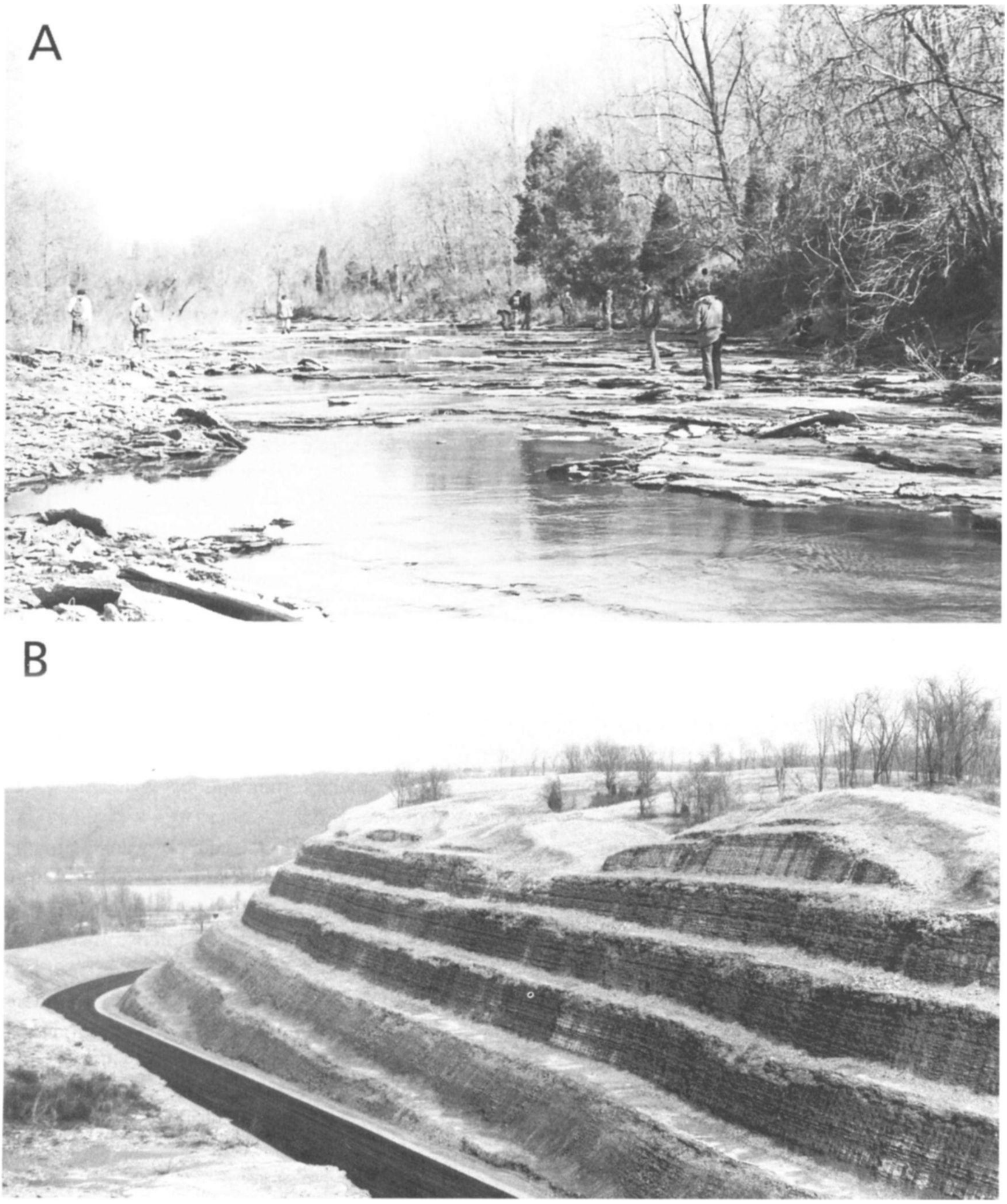


Figure 1.7. A. *Natural exposure of Cincinnatian strata in the bed of Stonelick Creek, Clermont County, Ohio. Streambed outcrops have wide surfaces of fossiliferous beds (bedding planes) that provide information about fossil distribution and orientation. Here, the fossil-rich Bellevue Limestone is exposed and examined by participants in a 1981 Geological Society of America field trip.* B. *One of the most extensive roadcut exposures of Cincinnatian strata, 1.3 km (0.8 miles) in length and about 75 m (250 ft) high, along Kentucky Route 3071, leading to the Ohio River, west of Maysville, Mason County, Kentucky. The lowest strata exposed are the lower Cincinnatian (Edenian Stage) Kope Formation, and the highest strata are the Bellevue Limestone (Maysvillian Stage). Photo by Paul E. Potter.*

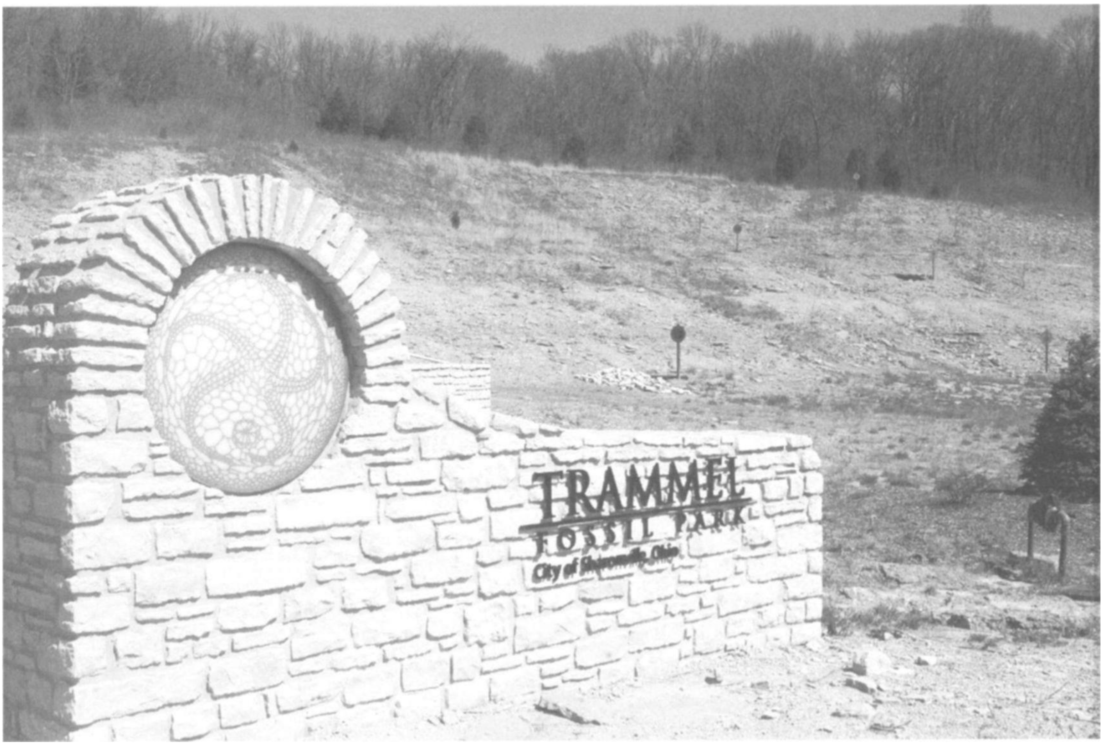


Figure 1. 8. *Trammel Fossil Park, Sharonville, Hamilton County, Ohio. This is a ten acre hillslope where construction exposed four fossiliferous formations: the Fairview Formation, Miamitown Shale, Bellevue Limestone, and Corryville Formation. The developer R. L. Trammel donated the site to the City of Sharonville as an educational, geological park where visitors can learn about the Ordovician geology and paleontology. The park has easy access, parking space, and includes interpretive signage and a protected, in situ fossil shell pavement. Because of the abundance of fossils, surface collecting of small specimens is permitted.*

(Figures 1. 7B, 1. 8) and quarries, provide access to the Ordovician bedrock throughout the region. In the Cincinnati Arch region we have a truly unique window to the past—easy access to ancient strata and fossils that elsewhere lie buried under thousands of meters of rock.

The foregoing overview shows that the abundance of fossils in the Ordovician rocks of the Cincinnati region is the result of many interacting factors. Because of this unique and fortunate combination of factors, the Cincinnati region became one of the earliest centers of intense interest and study of fossils in North America. Scores of Ordovician fossils were first discovered and described from this region, and main practices and concepts of paleontology and geology originated from research on Cincinnatian fossils and rocks. Because the Cincinnati region was one of the birthplaces of modern geological science, we will explore the early history of study of the fossils and rocks here in the following chapter.

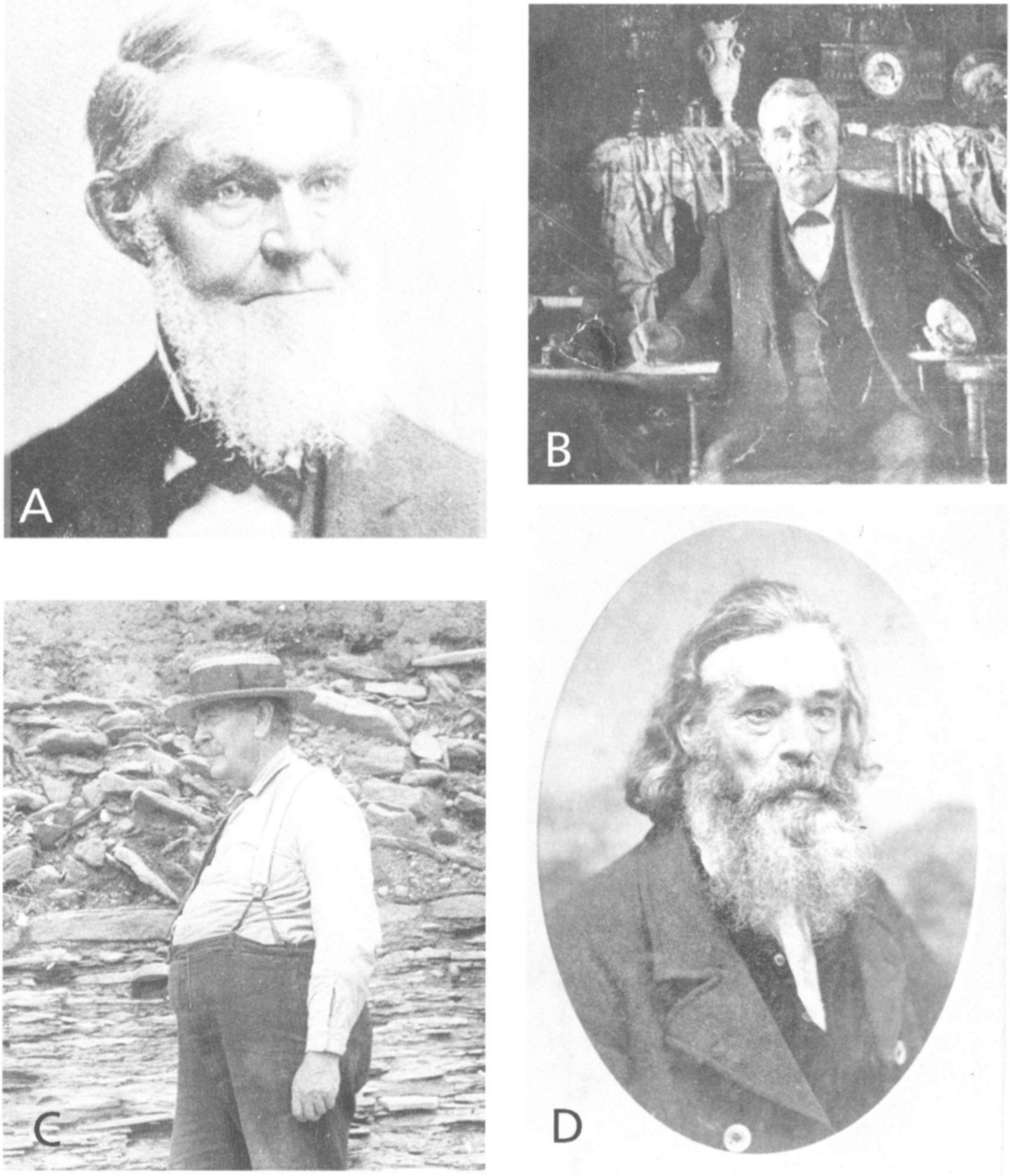


Figure 2.1. *Members of the Cincinnati School of Paleontology who were amateur paleontologists:* A. *U. P. James, publisher and owner of the James Book Store.* B. *S. A. Miller, attorney.* C. *Charles Faber, realfor.* D. C. B. Dyer; *who, after he retired as a maker of soap and candles, devoted himself to fossil collecting. Photograph of Dyer from an old album in the possession of Richard Arnold Davis (© Richard Arnold Davis); all others from the Department of Geology, University of Cincinnati.*

SCIENCE IN THE HINTERLAND: THE CINCINNATI SCHOOL OF PALEONTOLOGY

2

The rocks beneath and around Cincinnati were deposited in an interval of time universally called the Ordovician Period. This time unit was proposed formally in 1879. In the second half of the nineteenth century, beginning even before the Ordovician Period was named, there was in the region of Cincinnati, Ohio, a group of paleontologists who have been called the "Cincinnati School of Paleontology." There is no single, definitive list of the members of the Cincinnati School, and different authors have included different people as members, depending on the purposes of their compilations. Nor is there a definitive list of iron-clad criteria as to who should be considered a member and who should not. Nonetheless, the individuals included in the bod) of this chapter have a number of characteristics in common.

First, they were all serious collectors of local fossils. But they went beyond that. They did not just amass hordes of fossils. They also assiduously studied their finds and where they found them. But they went beyond that, too. They shared their finds with one another, and they shared their information about fossils and their thinking about fossils not only within the local fossil-collecting community, but with the world as a whole, through publication.

A significant number of the members of the Cincinnati School produced lists of fossils, indices, bibliographies, and other compilatory works. But these are just one aspect of an essential criterion for inclusion in the Cincinnati School, namely, publication.

Second, there is a geographic component. Whether born in Cincinnati or not, individuals spent a significant portion of their lives, especially their formative years, in the type-Cincinnatian outcrop area. Moreover, all or most of their published work was published locally—in scientific journals or in books or other publications that were printed in the Cincinnati area.

Third, they all were amateurs, in the sense that finding and publishing about fossils was not how they made their livings. This criterion is a bit difficult to apply consistently, however, because some did sell fossils and some did sell books and other published matter. Moreover, a lucky few went from humble, amateur beginnings in the Cincinnati area to become respected members of the geologic and paleontologic profession as a whole. But even they began as local amateurs.

Fourth, there is a time-and-place component. The Cincinnati School of Paleontology was essentially a phenomenon of the period between the American Civil War and shortly after the succeeding turn of the century. All of the members were associated with the Cincinnati Society of Natural History during that period (and some, with the Western Academy of Natural Sciences that preceded the society). In present-day "buzz-word" terminology, they comprised a "learning community. " They worked together; they shared resources; they communicated with one another; they encouraged one another; they competed against one another. Above all, they stimulated one another to perforin at a higher level than they otherwise might have done. The whole was more than the sum of its parts. There was true synergism in the Cincinnati School of Paleontology.

Although called a school, the Cincinnati School was not one, nor did it have any formal relationship with any college or university. (The University of Cincinnati, as such, was not founded until 1870, and there was no Department of Geology there until the first decade of the twentieth century, when the Department of Geology and Geography was initiated.)

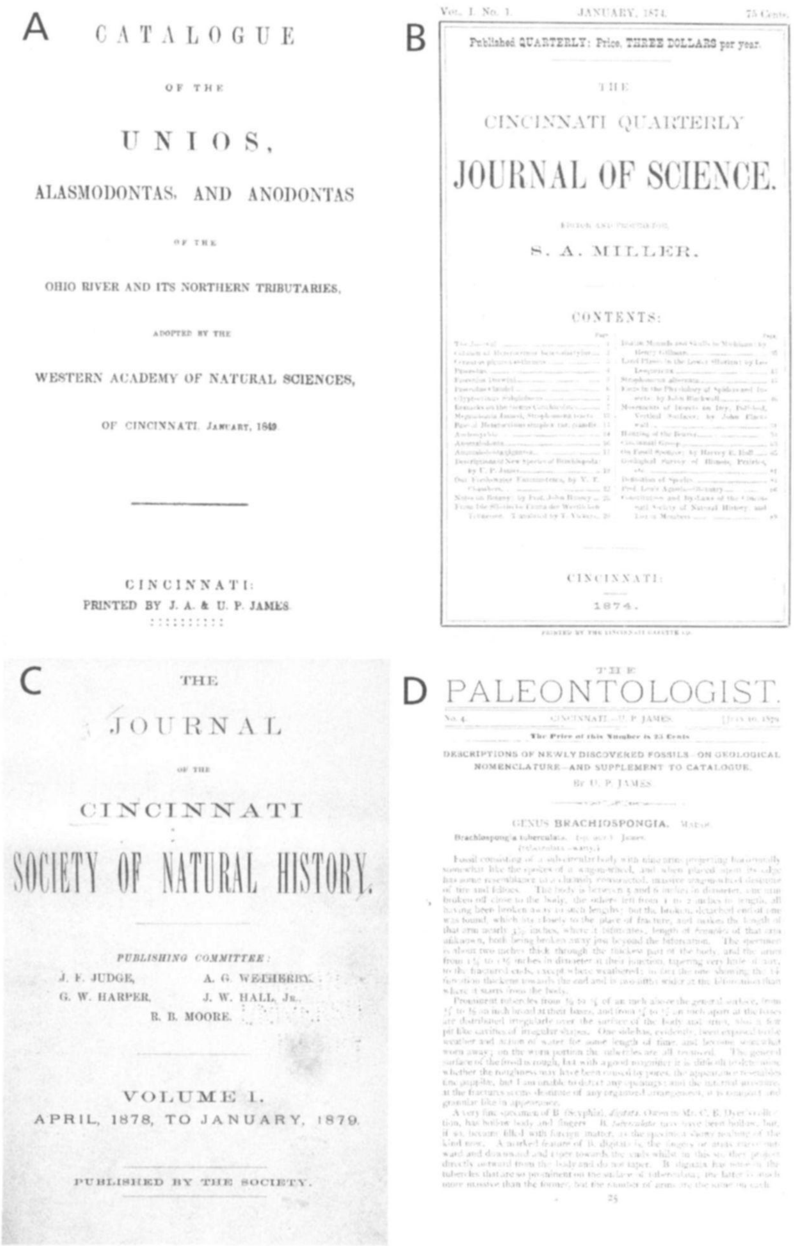
But we need to put the Cincinnati School into more of an historical perspective. In the second decade of the nineteenth century, Cincinnati was the largest city west of the Alleghenies, and a local physician, Daniel Drake, figured that the city needed a first-class museum. Hence, he spearheaded the establishment of the Western Museum. As part of the preparations for the opening of the new museum, a taxidermist and artist named John James Audubon was hired and worked for the organization for about a year, before moving on eventually to become the most famous bird artist the United States has produced. In any case, the Western Museum opened in 1820.

Unfortunately, there was a depression in the 1820s, and the Western Museum fell upon hard times. To make matters worse, Dr. Drake had left the area. Although able to continue its operations, the Western Museum sank to being little more than a chamber of horrors.

Daniel Drake returned to the area in the 1830s. He still figured that the city needed a first-class museum, so he spearheaded the establishment of the Western Academy of Natural Sciences. By the time the ink was dry on the document signed at Appomattox Court House that ended the American Civil War, the Western Academy of Natural Sciences was moribund, and the Western Museum was little more than a collection of curiosities and a chamber of horrors.

In the late 1860s the cultural and civic leaders of Cincinnati figured that the city needed a first-class museum, and the Cincinnati Society of Natural History was established in 1870. About a year after the founding of the Cincinnati Society of Natural History, the handful of remaining members of the old Western Academy of Natural Sciences decided to transfer all the assets of the academy to the new society, including its money, specimens, and library. In return, the members of the academy were to be members of the society for life. Thus came into being the Cincinnati Society of Natural History that was a part of the lives of all the members of the Cincinnati School.

Here follows an account of each of those members. (In appendix 2 are briefer entries for other individuals who had connections with the type-Cincinnatian area, with its rocks and fossils, or with both. Some of these people occasionally have been referred to as members of the Cincinnati School.)



CATALOGUE
OF THE
UNIOS,
ALASMODONTAS, AND ANODONTAS
OF THE
OHIO RIVER AND ITS NORTHERN TRIBUTARIES,
ADOPTED BY THE
WESTERN ACADEMY OF NATURAL SCIENCES,
OF CINCINNATI. JANUARY, 1849.

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CONTENTS:

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THE
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No. 4. CINCINNATI.—U. P. JAMES. JULY 10, 1879.
The Price of this Number is 25 Cents

DESCRIPTIONS OF NEWLY DISCOVERED FOSSILS—ON GEOLOGICAL NOMENCLATURE—AND SUPPLEMENT TO CATALOGUE.
BY U. P. JAMES.

GENUS BRACHIOSPONGIA.

Figure 2.2 A. Cover of an 7849 *publication of the Western Academy of Natural Sciences published by U. P. James, a member of the Cincinnati School of Paleontology, and his brother.* B. *Cover of the Cincinnati Quarterly Journal of Science, volume 1, number* 7, *published in January, 1874, by S. A. Miller, a member of the Cincinnati School of Paleontology.* C. *Cover of the Journal of the Cincinnati Society of Natural History, volume 1, number* 7. D. *Cover of The Paleontologist, Number 4, published in July 1879 by U. P. James, a member of the Cincinnati School of Paleontology.*

U. P. James

Uriah Pierson James (Figure 2.1 A) was born in the state of New York in 1811, the son of a carpenter. In 1831 he and his brother, Joseph, traveled to Cincinnati, where U. P. worked as a printer. By the end of the 1840s he was a publisher and the proprietor of the James Book Store. In the shop he always stocked the latest in geological books, and he displayed fossils in the windows.

U. P. James was very active in the intellectual life of Cincinnati. He served a term as president and was long-time treasurer of the Western Academy of Natural Sciences. When Charles Lyell, probably the foremost

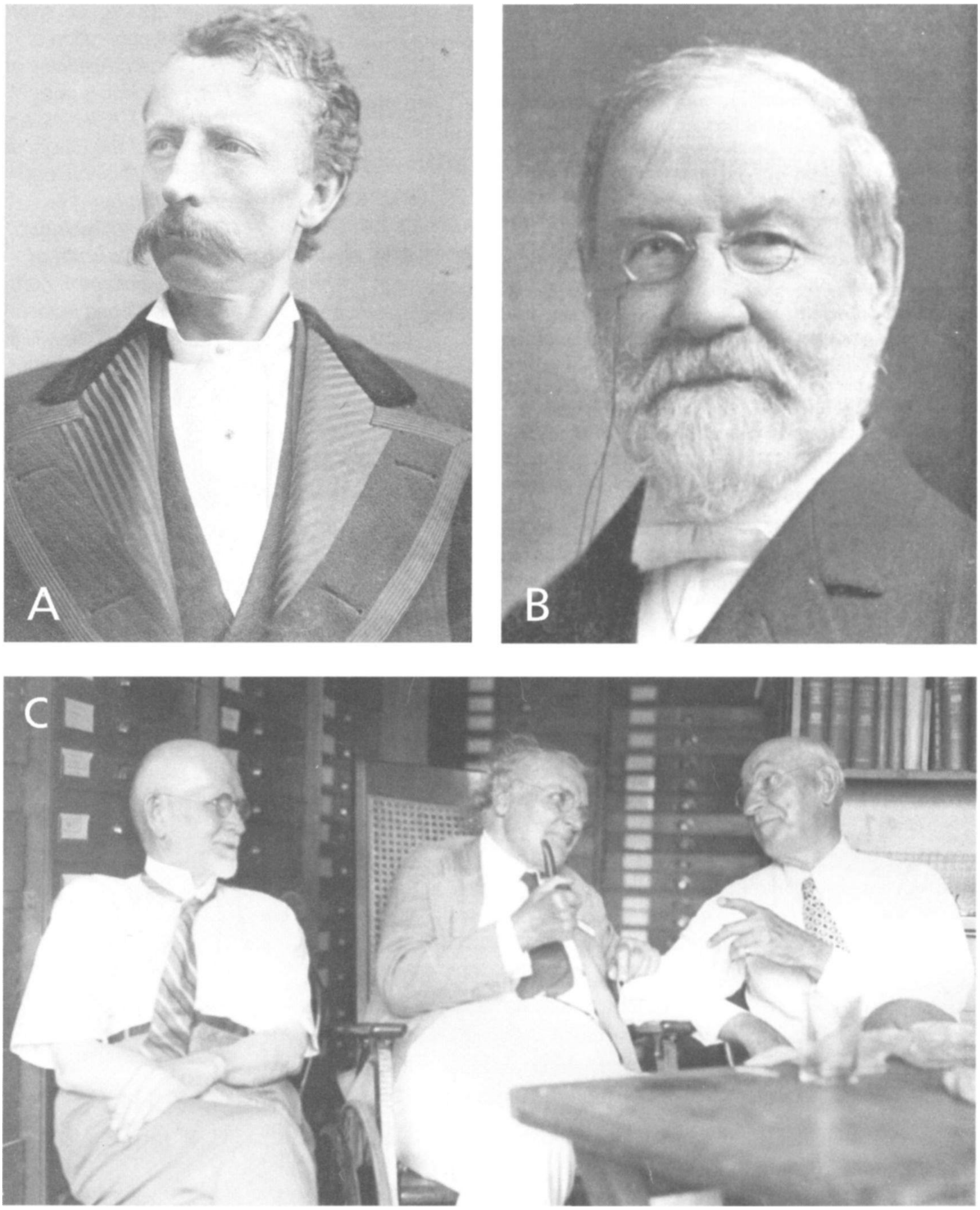


Figure 2.3. A. *Albert Gallatin Wetherby was professor of natural history at the University of Cincinnati before he relocated to Harvard University and malacology.* B. *George W. Harper, long-time principal of Woodward High School, where he facilitated the start of the careers of students Ray S. Bassler and John M. Nickles.* C. *"Friendly enemies": left to right, August F. Foerste, Amadeus W. Grabau, and Edward O. Ulrich, during the International Geological Congress in Washington, D.C, 1934 (picture taken by Ray S. Bassler). Photograph of Wetherby courtesy of the Museum of Comparative Zoology, Harvard University (© President and Fellows of Harvard College); that of Harper, courtesy of the Archives and Rare Books Library, University of Cincinnati; "Friendly enemies," from the Department of Geology, University of Cincinnati.*

Figure 2.4. *Field work in the early days.* A. *John M. Nickles (left) and Ray S. Bassler, collecting from an exposure of the Kope Formation, Cincinnati, Ohio, 1900.* B. *E. O. Ulrich at the contact between the Kope and Point Pleasant Formations on the banks of the Ohio River below Covington, Kentucky, 1901. These exposures are now underwater. (A and* B *from Bassler Archive, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C, courtesy of JoAnn Sanner.)*

Figure 2.5. *Four Cincinnatians who became leading professional paleontologists.* A. *Charles Schuchert, Professor, Yale University.* B. *John M. Nickles, U. S. Geological Survey, 1942.* C. *Ray S. Bassler, U. S. National Museum.* D. *E. O. Ulrich, U. S. Geological Survey. (All photographs from the Department of Geology, University of Cincinnati.)*

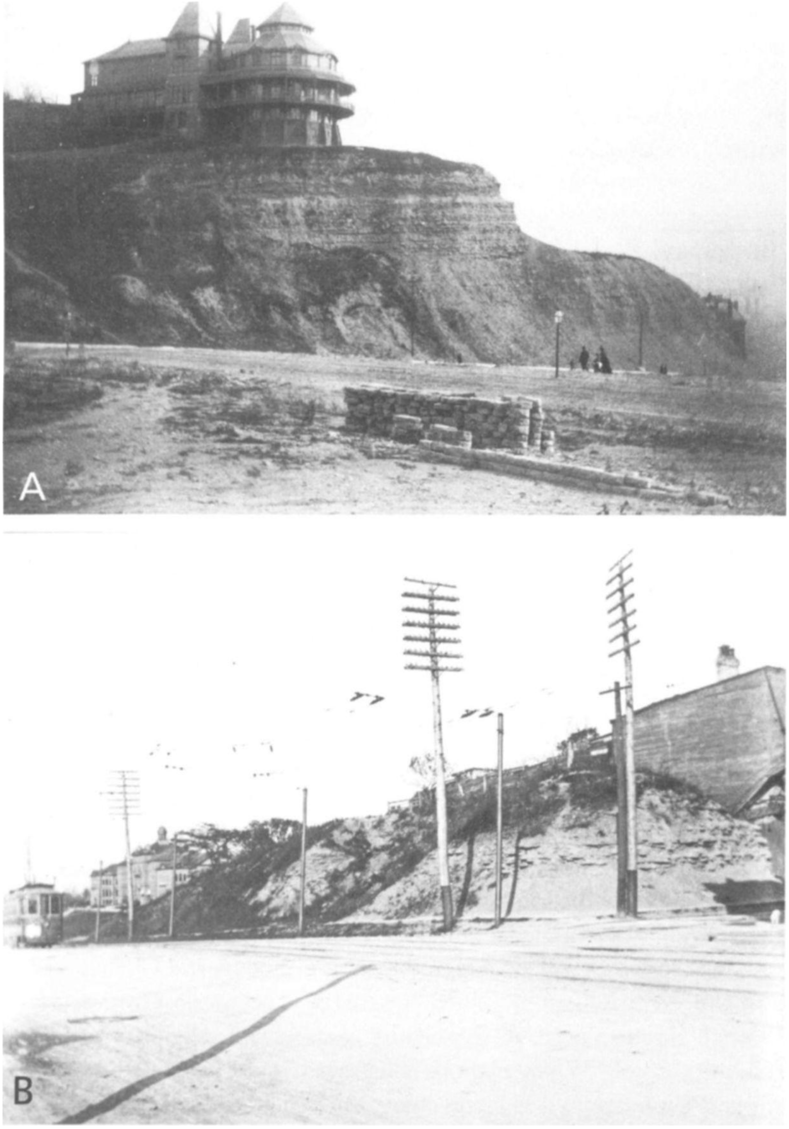


Figure 2.6. *Urban outcrops in Cincinnati, where members of the Cincinnati School found their inspiration.* A. *The Bellevue House, on the site of the present Bellevue Hill Park, ca. 1895. The stratigraphic section exposed below begins in the Kope Formation, spans the entire Fairview Formation and Miamitown Shale (a small "step" below crest), and is topped by the Bellevue Limestone. Clifton Avenue runs below the exposure, which was designated as the type section of the Fairview Formation by Ford (1967). (Image courtesy of the Cincinnati Historical Society Library, Cincinnati Museum Center.)* B. *Exposure of Maysvillian strata (probably Corryville and Mt. Auburn Formations) at corner of Clifton Avenue and Calhoun Street (right), Cincinnati, 1900. Note, at left, trolley car and McMicken Hall of the University of Cincinnati. This exposure has been leveled and is presently the site of the University of Cincinnati College of Law. (From the Bassler Archive, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C, courtesy of JoAnn Sanner.)*

geologist in the world, visited Cincinnati in the 1840s, James was one of his hosts. About the same time, U. P. James became one of the charter members of the Cincinnati Astronomical Society (according to a list at the Cincinnati Observatory, February 11, 2007). He was one of the surviving members of the Western Academy when it was dissolved and its assets were donated to the Cincinnati Society- of Natural History in 1872, whereupon he became a lite member in the society.

U. P. James's fossil collection was widely renowned. Louis Agassiz, one of the foremost paleontologists in this country, visited Cincinnati, and, after seeing James's collection, proclaimed it one of the finest he had ever seen. James's favorite fossils seem to have been bryozoans, which he considered to be corals. Many of the type-specimens in his collection ended up at the United States National Museum; other material went to the University of Chicago and to the University of Cincinnati.

Not only was James the author of many papers about local fossils, but he was the publisher of many others. Indeed, James was the publisher of the journal *The Paleontologist* (Figure 2.2), which ran for seven numbers, beginning in 1879. He also published a catalogue of Cincinnati freshwater mussels and another of local plants.

U. P. James retired from the bookstore business in 1886. He died in 1889 and was buried in Cincinnati's beautiful Spring Grove Cemetery. (Becker 1938; Bradshaw, pers. comm.; Caster 1951,1981,1982; Croneis 1963; Cuffey, Davis, and Utgaard 2002; Hendrickson 1947; Howe, Fisher, and Keekeler 1889; J. F. James 1889; Shideler [1952] 2002; Anon. 1849,1878.)

Joseph F. James

Joseph Francis James almost certainly was inducted into the wonders of fossil collecting by his father, U. P. James (above). However, Joseph's interests in natural history were broader than were his father's; the son published not only about fossils, but about physical geology, botany, and other subjects.

Joseph F. James began as a clerk in his father's bookstore, but he became the first of the Cincinnati School to gain professional status. He was elected to membership in the Cincinnati Society of Natural History in 1876 (Cincinnati Society of Natural History, 94), and he long was associated with that institution as a member, officer, staff member, and author of papers in its journal. After a two-year stint in business pursuits in California and adjacent states, he was elected custodian of the society in 1881 and held that position for six years. The position of custodian involved a good deal more than janitorial work; it would appear that he was in charge of day-to-day operations of the society's building. Meanwhile, he was also professor of medical botany at the Cincinnati College of Pharmacy.

In 1886 James was elected to the chair of Botany and Geology at Miami University in Oxford, Ohio, "but this position was lost two years later through the disruption of the faculty arising from religious prejudices" (Gilbert 1898, 2). "When religious beliefs were under fire at Oxford, professor James was accused of being an agnostic and defended as being essentially a Unitarian. So far as I knew it, his religion was an unswerving devotion to science" (Gilbert 1898, 3).

For one year, he was professor of natural history at the Agricultural College of Maryland, during which time he also did work for the United States Geological Survey. Then, in 1889 James was appointed assistant paleontologist with the United States Geological Survey in the Division of Paleozoic Paleontology, in Washington, D.C. Two years later, he became assistant vegetable pathologist with the U.S. Department of Agriculture, also in Washington, D.C, and served in that position for four years. During those four years, James devoted his evenings to the study of medicine and graduated with a medical degree from Columbian University (now George Washington University) in 1895. He spent the winter of 1895-1896 in New

York and London doing hospital work and bacteriological study, after which he set up in medical practice in Hingham, Massachusetts.

Joseph K James was a prolific author, not only in paleontology, but also in geology and botany. Not counting many items in newspapers and magazines, his output amounted to well over one hundred scientific papers about equally spread among those three areas, along with a number of others on miscellaneous subjects. Some of his paleontologic papers were co-authored with his lather, U.P. James. The younger James was the author or co-author of a number of taxa in the type-Cincinnatian, and at least one was named after him.

Joseph F. James died on March 29,1897, in Hingham, Massachusetts, and his ashes were buried in Cincinnati's Spring Grove Cemetery. (Becker 1938; Caster 19S2; Croneis 1963; Cuffey, Davis, and Utgaard 2002; Gilbert 1898; Shideler [1952] 2002; Anon. 1879,1882,1885b, 1886a.)

C. B. Dyer

Charles Brian Dyer (Figure 2.1D) was born on April 1, 1806, near Dudley Castle, Worcestershire, England. Having had to support himself and his mother, he had little formal education, if any. He came to Cincinnati in 1828 and set up as a manufacturer of soap and candles. Around 1850, having made what he considered to be a sufficient sum, he retired and devoted himself to fossil colleting.

Dyer was one of the original members of the Cincinnati Society of Natural History, and he co-authored papers with S. A. Miller (see below). One of these was the report of a committee on the geological nomenclature of the type-Cincinnatian appointed by the society (S. A. Miller et al. 1879); of the ten members of that committee, six of the individuals are generally recognized as members of the Cincinnati School, and all of them have been listed in one place or another as collectors of local fossils.

However, it is for his avid collecting of fossils that C. B. Dyer is best remembered. As a young man, he enjoyed hunting, but upon retirement he abandoned the gun in favor of the hammer—and live game in favor of long-dead fossils. He was a well-known collector of fossils during his lifetime, to the extent that, in the 1870s, fossils from his collection were figured in publications of the Ohio and New York Geological Surveys and elsewhere (Hall 1872a, b; Meek 1872a, b, 1873). In 1880 his personal collection, which weighed more than 17,000 pounds (!), was sold to Harvard University for its Museum of Comparative Zoology. "The arrangements for this fortunate disposition of important scientific material apparently were made possible by Nathanial Southgate Shaler" (Croneis 1963, 82).

However, C. B. Dyer is not only known for his collecting activities in the local area. Around 1857 he became interested in the beds at Crawfordsville, Indiana, famous for Carboniferous crinoids, and he made extensive excavations there. He also traded Ordovician fossils from the Cincinnati region to the Hovey Museum at Wabash College, in Crawfordsville. The crinoid collection thereby assembled by Dyer was sold by him to the British Museum of Natural History, and it was the first large group of specimens from Crawfordsville to be sent abroad (Van Sant and Lane 1964).

Through his work with S. A. Miller, C. B. Dyer was involved in the naming of many taxa of local fossils, including annelid worms, bryozoans, snails, sponges, starfish and other echinoderms, trace fossils, and others. Moreover, at least one genus and twelve species of fossils were named after him, including the well-known species of crinoids originally designated *Glyptocrinus dyeri* Meek, 1872, now assigned to ***Pycnocrinus.***

According to records at Cincinnati's Spring Grove Cemetery, C. B. Dyer died on July 11, 1883, in Harrison, Ohio, near Cincinnati. (Becker 1938; Byrnes et al. 1883; Caster 1982; Croneis 1963; S. A. Miller and Dyer 1878a, 1878b; Raymond 1936; Sherborn 1940; Shideler [1952] 2002.)

S. A. Miller

Samuel Almond Miller (Figure 2.1B) is certainly the most important of the "amateurs" of the Cincinnati School. He was born near Athens, Ohio, in 1837. By profession he was a lawyer; he had studied at the Cincinnati Law College and was admitted to the bar in 1860.

S. A. Miller was also involved in publishing. In 1861-1862 he published the Marietta, Ohio, *Republican,* which, interestingly enough, was a Democratic newspaper. In 1874 and 1875, he was the proprietor of the *Cincinnati Quarterly journal of Science; many* important papers on Cincinnatian fossils were published in that journal. After two years or so, Miller (and L. M. Hosea, who had become co-proprietor) ceased production of the journal alter eight numbers had appeared. When the Cincinnati Society of Natural History commenced its own journal in 1878, it was rather similar to Miller's defunct one. This is hardly surprising given that Miller had been a founding member of the society and had been campaigning for the society to publish its own journal (Anon. 1875). As an active member of the society, he served at various times as vice president, president, curator of paleontology, and an editor of their journal, in addition to presenting papers at their meetings. S. A. Miller was one of a committee of ten established by the society to consider the geological nomenclature of the type-Cincinnatian, and he was the first author of their report (S. A. Miller et al. 1879). As indicated in the section about C. B. Dyer above, six of the individuals on that committee are generally recognized as members of the Cincinnati School, and all of them have been listed in one place or another as collectors of local fossils.

Miller was active elsewhere in the community, too. He served on the local school board, ran for the U. S. Senate, and also for circuit court judge. He did not win his elections, however; it seems that he refused to take any contributions.

In 1882 Miller was considered for the position of Ohio state geologist, to succeed John Strong Newberry. Edward Orion actually got the job.) Miller was awarded an honorary doctorate by Ohio University, where, years before, he had been a student for one year.

Miller produced a great many publications devoted to fossils, often co-authored with other Cincinnati-area collectors, such as C. B. Dyer and Charles Faber. Lael Bradshaw concluded that Miller named over 1000 taxa (Bradshaw, pers. comm.). But Miller is perhaps best known for his compilations of knowledge: *The American Palaeozoic Fossils* (1877), *North American Mesozoic and Cenozoic Geology and Palaeontology* (1881), and *North American Geology and Palaeontology for the Use of Amateurs, Students, and Scientists* (1889, with supplements in 1892 and 1897). 'The last volume listed, according to Kenneth Caster, is probably the most used volume about American paleontology ever compiled and certainly was the most ambitious private publication in paleontology ever.

Miller's compilatory works were looked down upon by most professionals, but were used by them nonetheless. Caster recounted a story about his professor, G. D. Harris, to the effect that Harris's own professor, Henry Shaler Williams, was disdainful of Miller's works. In Caster's words: "'Yet,' said Harris, 'Miller's great *North American Geology and Paleontology* was always on Williams' desk, and on the desk of every other paleontologist of the land!'" (Caster 1982, 24).

Nor did S. A. Miller confine his work to fossils from the Cincinnati region. He also worked on those of Illinois, Missouri, and Wisconsin. Miller's fossil collection must have been fantastic: one newspaper account reported that it contained over a million specimens! According to Bradshaw, he rose early and worked on fossils until 10 AM, then went to his law office until supper; after supper he worked a couple more hours on fossils.

This schedule must have taken its toll, for Caster recorded that Miller was addicted to drink. According to the late Walter Bucher, one-time professor in the Department of Geology at the University of Cincinnati: "Miller often cadged a quarter from an advocate across the hall to buy a shot of bourbon" (Caster 1982, 25). Caster used to give an expanded version of the story: when thirsty for a drink. Miller used to go to the lawyer's office to borrow a quarter. The lawyer would take a type-specimen as collateral. The lawyer was supplied with money from the Walker Museum in Chicago. Miller lived long enough that every specimen marked "type" went to Chicago. Michael S. Chappars, curator at the University of Cincinnati Geology Museum in 1936, discovered that Miller had not marked all his types as such. Hence, the University of Cincinnati got about half of Miller's types by accident (Caster 1982, pers. comm.). On the other hand, a 1912 letter from Ray S. Bassler to C. D. Walcott said that Miller "sold whenever impecunious to Gurley" (Sherborn 1940, 97); and Sherborn indicated that most of Millers types were at the University of Chicago in the collection of W. K E. Gurley (with whom Miller had published a number of scientific papers).

S. A. Miller willed both his collection and his library to the University of Cincinnati. The library is intact, but is not easy to use because ". . . Miller had bound it into volumes, the only criterion of organization being enough papers of the same page-dimensions to make a conveniently sized volume. His interests ranged widely, and most volumes are highly eclectic" (Caster 1982, 26).

According to record 61331 at Cincinnati's Spring Grove Cemetery, where he is buried, S. A. Miller died on December 18, 1897, of "cancer of liver and uraemic poisoning." (Bradshaw, pers. comm.; Brandt and Davis 2007; Caster 1951,1981,1982, pers. comm.; Croneis 1963; Cuffey, Davis, and Utgaard 2002; Merrill 1924; Sherborn 1940; Anon. 1875,1878.)

By now it has become obvious that a number of threads of our story arc intricately intertwined. Various members of the Cincinnati School have tie-ins with the Cincinnati Society of Natural History, with the University of Cincinnati, or with both. Another thread in the skein is Woodward High School, as we shall see. But let us follow the University of Cincinnati thread for a bit.

A. G. Wetherby

Albert Gallatin Wetherby (figure 2.3A) was born in Pittsburgh, Pennsylvania, in 1833, but his family later moved to the Cleveland, Ohio, area. Alter graduating from college, he spent several years teaching in a country school, with summers spent farming. In 1861 he moved to Cincinnati and was appointed principal of Woodburn School, one of the public schools in the city, and spent some nine years there. In a eulogy written by George W. Harper, another member of the Cincinnati School, it is reported that Wetherby was appointed professor of natural history at the then new University of Cincinnati in 1870 and stayed there six years. However, according to the University ofCincinnati Record of Minutes No. 2, a volume in the archives of the University of Cincinnati, Wetherby's time at the university began in the autumn of1877, and he is listed as "Ass't. Prof A. C. Wetherby of Natural History." In January of 1878 he was appointed "Curator of the Museum in the University," and in March ofthat year, his title was changed to professor of natural history (Board of Directors, University of Cincinnati, 46, 65, 77, 80,100,117). Wetherby listed himselfas "A.M., Professor of Geology and Zoology, University of Cincinnati" (Wetherby 1880, 1881). His last entry in the catalogues of the University of Cincinnati is for 1884-1885: "Albert Gallatin Wetherby, A.M., Professor of Natural History."

Wetherby left the University of Cincinnati to pursue a career in business, first with the American and European Investment Company and, later, as a manager of some timber and mining lands of the Roan Ml. Steel and Iron Co. in North Carolina. He died on February 15, 1902, in Magnetic-City, North Carolina.

Wetherby's interests were many and varied. In addition to being a student of fossils, he was, at various times, curator of entomology and curafor of conchology at the Cincinnati Society of Natural History. He co-authored with another member of the Cincinnati School, John Mickleborough, a list of type-Cincinnatian fossils (Mickleborough and Wetherby 1878a, b). He authored a number of other papers on fossils, especially, but not exclusively, echinoderms (Wetherby 1879a, 1879b, 1880, 1881). In the first-cited of those, he named the genus ***Enoploura,*** and interpreted the animals of that genus to be crustaceans. Wetherby's failure to recognize that he was dealing not with crustaceans, but with echinoderms, brought down on him the wrath of Henry Woodward of the British Museum of Natural History. His contributions as a member of the Cincinnati School of Paleontology notwithstanding, most of Wetherby's publications are not about paleontology, but rather about present-day molluscs.

Wetherby is one of many examples of the fact that the lives and careers of the members of the Cincinnati School were intertwined, for example, John M. Nickles studied under Wetherby at the University of Cincinnati, and George W. Harper wrote a eulogy about Wetherby. Wetherby was one of a committee of ten who wrote a report on the geological nomenclature of the type-Cincinnatian (S. A. Miller et al. 1879); six of the individuals on that committee are generally recognized as members of the Cincinnati School, and all of them have been listed in one place or another as collectors of local fossils. (Brandt and Davis 2007; Caster 1982; Harper 1902; Johnson 2002; S. A. Miller et al. 1879; Mickleborough and Wetherby 1878a, b; Nickles 1956; Wetherby 1879a, 1879b, 1880, 1881; Anon. 1876, 1878, 1879.)

John Mickleborough

John Mickleborough, Ph.D., was the principal of the Cincinnati Normal School from 1878 until 1885. This school was a part of the Cincinnati public school system that was dedicated to training teachers. The Cincinnati Board of Education suspended the operation of the Normal School in 1900, but that was a decade and a half after Dr. Mickleborough had departed Cincinnati for New York, where he became the principal of the Boys High School in Brooklyn.

Mickleborough had been nominated for membership in the Cincinnati Society of Natural History in July of 1876 (Cincinnati Society of Natural History, 90), and he became an active member of the society; for example, he served on the Publications Committee and as a member of a committee on the nomenclature of the rocks of the type-Cincinnatian that included five other individuals generally recognized as members of the Cincinnati School (S. A. Miller et al. 1879). And as noted above, in the section about A. G. Wetherby, Mickleborough and Wetherby co-authored an important list of type-Cincinnatian fossils (Mickleborough and Wetherby 1878a, b). But his most significant publication is his 1883 paper on trilobites, which includes a description of a specimen of *Isotelus* from the type-Cincinnatian with preserved appendages. Mickleborough was rather ahead of his times in his realization that the appendages of trilobites are similar to those of present-day chelicerate arthropods.

In addition to authoring publications on fossils, Dr. Mickleborough, as a professional educator, also wrote in the field of education, for example, on a method of teaching addition and subtraction in the primary grades that was promoted by John B. Peaslee, superintendent of schools in Cincinnati, and called by Peaslee "The lens Method" and by Mickleborough "The Peaslee Method." (Bassler 1947; Brandt and Davis 2007; Caster 1982; Lathrop 1900, 1902; Mickleborough 1883; Nickles 1936; Shotwell 1902; Venable 1894; Anon. 1886.)

Charles Faber

Although the caption of his photograph in the Department of Geology at the University of Cincinnati indicates that Charles Faber (Figure 2.1C) was a realtor, Kenneth Caster (1982) claimed that he was a manufacturer of leather belting. But both sources recognized him as a fossil collector. In the 1880s and 1890s his name appeared as an author of record, both alone and as a co-author with S. A. Miller. As such, he was involved in the naming of a number of taxa of fossils from the type-Cincinnatian.

According to the same photograph caption, Faber lived until 1930, late enough that Shideler went collecting with him. According to Shideler ([1952] 2002, 3), Faber was, ". . . like the typical old timer he was[,] very secretive and suspicious. He wasn't telling anybody anything. It took me two years to get him softened up and educated so that he was willing to come out with his information. So we started going around to a number of the old secret localities where S. A. Miller got his types."

Like most of the other members of the Cincinnati School, Faber was associated with the Cincinnati Society of Natural History. In fact, he was proposed for membership in the society- in 1885, at the same time as Charles Schuchert and Ernst Vaupel, and he was duly elected.

Faber sold his original collection to the University of Chicago for $5000, according to Shideler, and it included specimens described by S. A. Miller. Being an inveterate fossil collector, however, he proceeded to amass a second collection. This one was bequeathed to the University ofCincinnati. The collection came with some money to provide for a curatorial position and for paleontological publications. The first holder of the curatorial position was Carroll Lane Fenton, who went on to write, along with his wife, what is arguably the best book of its time for amateur fossil collectors (Fenton and Fenton 1958). The late Kenneth E. Caster was also a well-known Faber curator. (Bassler 1947; Becker 1938; Caster 1982; Faber 1886, 1929; S. A. Miller and Faber 1892a, b, 1894a, b; Shideler [1952I 2002; Anon. 1885a, b.)

D. T. D. Dyche

Dr. Dyche, of Lebanon, Ohio, is one of the less well-known members of the Cincinnati School. He authored several papers on fossil crinoids of the type-Cincinnatian. In naming a species ofconodont, ***Prioniodus dychei,*** U. P. James honored Dr. Dyche as one "who has done so much in collecting and developing so many of the finest Crinoids, etc., found in the Cincinnati Group ..." (1884c, 147-148). There is, in the Warren County Historical Museum, in Lebanon, Ohio, what is labeled as the dental cabinet ofDavid Tullis Durbin Dyche. We have not been able to verify whether D. T. D. Dyche, the member of the Cincinnati School, is the same person as David Tullis Durbin Dyche, the dentist. (Becker 1938; Dyche 1892a, b, c; U. P. James 1884c.)

E. O. Ulrich

Edward O. Ulrich (Figures 2.3C, 2.4B, 2.5D) was born February 1,1857, in Cincinnati, but shortly thereafter the family moved to Covington, Kentucky, just across the Ohio River. The "O" stands for "Oscar, but it was not a name given to him by his parents; Edward Ulrich gave himselfthat name after a hero in one of the stories he read as a boy. He seems to have been a sickly- child, and was frequently absent from school. He was introduced to fossils by his minister, the Reverend Henry Herzer, when he was seven years old.

After quitting school, he was a surveyor for a couple of years and worked on the Eden Park Reservoir, which, to this day, supplies drinking water to downtown Cincinnati. He was a student at Baldwin-Wallace College for two years, but he did not finish college. During the 1876—1877 school year, he was a student in the Medical College of Ohio in Cincinnati, an independent institution at that time, but absorbed into the University of Cincinnati in 1915 (Broaddus, pers. comm.). Again, he did not finish work for a degree. Formal education and he did not get on too well, because "he insisted he was taught too much he didn't want and too little that he did" (Bassler 1945, 333).

In 1876, Ulrich was elected to membership in the Cincinnati Society of Natural History. The following year he was elected curator of paleontology, an unpaid position. About that time the society acquired its own building, and, in the minutes of the society- for the first meeting held in the new building on November 6, 1877 (Cincinnati Society of Natural History), it is recorded:

"The matter of appointing a janitor for the Building coming up, propositions were received from Messrs. F. O. Ulrich, Talbot, and J. C. Shorten.

"Professor Wetherby moved that the Society proceed to ballot for a janitor, the person elected to be subject to such rules as the Society may adopt, agreed to. The ballot resulted as follows: Mr. Ulrich received 28 votes. Mr. Shorten received 7 votes. Mr. Talbot received 3 votes and thereupon Mr. E. O. Ulrich was declared elected. Mr. Ulrich's proposition is as follows,

Cincinnati Nov. 6th 1877

To the Cincinnati Society of Natural History

The undersigned **is** an applicant for the position of Janitor or Custodian of the Society's building; am willing to devote my entire time to the interests of the Society, for the consideration of $300.00 per annum, and the Society to allow me one room for a sleeping apartment.

Respectfully yours,

E. O. Ulrich

Ulrich's association with the Cincinnati Society of Natural History-brought him into contact with U.P. James, Joseph F. James, Charles B. Dyer, S. A. Miller, and other members of the Cincinnati School. For example, Ulrich was one of six members of the Cincinnati School who served on a committee on the nomenclature of the rocks of the type-Cincinnatian (S. A. Miller et al. 1879). Nor did his contacts come only with Cincinnati folk. For example, as early as 1886, Ulrich went collecting with August F Foerste, who went on to become one of the foremost workers on fossil cephalopods in the United States. Although the position at the society was called "custodian," Ulrich apparently was in charge of day-to-day operations at their facility.

In addition to the labors associated with that job, and later on, Ulrich worked at various times as a carpenter, for various state geological surveys, and part-time for the United States Geological Survey in Tennessee. One of his main sources of income, however, was the production of thin-see-tions of bryozoans, which he sold to buyers both in the United States and Europe. In order to collect sufficient specimens and make thin-sections from them, Ulrich employed other local aficionados of fossils, including Bassler, Nickles, and Sehuchert. (Kenneth Caster *[1982]* has credited Ulrich with the trait of enlisting the assistance of local youths, therein changing their lives. This calls up the image of the kindly old man helping the local kids; it happens, though, that two of Ulrich's three best-known proteges, Sehuchert and Nickles, were only one and two years younger than Ulrich, respectively.)

In 1897, Ulrich was hired permanently by the United States Geological Survey and stayed there for the rest of his career, eventually becoming the head of the stratigraphic section, and in effect the arbiter of stratigraphic decisions in the country. Although specimens and thin-sections provided by Ulrich are present in many institutions all across the land, his personal collection went mainly to the United States Geological Survey and thence the United States National Museum. Ulrich officially retired in 1932, but continued scholarly work as an honorary associate in paleontology at the Smithsonian Institution.

Ulrich authored or co-authored many taxa of animals of all kinds. One of these was a species of ostracod crustacean named after the man of the cloth who had introduced him to fossils. Ulrich wrote: "I name it after Rev. H.Herzer, now of Berea, O., who was the first to awaken in me the latent love for nature that has since grown almost to a passion, and become an inexhaustible source of keenest enjoyment" (Ulrich 1891, 209).

Ulrich received main honors. Baldwin-Wallace College, which he had attended for a time, awarded him both an honorary master's degree and an honorary doctoral degree in 1886 and 1892, respectively. He was a member of the National Academy of Sciences and was awarded their Mary-Clark Thompson Medal. He was elected president of the Paleontological Society for the year 1915; this society was then and is now the premier professional paleontological organization in the United States. In 1932, Ulrich was awarded the Penrose Medal of the Geological Society of America, the highest honor to which a geologist may aspire.

On the other hand, Ulrich seems to have been involved in some less-than-honorable activities. The most surprising is that he backed an attempt to prevent the election of Charles Sehuchert to the presidency of the Geological Society of America, despite the fact that Sehuchert had been a protege and colleague of Ulrich from the old Cincinnati days. The proximate cause for this was that Ulrich had proposed recognition of two major chunks of rock between the Cambrian and the Ordovician Systems, the Ozarkian and Canadian. However, Sehuchert did not enthusiastically adopt the Ozarkian and the Canadian Systems in the prestigious textbook on historical geology of which he was co-author. There also was a dispute as to whether Ulrich or Sehuchert had "invented" the paleogeographic map (neither had, but it certainly was Sehuchert who made them famous).

The ultimate cause, however, was the fact that Ulrich was extraordinarily knowledgeable on all things stratigraphic and paleontologic. From childhood, he had had an uncanny memory. Kenneth Caster (pers. comm.) claimed that, decades after visiting a locality, Ulrich could recall the stratigraphic section there inch by inch, with great accuracy and precision, along with its fossil contents. Thus, Ulrich was supremely self-confident. In discussions, he "to put it mildly, made his position clear." He "was in congenital disagreement until the day of his death on Washington's Birthday, 1944" (Croneis 1963,85). However, one should not conjure up a picture of a grumpy old man. Ulrich was known for his genial disposition, and, indeed, was known as "Uncle Happy." (As it turned out, Ulrich's "new" systems never did gain widespread acceptance, but in the meantime, Schuchert did get elected.)

Ulrich was an early worker on Paleozoic ostracodes and conodonts. He is especially well known for his work with bryozoans, having been one of the pioneers in the use of thin-sections to understand the animals. However, his extensive record of publications includes scientific papers on representatives of almost every major group of invertebrates; not only the ones mentioned above, but also, annelid worms, brachiopods, molluscs, sponges, and trilobites. (Bassler 1945; Becker 1938; Bradshaw 1989; Brandt and Davis 2007; Byers 2001; Caster 1951,1981, 1982; Croneis 1963; Cuffey, Davis, and Utgaard 2002; Merrill 1924; Sherborn 1940; Shideler [1952] 2002; Ulrich 1891. Ulrich's personal bibliography is immense; a good place to start a search for his works is Bassler 1945.)

Charles Schuchert

Charles Schuchert (Figure 2.5A) was born in 1858, the son of a cabinet maker; the family was poor, and Karl (as he was christened) spent his life well into his twenties trying to keep body and soul together. He attended school through the sixth grade, then, at age twelve, went to a mercantile school to learn bookkeeping, at which point he began to work at his father's furniture factory. However, the factory burned down in 1877; Charles revived the enterprise, but it burned again in 1884. Meanwhile, Schuchert did take some drawing courses at the Ohio Mechanics Institute in Cincinnati, and he mastered lithography.

Schuchert's introduction to fossils came in 1866, when a laborer working near the Schuchert home tossed the eight-year-old lad a fossil that had come out of the excavation. Some time thereafter, Schuchert's father took him to see the roomful of fossils owned by one William Foster—"which opened to me an unknown world" (Becker 1938, 193). The boy was completely hooked. Then, at about age seventeen, Schuchert saw the fossils in the windows of the establishment of U. P. James. They met, and the elder James used some of the young man's fossils in his published work. Schuchert also heard about C B. Dyer's collection and sought out his acquaintance. In 1877, he met Ulrich, "who was to turn me from an amateur into a professional paleontologist" (Becker 1938,193).

As a serious amateur fossil collector, and as one trained in lithography, Schuchert was hired by Ulrich as the ideal assistant for preparing lithographs for the Illinois and Minnesota geological surveys. This was 1885 through 1888.

In that last year, James Hall, the dean of American paleontologists, visited Cincinnati and was so impressed by Sehuchert's collection that he hired him to become an assistant for the New York Geological Survey (and, incidentally, obtained his collection of fossils). In 1893, Sehuchert joined the United States Geological Survey, and, a year later, he went to the United States National Museum, also in Washington, D.C. Eventually, he came to occupy the most prestigious geological professorship in North America, that at Yale University.

Sehuchert began attending meetings of the Cincinnati Society of Natural History in 1878. However, it was not until 1885, after he had left the furniture business for good, that he formally was proposed as a member. As it happens, Charles Faber, Ernst Vaupel, and Sehuchert all were nominated at the same time.

Sehuchert was born in Cincinnati, but in some respects it is not fair to call him a member of the Cincinnati School, because he did not really publish anything locally. He had 234 scientific publications, but none appeared in the local journals. Although he did not invent the paleogeographic map, he brought it to its mature state. And, up until the time of his death, in 1942, he was also the foremost authority on fossil brachiopods of North America.

Like some other members of the Cincinnati School, Sehuchert was honored during his lifetime. He was awarded an honorary master's degree by Yale University in 1904, and honorary doctorates were awarded him by New York, Harvard, and Yale Universities. He was a member of the National Academy of Sciences, and was elected president both of the Paleontological Society and of the Geological Society of America, like Ulrich before him, Sehuchert was awarded the prestigious Penrose Medal of the Geological Society of America in 1934. Moreover, one of the medals awarded by the Paleontological Society bears his name. Not bad for a kid who never made it to high school! (Bassler 1945; Becker 1938; Brandt and Davis 2007; Byers 2001; Caster 1951, 1981, 1982; Clark 1943; Croneis 1963; Cuffey, Davis, and Utgaard 2002; Dunbar 1943; Kaesler 1987; Knopf 1952; Shideler [1952] 2002; Twenhofel 1942; Yochelson 1973, 1975; Anon. 1885a.)

John M. Nickles

John Milton Nickles (Figures 2.4A, 2.5B), on the other hand, clearly was a member of the Cincinnati School. Indeed, he was the first of the Cincinnati School actually associated with the University of Cincinnati; he received a bachelor's degree in 1882 and a master's degree in 1891. While at the university, he studied geology under A. G. Wetherby.

He had attended Woodward High School, in Cincinnati, and had been encouraged in his geological interests by George W. Harper, the principal, and by a fellow student. "My boyhood companion, Ernst H. Vaupel, inducted me into collecting fossils during my second year at Woodward High School. Previously we had together collected snail shells and fresh water mussels from the Ohio River at low water and then 'deer horns' (worn cyathophylloid corals) from the drift material fill of the Marietta and Cincinnati Railroad (now B & O) made through Mill Creek valley" (Nickles 1936).

By the time he graduated from high school in 1878, he had started a bibliographic work on the local bryozoans, and he already was acquainted personally with Ulrich and Schuchert. After stints of teaching in Arkansas and then Illinois, where he was a high school principal, he returned to Cincinnati, although for a number of summers he had spent vacations with Ulrich collecting bryozoans all over central and eastern North America.

In 1899 Nickles met Ray S. Bassler at the residence of E. O. Ulrich in Newport, Kentucky. Nickles and Bassler collaborated to produce United States Geological Survey Bulletin 173—*Synopsis of American Fossil Bryozoa* (Nickles and Bassler 1900). About the same time, Josua Lindahl, the director of the Cincinnati Society of Natural History and former state geologist of Illinois, asked Nickles to prepare a paper on the geology of Cincinnati; this was published in the society's journal in 1902 and is used to this day. In the summer of 1909, Nickles prepared a manuscript geologic map of the West Cincinnati Quadrangle for the proposed Cincinnati Folio of the United States Geological Survey; this has yet to be published.

In 1903 Nickles was appointed to the United States Geological Survey in Washington, D.C., apparently on the strength of the bryozoan bibliography that had appeared in 1900; of course, his friendship with Ulrich did not hurt. Until his death in 1945, he devoted himself to compiling bibliographies, including the *Bibliography of North American Geology,* the *Annotated Bibliography of Economic Geology,* and the *Bibliography and Index of Geology Exclusive of North America,* which were published over a number of years. In all, his contribution to these amounted to thirty-eight volumes, comprising a total of 14,361 pages—a fantastic accomplishment! (And it all was done "the old-fashioned way"—there were no computers in that far-distant day and age!)

Nickles authored a respectable pile of publications on bryozoans, but he deliberately sacrificed the paleontological reputation that would have been his in order to serve the science of geology in the thankless task of compiling the bibliographies, and it is for his bibliographies that the geological community forever will be indebted to him. (Bassler 1947; Brandt and Davis 2007; Caster 1951, 1981, 1982; Croneis 1963; Cuffey, Davis, and Utgaard 2002; Nickles 1902,1936.)

George W. Harper

George W. Harper (Figure 2.3B) was a brilliant pedagogue and amateur geologist. Actually, calling him a geologist is too narrow an assessment, for he was, at one time, the curator of entomology at the Cincinnati Society of Natural History and, al another, curator of meteorology, and his name is associated with the study of freshwater mussels in the Cincinnati area.

Harper was born in Franklin, Ohio, in 1832, but spent the vast majority of his life in Cincinnati. He graduated from Woodward College, in Cincinnati, in 1853, valedictorian of his class, and began teaching at Woodward. He was principal of Woodward High School from 1865 through 1900. Somewhere along the line he was awarded a master's degree from Denison College (now, Denison University) and a doctorate from Princeton University. In 1873, when the University of Cincinnati was still new, he assisted in organizing classes and in putting the institution in order; in fact, he is counted as an interim president of the university (Grace and Hand 1995, 139). Moreover, he served on the board and as president of the College of Medicine and Surgery of the university for a number of years.

Harper was elected to membership of the Cincinnati Society of Natural History in 1871 (Cincinnati Society of Natural History, 20). His association with the society was long and extensive. At various times he served as curator, librarian, member of the publishing committee, vice president, and president. Moreover, he served as a member of the committee on the nomenclature of the rocks of the type-Cincinnatian chaired by another member of the Cincinnati School and including four others (S. A. Miller et al. 1879).

Woodward High School, in Cincinnati, was headed by "kindly principal George W. Harper, a geologist in his own right, whose particular desire in life was to train students of geology" (Bassler 1947, iv). For example, he facilitated the progress of John M. Nickles and Ray S. Bassler by allowing them to re-arrange their schedules at the school so as to be able to work with Ulrich in paleontologic endeavors. Moreover, in 1896, he co-authored a paleontological paper with Bassler, then a high school senior (Harper and Bassler 1896). George W. Harper died in 1918. (Bassler 1947; Caster 1965,1982; Cuffey, Davis, and Utgaard 2002; Dury 1910; Harper 1886, 1902; Johnson 2002; Kramer 1918; Martin 1900; Anon. 1876,1878,1885b, 1886a, b.)

Ray S. Bassler

Raymond Bassler (Figures 2.4A, 2.5C), as he was christened, was born in Philadelphia in 1878. At the age of two he moved to Cincinnati with his family. His father, Simon Stein Bassler (that is, Sgt. S. S. Bassler, of the U.S. Army Signal Corps), was one of the founders of the United States Weather Bureau.

Although a handwritten card in the archives of the University of Cincinnati gives his full name as "Raymond Smith Bassler," he assumed the professional form of his name after having made acquaintance with the scientific works of John Ray and F. Ray Lankester, and, thereafter, he signed himself as "Ray S. Bassler" (Caster 1965, P167).

Bassler attended Woodward High School, where George W. Harper was principal. During his freshman year, he met Ulrich and became his technical assistant. Bassler was free to work for Ulrich in the afternoons, because Harper allowed him to compress his classes into the mornings. As previously noted, while only a high school senior, Bassler co-authored a paleontological paper with Harper in 1896.

In 1896 Bassler entered the University of Cincinnati, which had no geology department at the time. Bassler continued working with Ulrich, however. This work was invaluable experience; as Bassler said, "The thin-sections of Paleozoic Bryozoa prepared the hard way during our eight years association were equivalent to several college courses at least, and the time was not otherwise lost, for over a thousand slides were lett for future publications" (Caster 1965, P168).

Bassler spent considerable time at the facilities of the Cincinnati Society of Natural History. The late Ellis Yochelson related a story told to him by Bassler that the young man was alone in the building one day when a gentleman with a brilliant white beard showed up and asked to be shown around the place. Bassler did so, and, afterwards, the bearded visitor departed on his way back to Albany, New York. Thus, Bassler met James Hall (1811-1898), perhaps the foremost paleontologist in the country (Yochelson, pers. comm.).

Ulrich left the Cincinnati area for Washington, D.C, in 1900, and Bassler followed in March of 1901, withdrawing from the University of Cincinnati, before completing his senior year.

Bassler worked privately for Ulrich and went to school part-time at Columbian University (now George Washington University); he was able to transfer credits back to the University of Cincinnati and was awarded a bachelor's degree in June of 1902. About that same time, Bassler began working for the United States National Museum (where Charles Schuchert was his immediate supervisor). This association with the National Museum lasted for nearly six decades, as Bassler rose through the ranks to become head curator of geology in 1929. After his retirement, in 1948, he continued as an honorary research associate until his death in 1961. Meanwhile, he earned his master's and doctoral degrees at George Washington University, in 1903 and 1905, respectively; thereafter he was associated with the university for the next thirty-eight years, including service as professor and head of the Geology Department.

Bassler must have had a sense of humor. Kenneth Caster passed on a story he had heard from Bassler: As a professor in Washington, D.C, Bassler used to take classes to the zoo. One day he was leading such a group, and he noticed that an elderly lady, who seemed slightly familiar, was trailing along after the group. In any case, he stopped by a boulder of Pre-Cambrian rock on the zoo grounds and informed his students that the rock was one billion years old. At this point, the elderly lady interrupted: "But, Professor Bassler, I believe that you have made a mistake. It happens that I was here last year when you brought your students. At that time you said that the rock was a billion years old. So, this year, it must be a billion and one" (Caster, pers. comm.).

During the summer of 1909 Bassler did a manuscript geological map of the East Cincinnati Quadrangle for the proposed Cincinnati Folio of the United States Geological Survey. This map was never published.

During his life, Bassler was an author of over 200 papers, many of which were lengthy works. He was the foremost expert on Paleozoic bryozoans and was one of the pioneers in Paleozoic ostracodes and in conodonts. thereby encouraging the development of micropaleontology. It was Bassler's timely completion of the bryozoan volume of the *Treatise on Invertebrate Paleontology* that allowed that project to get off the ground, which might not have happened without the appearance of Bassler's volume (Bassler 1953). Among his most valuable works is a bibliography and index of American fossils from the Ordovician and Silurian (Bassler 1915).

Kenneth Caster used to call a 10X hand-lens a "Bassleroscope" (Caster, pers. comm.). According to Caster, Bassler refused to use a compound microscope; hence, his understanding of fossils was arrived at without the benefit of higher magnification (Caster 1965,1981). If that were true at one time, Bassler must have seen the light, at least with respect to bryozoans: ". . . we can not be sure of the position of any form in the scheme of classification until we have learned its internal structure by means of thin sections examined microscopically" (Nickles and Bassler 1900, 9). Moreover, according to Ellis Yochelson, Bassler had a compound microscope on his desk, and it appears in photographs Yochelson had seen (Yochelson, pers. comm.).

Bassler was recognized for his great accomplishments during his lifetime. He was elected secretary of the Paleontological Society and served in that position from 1910 to 1931, and then he became president of the society. In 1933, he was president of the Geological Society of America.

When Ray S. Bassler died in 1961, the Cincinnati School of Paleontology was no more—except in their vast numbers of fossils in museums around the world and in their publications in libraries. He was the last survivor. (Bassler 1933; Becker 1938; Brandt and Davis 2007; Caster 1965, 1981; Croneis 1963; Harper and Bassler 1896; Nickles 1936; Nickles and Bassler 1900; Shideler [1952] 2002.)

The Cincinnati School in Retrospect

Although a number of the members of the Cincinnati School of Paleontology did serve stints as school principals in real life, the Cincinnati School had no classrooms, nor did it offer courses. It did not even have a football team! Nonetheless, its members definitely made the grade. This is so despite the fact that, to the majority of the Cincinnati School, paleontology was not a profession, but rather an avocation. To call these individuals "amateurs" is at once true and unfair. Although they did not make their livings as paleontologists, their published works have held up as well as much of what was authored by the actual "professionals" of the day. Moreover, some of the members of the Cincinnati School did, in fact, go on to become amongst the leading "professionals" of their time.

It is primarily through the efforts of the Cincinnati School of Paleontology that the Cincinnati area is truly world famous for its fossils. It was due to their work that the Cincinnati region is the North American standard for the span of geologic time during which its rocks were deposited and the organisms that were to become its fossils lived.

However, it was not only the members of the Cincinnati School who have worked on the rocks and fossils of the type-Cincinnatian. There were, and continue to be, a great many others involved. In appendix 2 of this book, we have compiled brief biographies of some of these other individuals and of institutions associated with the study of the geology and paleontology of the Cincinnati region.

NAMING AND CLASSIFYING ORGANISMS

3

When people from a number of different countries endeavor to communicate with one another, eventually there is a problem, namely, language. Different peoples have different names for the same animal; for example, "chat," "felix," "gato," "gatto," and "Katze" all refer to the animal we call "cat." Moreover, the same word may be used to designate more than one kind of animal; for instance, we use the word "cat" when talking about a house cat, or a lion, or a tiger, or a bobcat, or a mountain lion, or. . . .

Beginning well over two centuries ago, it gradually was recognized that, if scientists around the world were to communicate with one another successfully, each kind of plant and animal must have its own unique name, and that each name must refer to one, and only one, kind of plant or animal. At that time, all educated Europeans knew Greek and, especially, Latin, so it was suggested that these plant names and animal names be in one of these classical languages; that way, no one modern language would be favored. For simplicity, however, it was decided that Greek letters would not be used; hence, only Roman letters were employed in these scientific names.

The name for each basic kind of plant or animal consists of two words. To illustrate this scientific naming, consider the common house cat, *Felis catus*. *Felis catus* is called a species name because each basic kind of organism is called a species. The last word, in this case *Felis,* is the generic name; the second word is called the specific name or trivial name. The species name, consisting of both the generic and the specific (or trivial) names, is called a binomen, literally "two names." The species name of an organism commonly is called its scientific name.

Note that the species name is in *italics*. This was agreed to by scientists: each binomen is to be put in a form that stands out from the writing around it. Generally this is done with italics, although sometimes with underlining. Remember, the species name must be in Roman letters, so that even in a Russian or Chinese scientific work, *Felis catus* will leap out of the page at you.

The initial letter of the generic name always is capitalized. If the species name of an animal is printed using both upper-case and lower-case letters, then the trivial name always is in lower-case throughout, even the initial letter. (This latter convention was not universally followed in former times, especially if a species was named after someone. For example, in 1872, F. B. Meek named the species Glyptocrinus *Dyeri* after C. B. Dyer, a well-known fossil collector in Cincinnati about whom we wrote in the previous chapter.)

In some scientific works, you may see a scientific name followed by a person's name, a comma, and a date, for example, *Felis catus L*innaeus, 1758. This means that it was Carolus (or Carl) Linnaeus who named the species in the tenth edition of his book *Systema Naturae,* published in 1758. Linnaeus invented the binomial system of naming organisms, and he did so in that book. Because of the great scope and importance of that work, it is common to abbreviate "Linnaeus, 1758" to "L." Hence, you might see *Felis catus* L.

(There has been some confusion as to Linnaeus's real name; see Davis [1992]. As was the custom in Sweden at the time, Carl Linnaeus's father, Nils, originally was called Nils Ingermarsson, after his father, Ingermar. As a young man, Nils intended to become a pastor, and, when he registered as a student, he was required to give a family name, rather than just the patronymic. He chose "Linnaeus," a Latin word referring to a lime tree—there was one growing in the family garden. After Carl was famous and ennobled by the king, he adopted the honorific form "von Linne." It is for this reason that the name "Linnaeus" sometimes is written "Linne" [Moore, pers. comm.].)

Actually, the regularization of biological nomenclature (the science of naming the groups into which organisms are classified) was only one of the contributions of Linnaeus. He also was the inventor of the system we use for that classification. It works like this: each basic kind of organism is called a species. Related species are joined together in a larger unit, a genus (the plural is "genera"). Related genera are grouped into an even larger unit, a family. And so on. In short, Linnaeus invented what now is called the Linnaean hierarchy, a system of categories in which smaller groups of related organisms are joined to form larger, more inclusive groups. Take the house cat, for example. *Felis catus* is the name of the species. The species *F. catus* and other, related cats belong in the genus *Felis.* The genus *Felis* and other genera of cats are assigned to the Felidae, the cat family. Cats, dogs, bears, skunks, and so on, make up the order Carnivora. The orders Carnivora, Insectivora (shrews, moles, hedgehogs, and their kin), Primates (monkeys, apes, humans, and their relatives), and all the other orders of hairy creatures comprise the class Mammalia. Mammals, birds, reptiles, amphibians, fishes, and so on, comprise the phylum Chordata. The chordates, cnidarians (corals, and so on), sponges, and more than twenty other phyla—plural of "phylum"—comprise the kingdom Animalia.

Let us summarize this in tabular form, using the common house cat as an example:

Kingdom	Animalia
Phylum	Chordata
Class	Mammalia
Order	Carnivora
Family	Felidae
Genus	*Felis*
Species	*Felis catus*

The entities listed in the left column are levels in the Linnaean hierarchy. Each word in the right column is the name of one group at that level in the hierarchy. Each of these groups is a taxon (the plural is taxa). So, for example, "family" is the level in the Linnaean hierarchy between "order" and "genus," and the "Felidae" is the taxon at the family-level to which ***Felis** catus* belongs.

All of this is within the realm of taxonomy—the science of assigning organisms to their proper biological groups. The word "taxonomy" comes from two Greek words, *taxis,* meaning "arrangement," and *norms,* meaning "law" or "science of" (Brown 1956); thus "taxonomy" literally means the "law of arrangement" or the "science of arrangement"; alternative names are classification and systematics. The real challenge of taxonomy is, of course, figuring out the biological relationships of the organisms being studied. After that has been done, and only after that has been done, can the groups be named in a truly meaningful fashion, at least, from a biological point of view. Although some scientists might separate "nomenclature," the naming of the groups, from figuring out the biological relationships, the two activities are irrevocably intertwined.

One purpose for the Linnaean hierarchy is to simplify the describing of kinds of organisms. Imagine if you had to describe a house cat COMPLETELY; it would take reams of paper and many months of time. Because of the Linnaean hierarchy, by saying *"Felis catus," you* convey to your listener all the characteristics of the species, genus, family, and so on, without having to use up paper and time in vast quantities. (Note that the name of the species is *Felis catus,* not just ***catus,*** which is only the specific name part of the species name.)

However, the Linnaean hierarchy is not merely a convenient way to save words and hours. The real significance is that it groups together organisms that are evolutionarily related to one another. Thus, the organisms joined together in a given taxon are more closely related to one another than they are to organisms of any other taxon at the same level in the hierarchy. Put another way, all members of a given taxon evolved from a common ancestor.

There are seven basic levels in the Linnaean hierarchy. When doing detailed work with a group of organisms, one commonly finds a need for more levels. As a result, extra levels have been invented. For example, several related families may be grouped into a superfamily. Or, going in the other direction, a family may consist of several related subfamilies, and a subfamily may be composed of several infrafamilies. Analogously, above the class-level, there can be superclasses, and below it can be subclasses and infraclasses. And so on for the other levels of the hierarchy. One does not have to use all the levels of the expanded hierarchy, however, just the ones necessary best to classify the creatures being studied.

One of the more commonly used levels of the expanded Linnaean hierarchy is the subspecies. *Platystrophia* ***ponderosa auburnensis*** is a subspecies of P. *ponderosa,* along with P. *ponderosa ponderosa.* Note that the subspecific name appears in print in exactly the same style as docs the specific name. The word "variety" sometimes is used as an alternative for "subspecies." (Note that "subspecies" is simply a level in the Linnaean hierarchy; there is no connotation that a "subspecies" is inferior in "quality" to a "species." Thus, if an organism is assigned to a particular subspecies, this means that the organism merely has been assigned to a particular subdivision of the species, not that the organism somehow is qualitatively inferior.)

What Funny Names!

. . . many learned words, half-Greek, half-Latin, and always difficult to pronounce, many unpolished terms that would scorch a poet's lips.

Jules Verne, [1864] 1992, *Journey to the Centre of the Earth,* **4**

If you have tried to wrap your tongue around the scientific names of fossils, you can identify with Jules Verne's one-liner about scientific terms (although he was referring specifically to mineralogical ones). Part of the problem is that the names of fossils do not seem to make sense—they appear to be random combinations of letters. Yes, they have a utilitarian significance in denoting taxa, but the names generally have "real" meanings, too. However, those meanings generally have their roots in ancient Latin or Greek or both, which is unfortunate for the vast majority of us, who are not schooled in these classical languages.

Some names are eponymous, that is, they arc derived from the names of people. There is a genus of common articulate-brachiopods found in the type-Cincinnatian called *Rafinesquina* after C. S. Rafinesque (1783-1840), a naturalist who taught at Transylvania College in Lexington, Kentucky. The crinoid *Pycnocrinus dyeri* was named in honor of local fossil collector C. B. Dyer (1806-1883). And so on.

Other names derive from places. For example, the edrioasteroids *Cincinnatidiscus* and *Isorophus cincinnatiensis* were named after a city that, once upon a time, was the capital of the old Northwest Territory. (The Latin suffix "-ensis" or "-ense" denotes place or locality.)

Each genus has what is known as a type-species; this was designated to represent the genus. In some cases, the trivial name indicates this special status, for example, the pelecypod *Cymatonota typicalis.* (Note, however, that not all genera have type-species that are named in such a way as to signal that status.)

In some instances, a name may derive from the rock-unit in which a taxon occurs. So, for example, the articulate brachiopod *Leptaena richmondensis* occurs in rocks of the Richmondian Stage.

Occasionally, a name is taken directly from the Latin or Greek. *Rana* is a common genus of frogs, and "rana" is Latin for "frog." The head of a specimen of the trilobite *Phacops rana,* "peeping" out of a rock, is strongly reminiscent of that of a frog.

Quite commonly a generic or trivial name is descriptive. The bryozoan *Constellaria* bears bumps that are disposed in star-shaped patterns ("stella," Latin for "star"). The shell of the inarticulate brachiopod *Trematis millepunctata* bears many holes ("trema" = "hole" [Greek]; "mille" = 1000 [Greek]; "punctum" = "small hole" [Latin]), *Thaerodonta rugosa* has wrinkles ("ruga" = "wrinkle" [Latin]). And so on.

Or the name may reflect the habits or habitat of an animal. The trilobite *Flexicalymene* commonly is found flexed into a ball. The inarticulate brachiopod *Petrocrania scabiosa* lived attached to other shells, rather like the scab attached to the shin you barked last week.

The message here is that generic and trivial names are not just cabalistic combinations of letters used to refer to taxa. They almost always have meanings beyond that—meanings that make sense! (For more information on the meanings of scientific names, see Brown [1956].)

Pronouncing Those Lip-Blistering Names

If you hear someone trying to talk about a subject, but that person routinely stumbles over technical terms or mispronounces them, you are bound to suspect that he or she does not know the subject very well. So how should one pronounce the names of taxa—so as not oneself to be labeled an ignoramus?

Proper pronunciation of words that are Latin or Greek depends on a knowledge of those classical languages. Alas! Very few people today have the requisite knowledge. To make matters worse, even among those who might lay a claim to being well-versed in Latin or Greek, not everyone agrees as to what constitutes correct pronunciation. For example, devotees of "Church Latin" and those of "Classical Latin" do not sing the same Christmas carols the same way. There are, however, some rules of thumb:

1. Unless you know otherwise, put the emphasis on the antepenultimate syllable (that is, the syllable before the syllable before the last). Thus, Brachiopoda is BrachiOpoda.
2. C's and G's are ordinarily hard (as in "cat" and "gun," respectively).
3. V's are pronounced as W's.
4. J's should sound like the Y in "your."
5. A "long i" in Latin is pronounced like a "long e" in English.
6. The diphthong "ae" in Latin is pronounced like a "long i" in English, ***viz.,*** "eye."
7. Y is pronounced rather like the "oo" in the word "look."

But the above "rules" can result in some strange-sounding names, for example, the name of the edrioasteroid *Cincinnatidiscus* would sound like "kinkinnatidiskus," and the snake *Virginia* would begin with the syllable "we're," followed by a hard G. (As an aside, a bunch of male graduates of a college or university are called "alumni," with the last syllabic being pronounced "nee," whereas their female classmates are "alumnae," with the last syllable rhyming with the English word "nigh.")

Names derived from the names of people can be a real complication. The well-known Cincinnati "horn-coral" ***Grewingkia*** was named for the Russian paleontologist Constantin Caspar Andreas Grewingk (1819-1887), who pronounced his name "gray-vink." Presumably, then, the generic name should be said "Gray-vink-ee-ah." However, most Americans would call it "Grew-wink'-ee-ah."

This raises the most-important concept in this section: the overarching goal of pronunciation is communication. It is important to pronounce the names so that those with whom you wish to communicate will understand what you mean. Listening to the experts in the field is generally a good way to learn how to pronounce the names, but the goal is communication. So, for example, if those with whom you are speaking refer to the common Cincinnatian brachiopod ***Zygospira*** with the "y" and the "i" each sounding like "eve," it is okay to do the same (even it your high school Latin teacher taught you that the "y" should sound like the "oo" in "look," and that the "i" should sound like "ee"). When in Cincinnati, do like the Cincinnatians!

Speaking of communication, sometimes one encounters words or phrases that look a bit like species names, but are not. For example, the term *nomen dubium* refers to the name of a taxon that was so poorly described and otherwise documented that it is not certain just what constitutes the taxon and how to recognize it. A dubious name, indeed.

Another such phrase is *nomen nudum.* With a term that literally means "naked name," a bit of background is necessary. When a species is named, the author is expected to follow certain conventions that have been agreed to by the community of the world's biologists. The author must indicate that he or she is naming the species for the first time (Genesis 2:19-20, notwithstanding). The species must have a diagnosis; this is a special kind of description that tells how individuals of the "new" species differ from all other members of the genus. And one or more type-specimens must be indicated.

Type-specimens serve as the material on which the species is based. They should be deposited in a *bona fide* museum so that scientists of future generations can study the exact specimens on which a given species is based. It used to be common to base a "new" species on a single specimen. Now, given the intraspecific variation that has been found to exist within all species, it is more common to designate a suite of type-specimens when a species is named. If all the type-specimens arc considered to be of equal value as representing the species, they arc said to be cotypes. On the other hand, if there is single type-specimen, or only one of a suite is considered to be the "name bearer" for the species, it is designated the holotype, and the others of the suite are paratypes.

Back to *nomen nudum:* It is a name of a taxon that does not have the associated verbiage, illustrations, designated specimens, and so on. Without such material, there is no way to know what constitutes the taxon, either conceptually or specimen-wise. Probably the most common way that a *nomen nudum* comes into existence is through the vagaries of the publication process. Suppose that a paleontologist is preparing two scientific papers for publication; one is to contain comprehensive descriptions and illustrations of "new" taxa. The other is just a tabulation of the fossils in a given rock-unit in a given area; it consists of just the names of the taxa formally described in the former. Alas! By a quirk of fate (or bad planning?), the list is published quickly, but the paper with the formal descriptions appears later, or, even worse, not at all. And a spate of *nomina nuda* are born.

The Game of "Musical Names"

Amateur fossil collectors commonly get more than a little aggravated at paleontologists for changing the names of fossils. Indeed, one of the bugaboos of all folks who study fossils is that the names sometimes change when you least expect it.

Take, for example, the case of a well-known local crinoid. In 1872, F. B. Meek recognized a species he named *Glyptocrinus dyeri.* The genus *Glyptocrinus* had been named by James Hall in 1847, and the type-species, the species that exemplifies the genus, is *Glyptocrinus decadactylus* Hall, 1847. Meek thought that *Glyptocrinus dyeri* belongs in the same genus as G. *decadactylus,* and so, quite properly, he used the same generic name. About the same time (1883, actually), S. A. Miller recognized what he considered to be a separate genus, and be called it *Pycnocrinus.* In subsequent years, experts on fossil crinoids decided that G. *dyeri* actually is more closely related to the type-species of *Pycnocrinus* than to that of *Glyptocrinus,* so the species named by Meek was re-assigned—from the latter to the former genus. Hence, its name was changed to *Pycnocrinus dyeri* (Meek, 1872)—the parentheses are shorthand to tell us that the species named by Meek in 1872, with the specific name "dyeri," was later transferred to the genus *Pycnocrinus.* (Although parentheses used in that way may not appear in some guide books for amateur fossil collectors, they can provide a valuable hint to the paleontologist trying to track down the nomenclatorial history of a particular species.)

On the other hand, sometimes the situation is the other way round. In 1935, Saburo Shimizu and Tadahiro Obata recognized a "new" genus of fossil cephalopods and named it *Orthonybyoceras.* In 1942, Rousseau Flower, an eminent expert on fossil cephalopods, recognized a "new" genus and called it *Treptoceras.* Later workers, for example, Curt Teichert, one of the most famous paleontologists of his clay and, it happens, an expert on fossil cephalopods, concluded that animals formerly recognized as belonging in the two separate genera comprised a single taxon. In such cases, biologists apply a convention called priority, *viz.,* when there is an older name and a younger name that both have been used to designate the same taxon. the older name becomes the official name of the taxon. So, because it is older, the name *Orthonybyoceras* Shimizu and Obata, 1935 was applied to the genus (Teichert 1964, K214).

Note that the guiding principle in both of these examples—and in all similar cases—is for a given taxon to have a single, unique name and that a given name should refer to a single, unique taxon. If two groups of organisms belong in separate taxa, then those taxa need to have separate names—in the above example, *Glyptocrinus* and *Pycnocrinus.* If two putatively separate groups of animals actually comprise a single taxon, then all should parade under a single name—in the above example, *Orthonybyoceras.*

Names are not changed for frivolous reasons. All creatures with the same species name belong in the same species. All creatures with the same generic-name belong in the same genus. That way, when a particular genus or species is mentioned by name, everyone everywhere knows exactly what is being discussed. The goal of zoological nomenclature is communication!

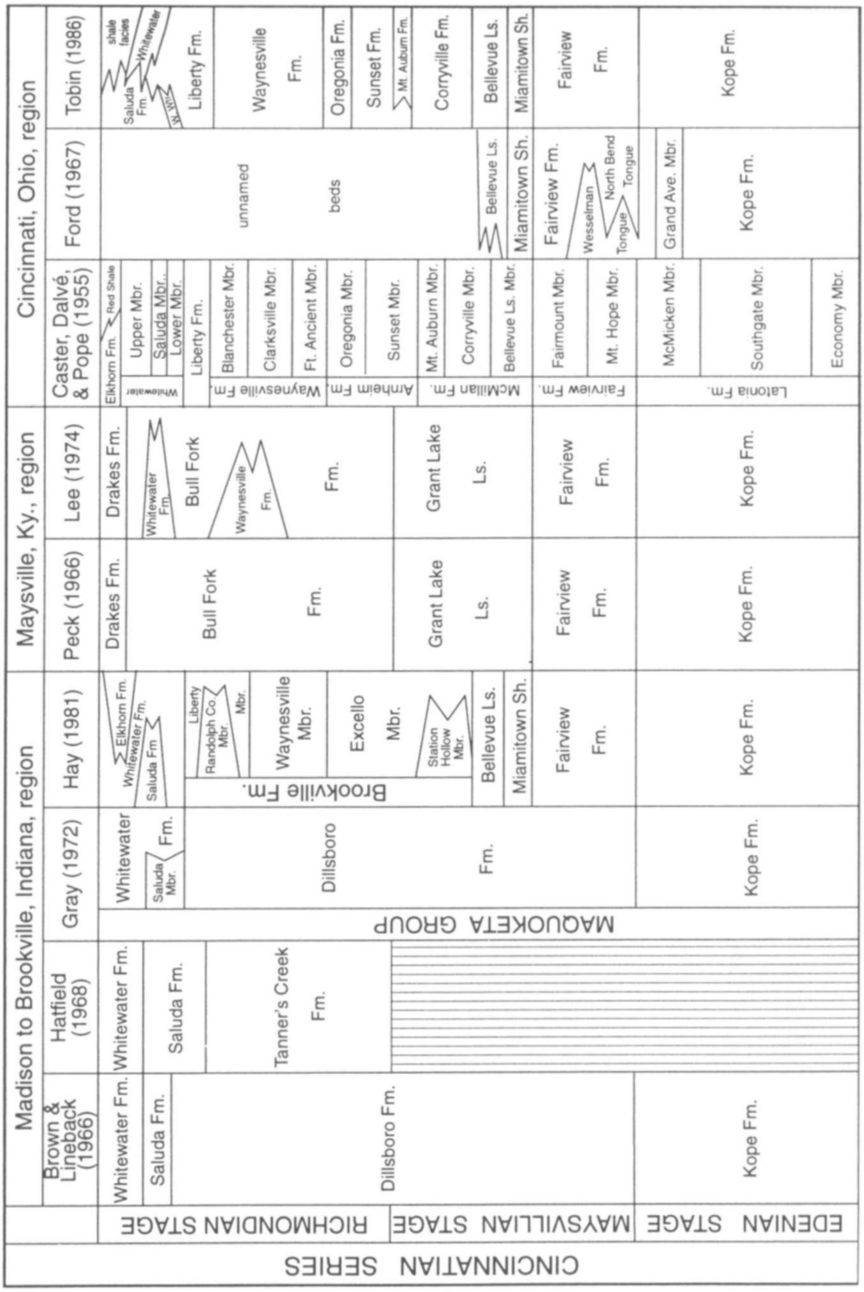


Figure 4.1. *Cincinnatian stratigraphic nomenclature from 1955 through 1986. From Davis and Cuffey (1998). From Schumacher (1984, figure 2), courtesy of the Ohio Department of Natural Resources Division of Geological Survey. This chart shows stratigraphic subdivisions of the Cincinnatian Series proposed by different researchers for different parts of the Cincinnati Arch region. Subdivisions in the Caster et al. (1955) column were based largely on differences in fossil content. Broader subdivisions such as those of the Brown and Lineback (1966), Hatfield (1968), Gray (1972), Peck (1966), and Lee (1974) columns were based on general characteristics of the rocks (lithology) and bedding. Hay (1981) and Tobin (1986) used both lithologic as well as paleontologic aspects. In the Hatfield column, the vertical lines indicate parts of the section excluded from his study. Units separated by jagged lines indicate lateral changes in rock characteristics (faces)*

ROCKS, FOSSILS, AND TIME

4

Fossils in many collections and museum exhibits are often impressive for finely preserved detail and even beauty, because they have undergone painstaking preparation by which every trace of the stony matrix has been removed. However, a fossil so isolated from its embedding matrix also loses much of its significance as a means by which to understand when and how it lived. Only through investigation of *the fossil in the rock* can we attain a clear understanding of the significance of the abundant Ordovician fossils of the Cincinnati Arch region, or any fossils for that matter. In this chapter we will explore the nature of the rocks in which Cincinnatian fossils are found, the means by which they are subdivided, and the applications of this study to understanding the environments in which they were formed and to determining their geologic age.

Two words effectively describe the bedrock of the Cincinnati Arch region for even first-time observer: *monotonous* and *layered.* Cincinnati rocks are indeed monotonous as their entire thickness of over 250 m (820 feet) consists of apparently similar blue-grey limestones and shales. These two common sedimentary rocks form thin, alternating layers (beds or strata) that appear to be horizontal and continuous across an exposure such as a roadcut. The overall impression is that of a layer cake, and in fact Cincinnatian bedrock has long been known as a classic of "layer cake geology." Closer examination by scores of geologists over more than 150 years revealed that like most first impressions, the actual character of Cincinnatian strata is quite different. Geologists vigorously pursued the detailed description, subdivision, and classification of these seemingly uniform strata for a variety of purposes, resulting in a long and complex history of study. Geologists employ different methods to describe and subdivide rocks. For layered sedimentary rocks, the chief methods arc *relative age, rock type,* and *fossils.*

Geologic Time Units

Although the history of the Earth is part of a continuous flow of time, the evidence we have for that past history, the rocks and fossils, represents only fragments of that history. For this reason, geologists use a dual set of terms for divisions of continuous time and the rocks that represent preserved intervals of time (see Figure 1.1). The continuous flow of geologic time is divided into major divisions called eons, which are in turn divided into eras and periods, the fundamental units of Earth history. Periods are subdivided into epochs (Early, Middle, Late), and ages. In geologic time terms, the Cincinnatian is part of the Late Ordovician Epoch of the Ordovician Period. The Ordovician Period is the next-to-oldest period of the Paleozoic

Era, and the Paleozoic Era is the earliest era of the Phanerozoic Eon (meaning "time of revealed life," for the abundance of fossils in those strata). The other set of terms, time-stratigraphic units, applies to the actual rocks that geologists assign to particular intervals of the geologic time scale, and are roughly equivalent to the divisions of continuous time, except that there are many gaps in the record of time that result from incomplete preservation.

Relative Age

According to a fundamental principle of geology, superposition, the lowest rock layers in an undisturbed vertical sequence were deposited before layers lying above them. Thus, for the Cincinnati "layer cake," we know that layers exposed in the bed of the Ohio River formed before layers exposed higher along the hillsides, but we do not know exactly *how old* the layers are, or *how much older* are lower layers than higher layers. We know only that lower layers are *relatively older* than higher layers. Geologists established the relative age sequence of the major sedimentary layers of the Earth's crust long before analytical methods (chiefly radiometric dating) were developed to determine the absolute age of rocks.

Time-Stratigraphic Units

Rocks that formed during a particular interval of geologic time are called time-stratigraphic units. Thus, rocks deposited during the Ordovician Period constitute the Ordovician System, which is subdivided into Series (usually Lower, Middle, and Upper, but sometimes named, as in the Cincinnatian Series). Stages are the fundamental subdivisions of series used for correlation on a continental and intercontinental scale. Cincinnatian stages are the Edenian, Maysvillian, and Richmondian, in order from oldest to youngest.

Rock-stratigraphic or Lithostratigraphic Units

Rocks can also be subdivided or classified by rock type or lithology. Lithology usually includes the composition of the rock, its constituent particles, their size, shape, and arrangement. The fundamental lithostratigraphic unit is the formation, defined by a distinctive lithologic character as well as a thickness sufficient to be shown at a convenient scale of geologic mapping. Formations can be combined as groups, or subdivided into members. Formations do not necessarily coincide with a specific interval of time, and indeed are often time-transgressive, that is, their lower or upper boundaries are not time-equivalent or isochronous surfaces.

Biostratigraphic Units

Rocks can be subdivided on the basis of fossil content. The thickness of strata in which a particular kind of fossil occurs defines the fossil zone (or biozone), which is the fundamental biostratigraphic unit. The lower and upper limits of a particular fossil do not necessarily represent the same time horizons in different stratigraphic sections. However, through the use of the overlapping range zones of many species, biostratigraphers establish the boundaries of time-stratigraphic units such as stages.

Early Studies

The earliest studies of the rocks and fossils of the Cincinnati region date to the early 1800s (Drake 1825; Riddell 1837; Locke 1838; Lyell 1845) and coincide with the very beginnings of geology as a science. These early workers made no attempt to subdivide the strata around Cincinnati, and referred to them simply as the "Blue Miami Limestone" (Riddell 1837), "Blue Limestone" (Locke 1838), or "Great Limestone Deposite" (Briggs 1838). F. B. Meek and A. H. Worthen (1865), both pioneers of American paleontology, first used the term Cincinnati Group for the Ohio strata. Edward Orton (Orton 1873), Ohio's third state geologist, proposed a fourfold subdivision of what he termed the Cincinnati beds proper: River Quarry Beds (lowermost), Middle (Eden) Shales, Hill Quarry Beds, and Lebanon Beds (uppermost).

Subdivision Based on Fossils

The abundant and well-preserved fossils of the Cincinnati region attracted more and more attention during the latter part of the nineteenth century, and as a result, detailed knowledge of the distribution of particular fossil species in the strata was accumulated through the efforts of the Cincinnati school of early paleontologists (see chapter 2). In 1902 John M. Nickles published a comprehensive report on the geology of Cincinnati, an excellent review and compilation of earlier studies (Nickles 1902).

By the time of Niekles's report, the Cincinnati Group had come to be recognized as "one of the major divisions of the Ordovician or Lower Silurian Era, with the title of Cincinnati Period" (Nickles 1902, 64). Nickles subdivided the Cincinnati Period into three major div ISIONS. each termed a group: Utica group (lowermost, 260 feet thick), Lorraine group (310 feet thick), and Richmond group (uppermost, 200-300 feet thick). The terms Utica and Lorraine were both derived from comparisons with the Ordovician of New York. Winchell and Ulrich (1897) had proposed the term Richmond (from excellent exposures at Richmond, Indiana) for the uppermost Cincinnati strata because Lebanon had previously been used for older Ordovician strata in Tennessee. The following section from Niekles's report contains fundamental statements that were the basis for subdivision of the section:

> There is considerable variation in the different groups in the proportions of limestone and shale. Shale greatly predominates in the Utica, but from the lower beds of the Lorraine on, the proportion of limestone gradually increases. This shows that there was a gradual change from more or less turbulent conditions prevailing at the close of the Trenton to the time of the Lower Richmond, when quiet seas permitted the accumulation of the materials for closely succeeding beds of limestone. As the period came to a close, there came anew turbulent conditions. The fauna of the different groups indicates the same succession of changes. (Nickles 1902, 65)

Both the character of the rock (lithology) and the fossil content differentiate subdivisions. Nickles listed species that could be found throughout the entire section, but these were only 4 percent of all forms known from the Cincinnati period, and "the great bulk of forms usually have a limited vertical range" (Nickles 1902, 65). His further subdivision of the groups was based on a combination of lithologic and paleontologic criteria. The Utica group ". . . may be divided into three subdivisions, more easily recognized faunally than lithologically, though close study shows lithological differences, which soon come to be felt, but are not easily described" (Nickles 1902, 69) These were named the Lower Utica or *Aspidopora newberryi* Beds, the Middle Utica or ***Batostoma jamesi*** Beds, and the Upper Utica or *Dekayella* ***ulrichi*** Beds. The Lorraine was likewise subdivided into six "beds," each given a local geographic name as well as a characteristic fossil species, and he indicated that the group ". . . is easily separable on faunal grounds, with corresponding more or less well-marked lithological characters" (Nickles 1902, 75) He divided the Richmond into lower, middle, and upper divisions based on their faunas, but indicated that study has been insufficient to establish their boundaries or lithological characters.

In 1903 August F. Foerste introduced for the first time the term Cincinnatian Series for the entire section, and referred to the Utica, Lorraine, and Richmond as stages (Foerste 1903). Foerste (1906) termed the same three groups formations, with their subdivisions as members. He also discarded the New York term Lorraine and replaced it with Maysville. In the same year Ray S. Bassler (1906) elevated the narrower subdivisions to formations and defined the Covington Croup to include the Utica, Eden, Fairview, and McMillan Formations, overlain by the Richmond Croup, including the Arnheim, Waynesville, Liberty, Whitewater, and Saluda Formations. In time, further subdivisions of these formations were designated as members, although different workers continued to utilize different stratigraphic classifications (Weiss and Norman 1960b).

A guidebook to the fossils and strata of the Cincinnati area prepared in 1939 by Prof. Walter H. Bucher, with illustrations by Kenneth F. Caster, assisted by Stewart Jones, was first printed informally by the Department of Geology of the University of Cincinnati (Bucher et al. 1939). The booklet was published in 1945 by the Cincinnati Museum of Natural History under the title *Elementary Guide to the Fossils and Strata in the Vicinity of Cincinnati, Ohio* (Bucher et al. 1945); later revised by Caster, Dalve, and Pope (1955, 1961), it became the standard for what has become known as the "traditional" or "biostratigraphic" classification of the Cincinnatian (Figure 4.1). These editions of the *Elementary Guide* include the statement that "The lithology, i.e., rock characteristics, of the beds as indicated on the charts varies considerably when traced away from the Tri-State Area. Therefore, lithologic identification of the Cincinnatian formations and beds is unreliable. However, the sequence of fossils persists throughout the area and furnishes a reliable basis for identifying equivalent beds, and thus the position in the stratigraphic sequence" (Caster, Dalve, and Pope 1955, 15; Caster, Dalve, and Pope 1961, 15). Subsequent revisions of this book by R. A. Davis (1985, 1992), under the title *Cincinnati Fossils* retained the time-honored Cincinnatian stratigraphic chart of the older work, but pointed out how it differs from modern stratigraphic usage.

Modern practices in the field of stratigraphy emerged during the post-World War II era as efforts were made to eliminate confusion resulting from non-uniform usage and to standardize stratigraphic classification and terminology. The history of Cincinnatian stratigraphy (Weiss and Norman

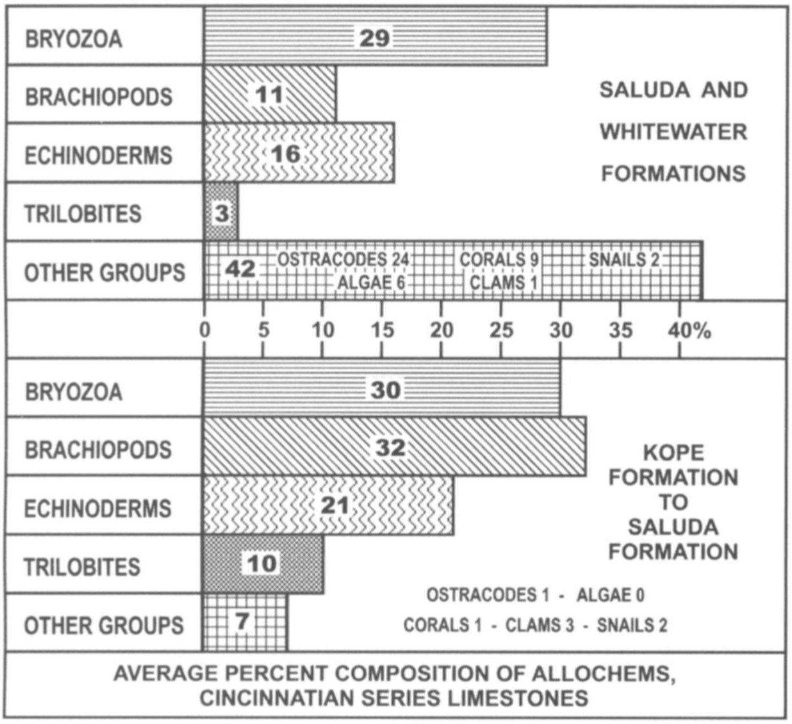


Figure 4.2. *Average percent composition of the allochem fraction of faunal groups and algae in the upper (Saluda and Whitewater Formations) and lower (Kope Formation to Saluda Formation) parts of the Cincinnatian Series. (Allochems are fragments of fossils or other discrete grains in limestones.) Adapted from Martin (1975), courtesy of Wayne D. Martin.*

1960b) provides a strong case demonstrating this need! Gutstadt (1958) and Weiss (1961) pointed out that traditional Cincinnatian stratigraphic classification was essentially a biostratigraphic zonation, sorely in need of revision in keeping with new concepts and practices. Publication of the Code of Stratigraphic Nomenclature (American Commission on Stratigraphic Nomenclature 1961) and the International Stratigraphic Guide (Salvador 1994) culminated many years of collaborative work between earth scientists in the United States and worldwide.

Cincinnatian lithostratigraphic units are defined by data on the following characteristics obtained from measured sections: limestone types present, clastic ratio, and bedding features. Limestones in the Cincinnatian display wide variation, ranging from fine-grained to coarse-grained and composed of varying mixes of fossils (Figures 4.2, 4.3). Accelerated research in limestone (carbonate) petrography enabled greatly refined description of Cincinnatian limestones (Weiss and Norman 1960a; Martin 1975; Tobin 1982). The elastic ratio is the proportion of shale thickness in relation to limestone thickness in a section. Bedding features include the bedding index, calculated as the number of beds (x 100) in a given interval divided by the thickness of the interval, and bed form, such as planar or wavy. These lithologic characteristics can be quantified and plotted on vertical sections or maps.

The new clarification and codification of stratigraphic usage meant that Cincinnatian formations that had been defined largely on the ranges of characteristic fossils were invalid. The distinction was much more than a semantic problem: attempts to recognize the traditional Cincinnatian stratigraphic formations beyond the immediate vicinity of Cincinnati were

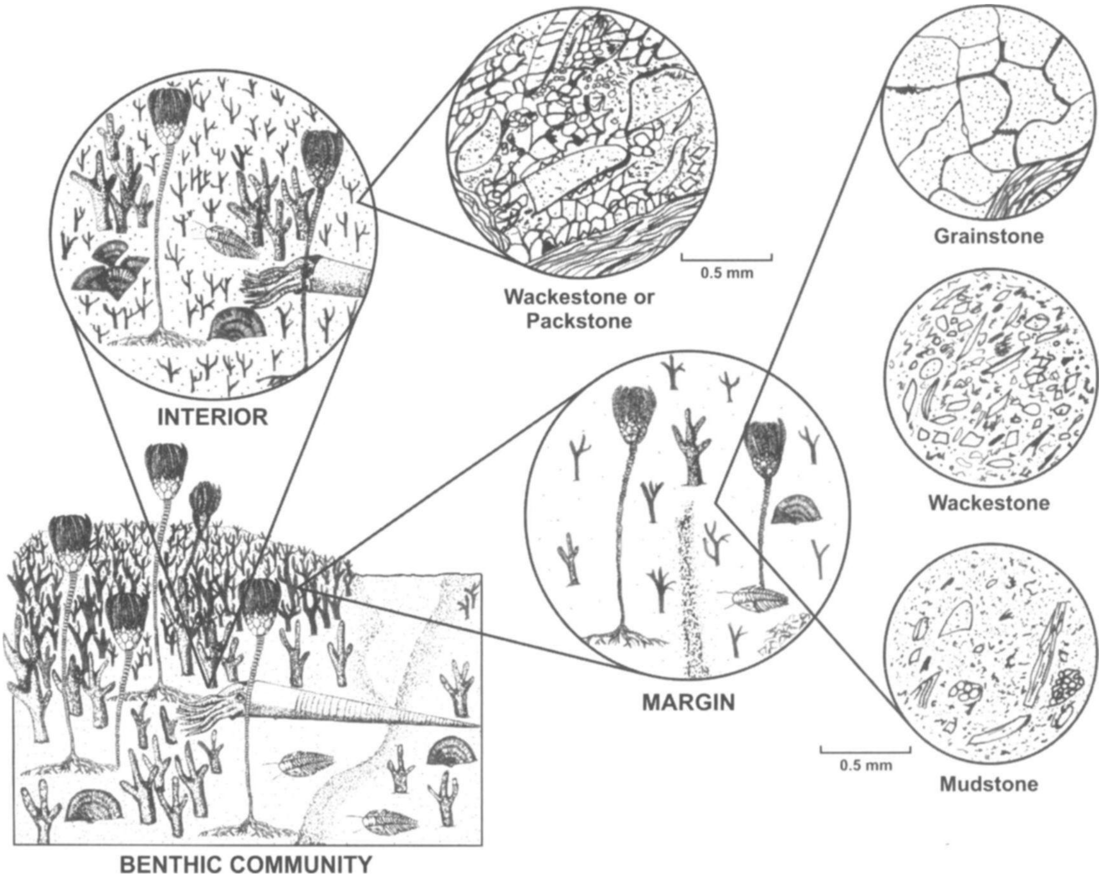


Figure 4.3. *Variation in limestone deposition in relation to benthic fossil assemblages. Smaller circles depict the character of different limestone types as seen in petrographic thin section under the microscope. All limestones are not the same. Different types of limestone will form depending on the relative contributions of skeletal grains and other allochems, fine-grained carbonate sediment (mud), and calcium carbonate cement (spar). A packstone has skeletal grains in contact (grain-supported) with mud filling the spaces between grains. A grainstone is grain-supported with cement filling the intergranular spaces. A wackestone has skeletal grains "floating" in a mud matrix (mud-supported) with more than 10% grains, and a mudstone has less than 10% grains. In the interior of a benthic assemblage, water movement is retarded by the dense growth of organisms, causing fine-grained sediment to be deposited along with skeletal grains, resulting in either packstones or wackestones. More variable water movement at margins of assemblages will produce a wider variety of limestones. A grainstone usually reflects the highest level of water motion, by which mud is winnowed, leaving only skeletal grains to be cemented. From Martin and Hauer (2006), courtesy of Wayne D. Martin.*

fraught with difficulties. Even the internationally recognized Cincinnatian stages (Edenian, Maysvillian, and Richmondian) could he called into question as valid time-stratigraphic units because they were equivalent to the Eden, Maysville, and Richmond "Croups" which comprised "formations" that lacked time-stratigraphic significance. Consequently, geologic-research on the Cincinnatian during the 1960s resulted in major revisions of the stratigraphic classification and nomenclature.

Lithostratigraphy and "Stateline Boundaries"

Three major research programs of the 1960s marked a new phase in the development and understanding of Cincinnatian stratigraphy; all were initiated outside of Cincinnati. Several geologists at The Ohio State University (notably Stig M. Bergstrom, Walter C. Sweet, Malcolm P. Weiss, and their students) published a series of papers aimed at revising the American Upper Ordovician Standard in both lithostratigraphic and biostratigraphy terms. In the 1960s the Kentucky Geological Survey and the United States Geological Survey initiated a major project to provide new geologic maps of the entire state of Kentucky at scale of the 7.5 minute quadrangle (1:24,000 scale). In order to accomplish this enormous task, it was necessary to provide a uniform stratigraphic classification of mappable lithostratigraphic units. In keeping with the new Stratigraphic Code, geologists associated with the mapping program developed a new stratigraphic classification for the Ordovician rocks of Kentucky based on mappable, lithologically defined formations. New formational names were proposed, such as the Kope Formation, based on type sections in Ohio and Kentucky, which replaced the old Latonia or Eden Formation (Weiss and Sweet 1964). Some traditional names, such as the Fairview (Ford 1967), were retained and given formal definition as formations. In Kentucky most of the new formations were thick packages of strata comprising equivalents of older, thinner units that either could not be traced into Kentucky or else had been based on fossil content (Figure 4.1). Also in the 1960s the Indiana Geological Survey undertook restudy of the Upper Ordovician in southeastern Indiana. This work produced a revised lithostratigraphic classification in which a single formation, the Dillsboro, spanned the Maysvillian and Richmondian Stages (Figure 4.1; Brown and Lineback 1966).

Although the new research programs yielded stratigraphic units in keeping with modern lithostratigraphic practice, the status of Cincinnatian stratigraphy in the late 1960s presented new challenges to an overall understanding of Cincinnatian geologic history. Creation of such thick, broadly defined formations tended to obscure many changes occurring at smaller scales of stratigraphic resolution, and the abundant fossil content of these rocks was largely ignored. Any attempt to map the Cincinnatian over the entire tri-state region revealed that formations ended abruptly at state lines, resulting in confusion not unlike that of a visitor to the city of Cincinnati who finds that many street names change across major intersections! One might also be led to conclude that major faults followed the state boundaries or the course of the Ohio River! Stratigraphic columns established for the Cincinnatian section in each state of the tri-state region had to be correlated.

New Advances in Biostratigraphy

Although the early zonation of the Cincinnatian based on such groups as bryozoans and brachiopods had proven inadequate for correlation very far outside the local Cincinnati area, beginning in the late 1950s, new research into the biostratigraphy of the Cincinnatian enabled a single time-stratigraphic framework to be applied across the entire region. In order to understand how this new advance came about, we must consider what characteristics are required for a fossil to be a reliable tool for long distance correlation of strata.

Fossils that are most useful for correlation of strata over great distances ideally must have two characteristics: a short vertical (time) range and a wide lateral distribution. Fossils having a short vertical range will be groups whose preservable morphology evolves relatively rapidly over time. Fossils with a wide lateral distribution will be groups that either tolerate a broad range of environments or else are capable of wide dispersal through a free-swimming larval stage or adult mode of life. The short vertical range of many Cincinnatian fossils produced a detailed biostratigraphic subdivision of the strata. However, as already mentioned, many of the fossil zones established in the immediate Cincinnati area could not be traced very far. Because lithologies also changed laterally, it is very likely that the fossils (chiefly bottom-dwelling bryozoans and brachiopods) are strongly controlled by environmental change. Modern techniques in biostratigraphy showed that groups such as microplanktonic algae (chitinozoans and acritarchs), conodonts (Sweet and Bergstrom 1971), and graptolites (Mitchell and Bergstrom 1977; Goldman and Bergstrom 1997) are better suited for long distance correlation (even intercontinental) of Ordovician strata because they have very wide dispersal. (Most of these groups lived in the water column above the sea floor, either drifting as plankton or actively-swimming.) The vertical ranges of these groups through the Ordovician tend to be rather long, so that they cannot be used to subdivide the Cincinnatian very effectively below the stage level, but they do form the basis of modern time-stratigraphic correlation of the Cincinnatian in relation to other regions of North America and worldwide (Webby et al. 2004).

Cycles and Depositional Sequences

Despite the apparent monotony of Cincinnatian limestones and shales, major repeated patterns in the lithologies had been recognized since the earliest work of Orton (Orton 1873). Nickles (1902) related these lithologic patterns to changes in turbulence. In 1969 Anstey and Fowler recognized that a transition from the limestone-rich Lexington Limestone underlying the Cincinnatian to the shale-dominated Eden Shale (now the Kope Formation) traceable throughout the tri-state area of Ohio, Indiana, and Kentucky, corresponded to a transition from shallow water, more turbulent conditions to deeper water, more quiescent conditions. In shallow water, greater wave-generated turbulence was expected to prevent settlement of fine-grained sedi-

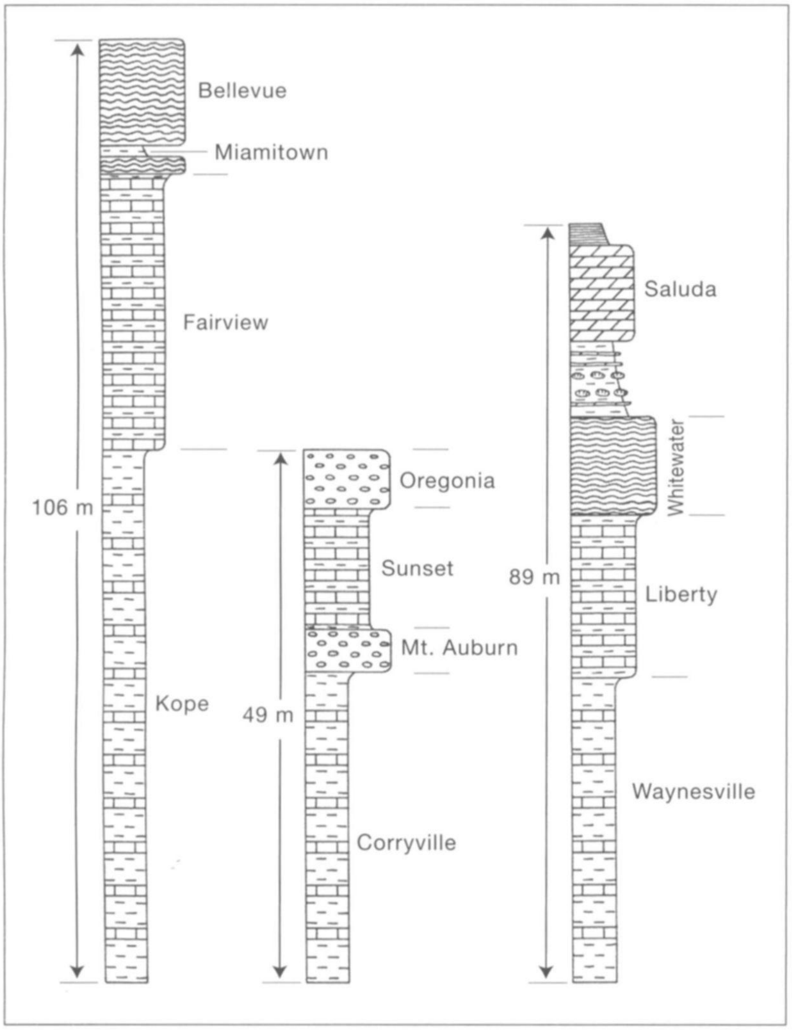
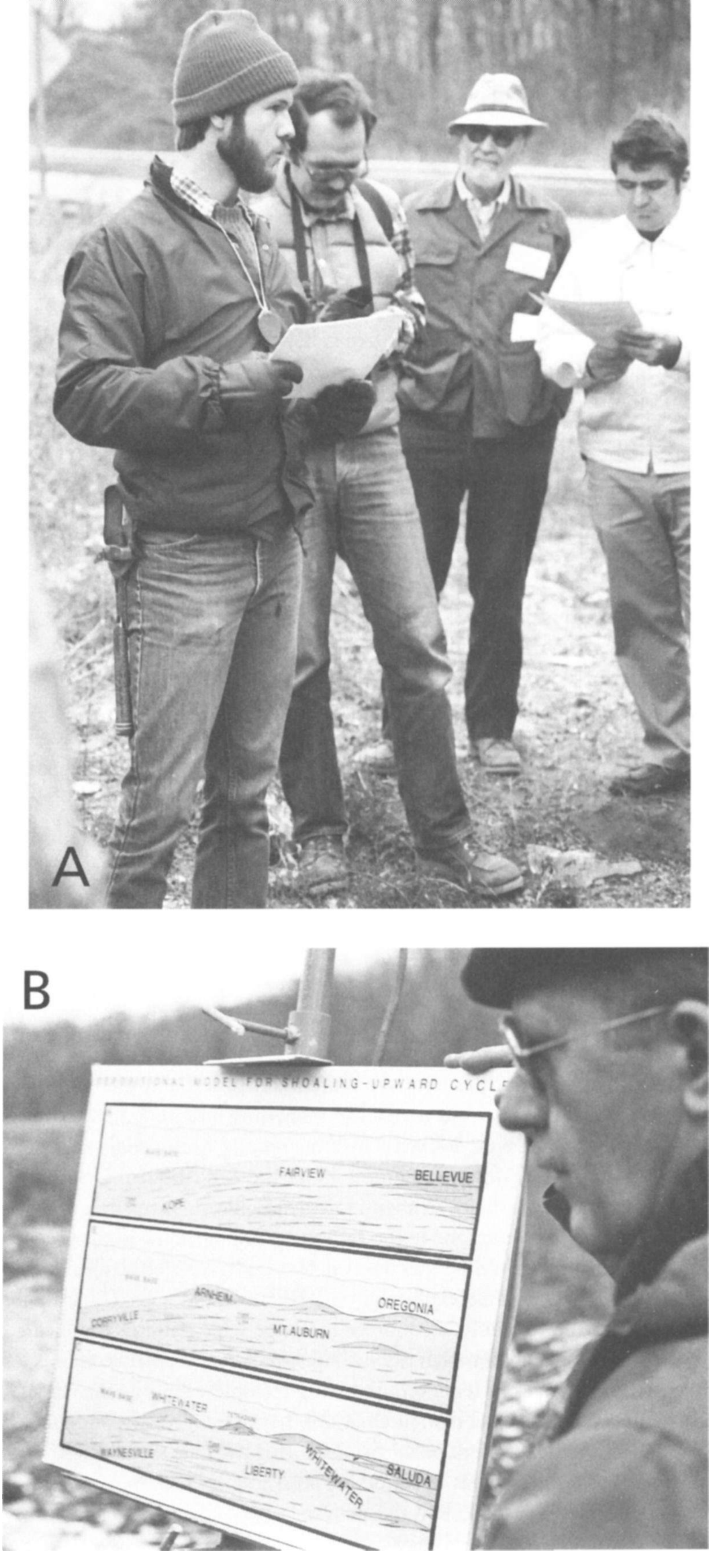


Figure 4.4. *Cincinnatian shoaling-upward cycles. From Tobin (1982, figure 74). The base of the Cincinnatian is at the base of the Kope Formation in the left-hand column; the Corryville Formation continues above the Bellevue Limestone, and the Waynesville Formation overlies the Oregonia Formation and continues to the top of the Cincinnatian (Saluda Formation). Arrows indicate thickness of each major cycle in meters. Note that in each cycle, shale is replaced by limestone toward the top, indicating a shallowing upward transition. Rock symbols are: brick pattern = limestone, dashed pattern = shale, wavy pattern = wavy-bedded limestone, rhombic pattern = dolomite, small circles = nodular limestone. More recent work by Holland has recognized six major shoaling-upward cycles or sequences over the same stratigraphic interval in which Tobin delineated three cycles (see Figure 15.1).*

merits, leaving coarser, shelly sediment, while in deeper water, fine-grained sediments, chiefly clay particles, are more likely to settle to the bottom. A return to shallower water was marked by increasing limestone in the overlying Fairview to Bellevue, followed by a deepening in the shale-rich Corryville and a shallowing in the limestone of the Mt. Auburn. Deepening again occurred in the shales Arnheim to Waynesville, followed by a shallowing with increasing limestone in the Liberty to Saluda, and a slight deepening in the uppermost Whitewater interval. Hay (1981) and Tobin (1982) recognized basically the same cyclic patterns (Figures 4.4, 4.5). Thus, major changes in sea level could account for the large-scale patterns of repeated lithologies of the Cincinnatian Series. There are several possible causes for these major changes in sea level, including tectonic events in the Appalachian orogenic belt to the cast, fluctuations in sediment supply, and growth of ice sheets in the southern polar regions during the Late Ordovician.

The modern concepts of sequence stratigraphy use the importance of sea level changes to explain the patterns of repeated deposition in the

Figure 4.5. *Geological Society of America Field Trip, 1981.* A. *Left to right: leader Rick C. Tobin, participants Tim Carr, Thomas W. Amsden, and Robert F. Dill.* B. *Professor Wayne A. Pry or with poster illustrating Cincinnatian shoaling-upward cycles and fades relationships.*



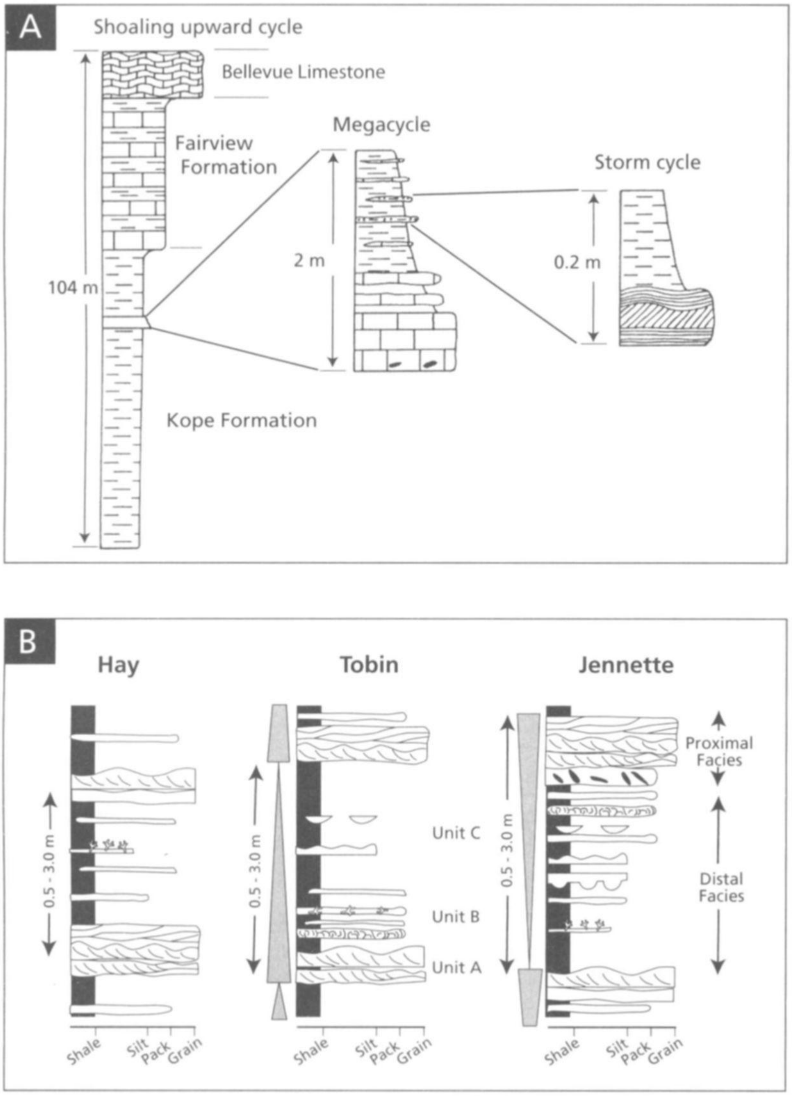
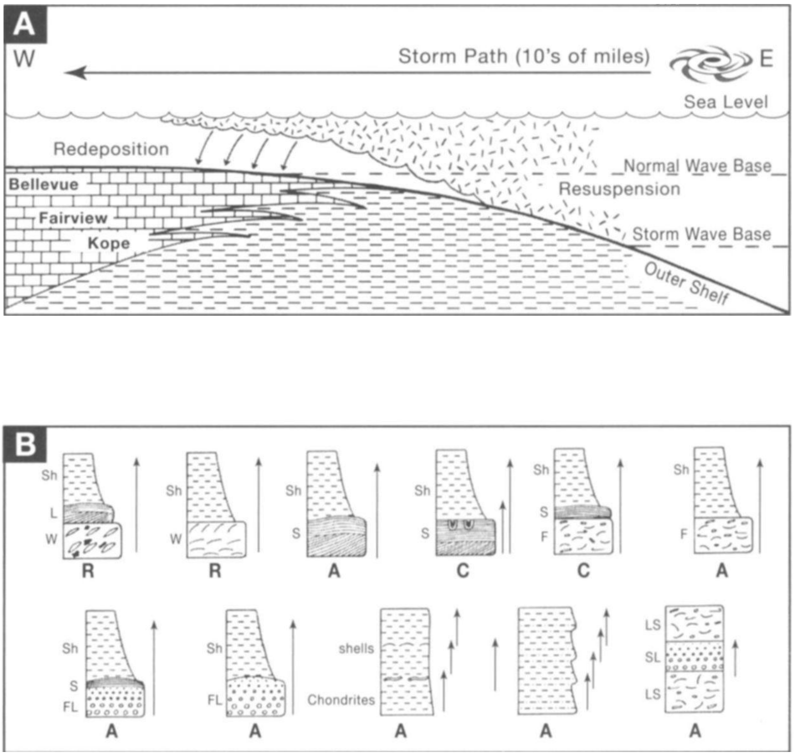


Figure 4.6. A. *Three scales of Cincinnatian stratigraphic cyclicity. From Tobin (1982, figure 30). In storm cycle, basal bed with wavy and oblique lines indicates cross-stratification produced by storm-induced currents and waves.* B. *Comparison of three concepts of Cincinnatian meter-scale cycles. From Holland et al. (1997, figure 1), courtesy of the Journal of Geology. In each column, width of bed pattern indicates lithology as shown in scale (pack = packstone, grain = grainstone). Arrows indicate thickness of cycle in meters. Tapering wedges beside each column indicate direction of shallowing (wider = shallower). Distal facies contain material transported farther from place of formation than proximal fades.*

Cincinnatian, as well as the marked lateral changes that had so greatly frustrated earlier efforts to achieve a single stratigraphic framework for the entire outcrop region. Because the Ordovician sea floor was a gentle ramp that generally became deeper from south to north, presumably eustatic (global) changes in sea level brought about different depositional conditions over different parts of the region at the same time. The abrupt transitions from shallow to deeper water mark sequence boundaries that can be used to correlate sections located on different regions of the paleoslope. Holland (1993, 1997, 1998) recognized six major depositional sequences within the Cincinnatian that cut across lithostratigraphic contacts (see Figure 15.1). The Cincinnatian comprises mainly the lower four sequences. The C1 sequence (Edenian) comprises the Kope Formation in the Cincinnati area. The **C2** sequence (Maysvillian) comprises the Fairview-Bellevue sequence, and the **C3,** Corryville-Mt. Auburn sequence. The Richmon-

Figure 4.7. A. *Storm deposition and erosion across the Cincinnatian sea floor. From Tobin (1982, figure 37). Note that hurricane rotation is correct for the Southern Hemisphere.* B. *Variations in Cincinnatian storm cycles. From Tobin (1982, figure 36). Arrows indicate layers of sediment deposited by single storm events. Sh = shale, L = laminated unit, W = whole fossil limestone, S = siltstone, F = fragmental limestone, FL = fine-grained limestone, SL = storm layer, Ls = any limestone. Chondrites is a trace fossil. A = abundant, C = common, R = rare.*



dian consists of three sequences: C4, Sunset-Oregonia, C5, Waynesville-Liberty-Whitewater, and C6, Upper Whitewater-Elkhorn, truncated by the erosional unconformity with the Silurian.

Within these six major Cincinnatian sequences, cyclic patterns of stratification also occur on smaller scales (figure 4.6A). Couplets of limestone and shale beds on a scale less than one meter thick are very characteristic of much of the Cincinnatian. Hay (1981) and Tobin (1982) first recognized that at least some of these couplets were the product of storm processes (Figures 4.6A, 4.7). The shallow, subtropical Cincinnatian sea floor must have been swept frequently by large storms, even hurricanes. During these storms, waves and strong bottom currents disrupted sea floor communities of organisms, sweeping fine-grained sediments into suspension while leaving shells and other skeletal debris as coarse calcareous lag deposits. As the storm subsided, fine-grained sediments settled onto the sea floor, smothering communities and forming what would become a shale bed overlying a fossiliferous limestone (see Figure 15.2). Tobin (1982) recognized that the Cincinnatian contains a wide variety of these storm cycles, some consisting of simply a shale bed overhang a limestone, in addition to other more complex patterns (Figure 4.7B). Some paleoecologists like Harris and Martin (1979) envisioned an ecological succession following such storm events, in which shelly organisms repopulated the muddy bottom and were in turn colonized by encrusting and attached epifauna (Figure 4.8). Many cases of completely preserved fossils such as crinoids, edrioasteroids, and trilobites in the Cincinnatian are undoubtedly the product of

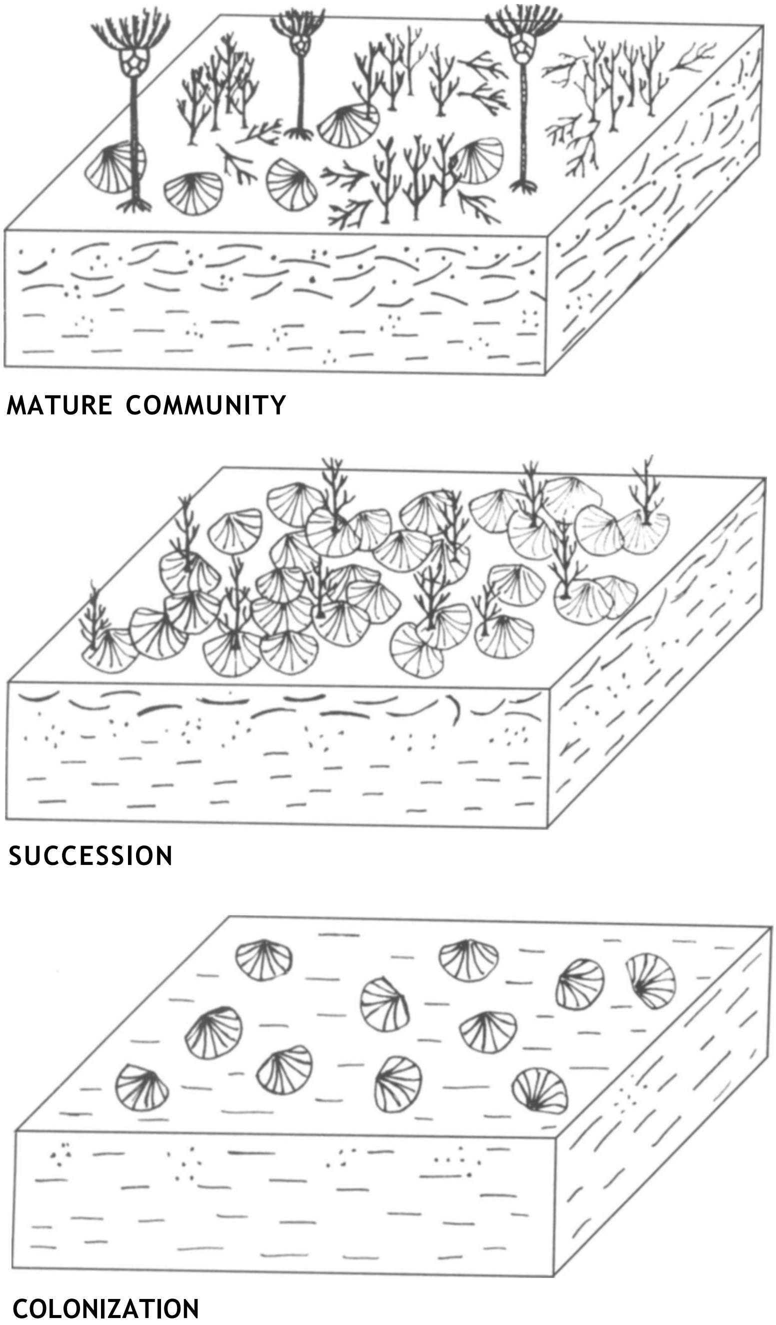


Figure 4.8. *Colonization of a soft mud substratum by Dalmanella (low diversity) is followed by the development of a shell pavement and succession of erect bryozoans. Higher diversity is achieved in the mature community by crinoids growing on a firm substratum. From Harris and Martin (1979) and reprinted by permission of the Society for Sedimentary Geology.*

rapid burial by fine-grained sediments during storm events (Brandt 1985; Meyer 1990; Schumacher and Shrake 1997; Hughes and Cooper 1999).

In many parts of the Cincinnatian section, particularly the Kope Formation, cyclicity at a scale of about one to three meters is very apparent as one passes long highway roadcuts. Different workers have interpreted this cyclicity in different ways. Hay (1981) recognized a regular spacing of coarse-grained limestone bundles (Figure 4.6B). Tobin (1982) termed this


A


B

scale of cyclicity the megacycle, and described it as a "fining-upward" packet having a basal component of coarse-grained limestone (grainstone), a middle component with thin interbedded limestones (packstones) and shales, and an upper shale-rich component (Figures 4.6A, B). Jennette and Pryor (1993) felt that the cycle was "coarsening-upward," beginning with shale, overlain by interbedded thin limestone and shale, and capped by coarse-grained limestone (Figure 4.6B). In their interpretation the cycle was of a regressive nature, corresponding to short-term fluctuations of sea level. More recent studies by Holland and others (1997) have continued to recognize storm-related features within these meter-scale cycles, but note that no single pattern of coarsening or fining upward is dominant. The high variability in cycle character probably reflects a complex interplay of sea level change and fluctuations in storm intensity and frequency. A remarkable result of all these studies is that despite the long-held view that individual strata within the Cincinnatian are not laterally persistent, meter-scale cycles within the Kope Formation can indeed be correlated over virtually the entire outcrop area for tens of kilometers (Brett and Algeo 2001b; Holland, Miller, and Meyer 2001; Webber 2002). Variations in proportions of limestone to shale within the Kope and Fairview Formations define even larger-scale cycles, on the order of 10-20 m thick ("decameter-scale cycles") that enable lateral correlation over long distances (Figure 4.9; Jennette and Pryor 1993; Dattilo 1996; Holland et al. 1997; Brett and Algeo 2001b).

Figure 4.9. *Kope cyclicity and Kope-Fairview formational contact traceable over broad area of Cincinnati Arch.* A. *Geological Society of America Field Trip, 1981. Participants examining meter-scale cyclicity in the Kope Formation along Kentucky Route 445 near the Ohio River, Campbell County, Kentucky.* B. *Contact of Kope Formation with overlying Fairview Formation (arrow) along Radcliff Drive, Cincinnati, Ohio. Photo by Paul E. Potter.*

Tracing Biofacies and Event Beds

The most recent studies of the Cincinnatian have, in a sense, come full circle in returning to its abundant fossil content as a key to understanding how Cincinnatian strata were deposited. In contrast to earlier lithostratigraphic studies in which thick units were defined on the basis of limestone-to-shale ratios with few internal subdivisions, the latest studies are based on high resolution, bed-by-bed logging of stratigraphic sections in terms of lithologic as well as paleontologic features. In the Kope Formation, long regarded as a single, thick and monotonous shale-rich unit, high resolution censuses of fossil assemblages (biofacies) revealed trends that are not immediately obvious from lithologic features (lithofacies) (Holland, Miller, Meyer, and Dattilo 2001). These biofacies trends appear to reflect depth-related faunal preferences and can be traced within the Cincinnati area and also eastward to Maysville, Kentucky (Holland et al. 2001; Webber 2002). Within another shale-rich unit, the Miamitown Shale, Dattilo (1996) also demonstrated the utility of fossil assemblages, together with lithofacies analysis, in correlation of meter-scale cyclicity within a 30 km radius.

Earlier Cincinnatian workers recognized many thin beds characterized by an abundance of a particular fossil species and restricted in stratigraphic occurrence. These are marked in the traditional biostratigraphy section (Davis 1992) and are well known among local collectors, yet found little use during the phase of Cincinnatian Lithostratigraphy. Exceptions were the "shingled *Rafinesquina*" beds in the Miamitown Shale and a thin zone of abundant *Platystrophia ponderosa* occurring at the base of the Mt. Auburn that were used by Ford (1967) as marker beds that were useful for correlation.

In recent years several paleoecologic and taphonomic studies brought renewed attention to thin, fossil-rich horizons that are traceable over a wide area. Frey (1987b) traced the nautiloid-rich ***Treptoceras d***_useri_ shale within the Waynesville Formation in Warren and Clinton Counties, Ohio, and correlated it with a lithologically equivalent trilobite-rich shale to the west in Indiana. A strophomenid brachiopod shell pavement encrusted by the same three edrioasteroid species occurs in the upper Corryville formation at Florence, Kentucky, and again 22 km to the north near the I-275 beltway northwest of Cincinnati (Meyer 1990). In the upper Kope formation, a persistent bed of calcareous siltstone replete with the U-shaped trace fossil *Diplocraterion* provided a key marker horizon for correlation from northern Kentucky to southwestern Ohio (Jennette and Pryor 1993). Several examples of paleontological event horizons in the Cincinnatian are discussed in Brett and Baird (1997). These include: a traceable storm horizon (Miller 1997); a one-meter thick interval characterized by the brachiopod ***Onniella*** *meeki* traceable 135 km from Ohio into Indiana (Frey 1997b); the Richmondian faunal "invasion" (Holland 1997);and Isotelus-bearing shales in the Waynesville formation that can be traced for at least 40 km across southwestern Ohio (Schumacher and Shrake 1997). Dattilo (1996) used the restricted occurrence of the brachiopod ***Heterorthina fairmountensis*** as a datum for correlation of the Miamitown Shale from southwestern Ohio to northern Kentucky. Brett and Algeo (2001b) discussed several other key fossil beds or epiboles in the Kope and fairview formations that facilitate correlation over a wide area in Ohio and Kentucky. All of these marker beds are exceptional for their wide geographic distribution, but have a variety of causes. Some resulted from conditions favorable to a particular species for a short time. Others reflect a widespread event such as a storm that smothered the sea floor over a wide area. The wide extent of these beds is also related to the very gradual change in depth over the entire region, creating vast areas of similar depth and bottom type.

Other types of event horizons in addition to zones of restricted fossil occurrence are also widely traceable across the Cincinnati Arch region. In particular, Jennette and Pryor (1993) used a bed with well-developed basal gutter casts as a datum for cycle correlation near the top of the Kope formation in the vicinity of Cincinnati and northern Kentucky. Cutter casts are sediment fillings of troughs eroded into the sea floor. More recently Brett and Algeo (2001b) demonstrated the utility of several l\ pes of event horizons in the Cincinnatian. Tempestites or storm beds include a variety of sedimentary features such as shingled brachiopod beds, rippled beds, graded beds, gutter casts, and smothered bottom or obrution deposits—all products of short-term but widespread episodes of intense disturbance of the sea floor. Other event horizons include distinctive trace fossil horizons (the aforementioned *Diplocraterion),* brachiopod shell pavements, concretionary layers, hardgrounds (beds formed by early cementation on the sea floor), and beds indicative of seismic events. Features possibly caused by seismic deformation of the sea floor including beds with intense internal deformation and so-called ball and pillow structures occur over a wide area in southern Ohio and northern Kentucky (Schumacher 1992; Pope et al. 1997). These seismites may have resulted from earthquakes caused by tectonic activity in the rising Appalachian mountains far to the east. Using all of these event horizons, Brett and Algeo (2001a) were able to correlate decameter and meter-scale cycles within the Kope and Fairview Formations for distances up to 80 km along the AA Highway (Kentucky Route 9) in northern Kentucky.

To a certain degree, the most recent studies of Cincinnatian stratigraphy confirm and vindicate the heavy emphasis that was placed on fossil content by generations of earlier workers in the Cincinnatian. Clearly, no study of Cincinnatian stratigraphy can afford to ignore the plethora of information offered by the abundance and diversity of fossils throughout the region. At the time of this writing, efforts to develop a highly detailed regional stratigraphic framework for the Cincinnatian rely on a synthesis of all evidence available, including lithology, sedimentology, and paleontology. Studies incorporating this "total evidence" approach include those of Dattilo (1996), Holland (1993 Holland (1997) Holland. Miller, and Meyer (2001), Brett and Algeo (2001b), Webber (2002), and McLaughlin and Brett (2007).

Through these studies, the recognition that the Cincinnatian is constructed of a series of stratal "packages" delimited by relatively short-term sea level changes that mark sequence boundaries also to some extent revives the old concept of the stratigraphic "layer cake" that typified much of the original work on the Cincinnatian (Algeo and Brett 2001). Clearly the Cincinnatian is not merely a jumbled mosaic- of carbonate and shale facies with poor lateral continuity. Although lateral facies variations do exist, they can be understood in the context of regional paleobathymetry and sequence architecture. Sequence, cyclic, and event stratigraphy offer great promise for development of a high resolution time-stratigraphic framework for the Cincinnatian in which many interesting questions of evolutionary paleontology, paleoecology, and sedimentology can be addressed.

Age of the Cincinnatian

How old arc the fossils of the Cincinnatian? How long ago did the Cincinnatian Age begin, and when did it end? How much time does any part of the Cincinnatian Series—a formation, a sequence, or a single bed—represent? These are questions of the absolute age of Cincinnatian fossils and strata.

To say that the Cincinnatian is Late Ordovician in age is to make a statement about its relative age. The geologic time scale of eons, eras, and periods was constructed during the nineteenth century on the basis of superposition and fossil succession. Initially, pioneering geologists like the Englishman William Smith recognized that fossils could be used to characterize strata and correlate them from one region to another. Through the work of Smith and other pioneers like Cuvier and Brogniart in France the geologic-succession of strata was established by recognizing that strata with characteristic sets of fossils always occurred in the same vertical sequence from oldest to youngest. The principle of organic evolution as later put forth by Charles Darwin and others was unknown to these founders of geology, but they were able to use the changing makeup of lite on Earth as a relative gauge of ancient history. Organic evolution is the underlying mechanism that provides a directional component, a sort of clock, by which to place fossils and their encasing rocks on the geologic time scale. However, the rate of evolutionary change varies greatly among living organisms, and some groups show marked change through a vertical succession of strata while others do not; consequently, different groups have different clocks. Evolutionary change thus cannot provide a uniform measure of time by which to estimate the absolute age of fossils (despite the modern use of "molecular clocks" to set the age for common ancestors of different living groups).

Absolute age dating of ancient rocks relies on the constant rate of radioactive decay of unstable isotopes of certain elements contained in minerals found in volcanic and other types of igneous rocks. Because these minerals do not usually form in the shells and skeletons of organisms or in the sediments, direct dating of fossils and most sedimentary rocks is very difficult. At best, we can hope to find datable layers such as volcanic ash beds or lava flows interbedded with fossiliferous strata. It may then be possible to state that a fossil-bearing layer lies either above or below a dated horizon, making the fossil either relatively younger or older. In the marine sedimentary record the best opportunities for this method of age determination come from unique potassium-rich clay beds known as K-bentonites, formed through chemical alteration of volcanic ash falls into the sea. K-bentonites contain biotites and zircons that are datable using uranium-lead and potassium-argon dating techniques.

In North America, ash beds preserved as K-bentonites are found throughout the Ordovician but are particularly well known from the Middle Ordovician (Huff et al. 1992). The closest dated K-bentonite to the Cincinnatian is a remarkable bed known as the Millbrig K-bentonite occurring at the base of the Middle Ordovician Lexington Limestone of Kentucky Ordovician (Huff et al. 1992). The Millbrig is found throughout much of the eastern mid-continent of North America and is equivalent to an ash bed found widely in western Europe. Radiometric age dates (U-Pb and $_{40}$Ar-$_{39}$Ar methods) of about 454 million years for this bed in North America and Europe indicate that it represents one of the largest ash-producing volcanic eruptions known in the Phanerozoic record. The eruption took place during the Taconian orogenic event as the ancient continents Baltica and Laurentia collided, closing the ancient Iapetus Sea. On the basis of this dated horizon, the Cincinnatian Age began sometime more recently than 454 million years ago.

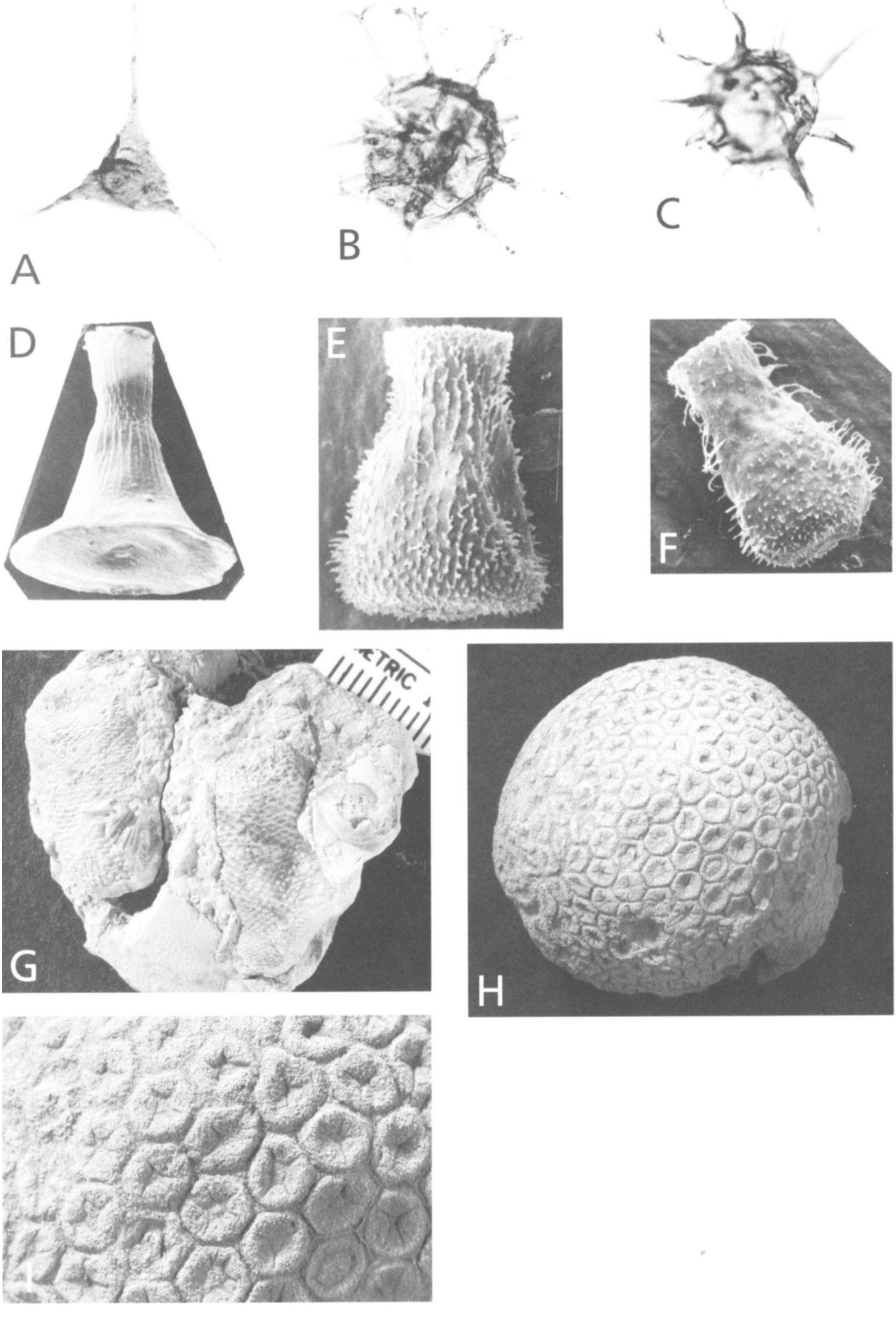
Unfortunately for a closer dating of the Cincinnatian, K-bentonites are scarce in the Upper Ordovician in both North America and Europe (Bergstrom, pers. comm.), probably reflecting a lull in tectonic activity between the Taconian and Acadian (Middle Devonian) orogenic (mountain building) pulses. However, a zone of two or three impure K-bentonites, known as the Bear Creek K-bentonite zone, occurs within the Point Pleasant Formation from 12.5 m to 13.7 m above the Lexington/Point Pleasant contact, and just below the base of the Cincinnatian (Schumacher and Carlton 1991). This zone has been identified in cores in Ohio and northern Kentucky, and in the Bear Creek Quarry, Clermont County, Ohio, but has not been dated, as it contains no zircons. The only bentonite known to occur within the Cincinnatian itself was recorded in the lower Richmondian from a drillcore in Seneca County, Ohio (Bergstrom and Mitchell 1992), but it, too, has not been dated.

By using radiometric dates from other regions to calibrate the time-stratigraphic record based on ranges of conodonts and graptolites, it is possible to place further constraints on the Cincinnatian time interval. The beginning of the Ordovician is now dated at about 488.3 +/-1.7 million years ago and its end at 443.7 +/-1.5 million years ago (International Commission on Stratigraphy 2004). The time scale produced by the UNESCO-sponsored International Geological Correlation Programme (Webby, Cooper, Bergstrom, and Paris 2004) places the beginning of the Cincinnatian at about 452.5 million years ago. However, the top of the section in the Cincinnati Arch region does not include the uppermost Ordovician record because of pre-Silurian erosion, and an entire stage, known as the Hirnantian, is missing. According to the timescale provided by Webby, Cooper, Bergstrom, and Paris (2004) the base of the Hirnantian is at about 445 million years ago. These considerations yield an approximate duration for the Edenian, Maysvillian, and Richmondian of about 7.5 million years (452.5 my—445 my). The fact that dates for neither the lower or upper boundaries of the Cincinnatian come from samples in the local region should alert the reader for future refinements! However, the dates and 7.5 million year estimate seem to be the best information currently available.

Holland and Patzkowsky (1996) calibrated biostratigraphic zonation of the Cincinnatian based on conodonts (Sweet 1984) with a radiometrically dated K-bentonite to derive estimates of the duration of the six Cincinnatian stratigraphic sequences. By their estimates, the duration of the C1 sequence (Edenian) was about 2.5 million years, that of the C2 sequence (Fairview-Bellevue) about 1.7 million years, that of the C3 sequence (Corryville-Mt Auburn) about 0.6 million years, that of the C4 (Sunset-Oregonia) sequence about 0.8 million years, that of the C5 sequence (Waynesville-Liberty-Whitewater) about 1.5 million years, and that of the C6 sequence (Upper Whitewater-Elkhorn) about 0.7 million years. Their total duration for the six sequences is 7.8 million years—very close to the more recent estimate of 7.5 million years.

If the Cincinnatian can be bracketed in time between 452 and 445 million years ago, is it possible to assign dates to subdivisions of the Cincinnatian, and to determine the amount of time represented by individual cycles or beds? Unless any directy datable components, such as ash beds, are found within the Cincinnatian, no absolute ages can be determined. Instead, we arc forced to rely on a process of interpolation, working up from the earliest radiometrically determined calibration point or down from the terminal calibration point. Assuming that sedimentation rates were constant during the Cincinnatian, one could assign intermediate dates based on stratal thickness. However, there is abundant evidence from studies of modern sedimentation rates that the assumption of uniform sedimentation rate cannot be made. A single bed of Cincinnatian limestone might well represent the product of a single major storm event, or it could represent a long-term accumulation of shell material. Likewise, a shale bed could he the product of a single depositional event, or alternatively represent very slow accumulation. Each bedding contact itself potentially represents a break in sedimentation or Hiatus of indeterminate duration—days, months, years, or more. Many Cincinnatian limestones have irregular, pitted upper surfaces, sometimes bearing encrusting organisms, which strongly suggest formation of a hardground on the sea floor over a long time interval during which very little sediment accumulated. In general, given the abundance of evidence for storm-related deposition in the Cincinnatian (Tobin 1982; Jennette and Pryor 1993). most limestones probably represent more time than the interbedded shales, but determination of absolute durations is very uncertain.

Wherever sedimentary strata display a strongly cyclic pattern of repeated sets of beds having uniform thickness or variation in lithologies, geologists have sought a possible link to cyclic or episodic causes reflecting seasonal, annual, or longer timescales of periodicity. Most intriguing is the possibility that variations in the Earth's orbital parameters could exert influence on climate changes that in turn cause cyclic or periodic sedimentation processes (Grotzinger et al. 2007). If sedimentation could be shown to respond to this kind of astronomical metronome, interpolation between calibration points on the timescale could be made accurately, and the amount of time represented by particular sets of strata could be determined. However, cycles of this type, known as Milankovitch cycles, have not as yet been demonstrated to exist within the cyclic Cincinnatian strata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ALGAE: THE BASE OF THE FOOD CHAIN

5

Algae are uncommon fossils in the Cincinnatian, but are potentially significant as primary producers of the Ordovician ecosystem and as indicators of important environmental conditions such as water depth. Algae include single-celled as well as multi-celled plants that are confined to aquatic or moist habitats because they lack internal canals for water storage and transport. They are therefore termed nonvascular. Because they obtain their energy through photosynthesis, algae require adequate exposure to sunlight. This essential requirement generally restricts them to very shallow water. Algae include the blue-green algae (division Cyanophyta), green algae (division Chlorophyta, single- and multi-celled), red algae (division Rhodophyta), and the brown algae (division Phaeophyta).

Blue-green algae are ubiquitous in modern marine environments, where they form a "turf" or mat of very fine filaments less than 1 mm in length. These mats are an important food source for many grazing animals such as gastropods. Although algal filaments are not often fossilized, the presence of algal mats is commonly recorded in the geologic record as finely laminated mounds or sheets called stromatolites. Algal mats have sticky, velcro-like surfaces that trap very fine sediment. As each thin layer of sediment accumulates, the algal filaments grow through it to form a new mat, and the process can be repeated indefinitely. Over time the layers (laminae) can be cemented, sometimes with the help of the algae, to form a stromatolite. Stromatolites are among the oldest known evidence of life, dating to over 3.5 billion years old, and are especially characteristic of Precambrian sedimentary rocks. At the end of the Precambrian, stromatolites declined drastically in abundance and variety of growth forms, possibly as a consequence of the evolution of large grazing animals. After the beginning of the Paleozoic, stromatolites became even less common and were usually restricted to very shallow water environments, such as tidal flats, where algal mats were less susceptible to grazing. Interestingly, stromatolites are virtually absent from Cincinnatian strata, although they occur in the tidal flat facies of the Middle Ordovician High Bridge Group near Lexington, Kentucky (Cressinan and Noger 1976). One blue-green alga that is preserved as calcareous filaments, ***Girvanella,*** occurs in the Whitewater Formation in the uppermost Cincinnatian in a zone containing biscuit-like laminated oncolites also attributed to algae (Blackwell et al. 1984).

Among the many species of green algae are some species capable of precipitating calcium carbonate within their plant tissues. Sand-sized flakes and minute needles produced by these algae are responsible for huge accumulations of calcareous sediments in modern shallow tropical seas. One

Figure **5.1.** A-C. *Cincinnatian acritarchs, all Edenian, Kope Formation, Wayne County, Indiana.* A. *Veryhachium edenense Colbath,* x *569 (from Colbath [1979, plate 13, figure 1]).* B. *Ordovicium gracile Colbath,* x *507 (from Colbath [1979, plate 8, figure 4]).* C. *Multiplicisphaeridium micraulaxum Colbath,* x *1038 (from Colbath [1979, plate 7, figure 10]).* A-C *reprinted by permission of E. Schweizerbart'sche. Note: in all figures,* x *indicates the magnification factor.* D-F. *Cincinnatian chitinozoans, all Maysvillian.* D. *Cyathochitina sp. cf. C. campanulaeformis, OSU 32534,* x *747 (from Miller [1976, plate 5, figure 6]).* E. *Hercochitina turnbulli Jenkins, OSU 32568,* x *516 (from Miller [1976, plate 13, figure 2a]).* F. *Conochitina hirsuta Laufeld, OSU 32542,* x *287 (from Miller [1976, plate 8, figure 1]).* G-I. *Cincinnatian dasycladacean algae.* G. *Lepidolites dickhauti Ulrich, William Heimbrock collection, Edenian, Kope Formation, Kenton County, Kentucky,* x *3.8.* H. Cy-

clocrinites darwinii (Miller), Stephen Felton collection, Maysvillian, Mt. Auburn Formation, Butler County, Ohio, x *1.3.* I. *C. darwinii, surface detail of H, polygonal facet diameter ~0.4 mm.*

group, the Dasycladaceae, is represented in the Cincinnatian by several species (Cross et al. 1996). Modern dasyclads occur no deeper than about 30 m, and frequently less than 5 m (Wray 1977). *Cyclocrinites* is the largest and most common dasyclad, found in the Bellevue Limestone and throughout the Richmond Group (Figures 5.1H, I). This alga resembles a golf ball in size, shape, and its dimpled surface. In well-preserved specimens the dimpled surface reveals a pattern of rhomboidal plates. These plates are actually expanded ends of branches that radiate from a central axis. Several species were originally described under the name *Pasceolus,* but Nitecki (1970) referred most of these to a single species, *Cyclocrinites darwini* (Miller).

Three other genera of dasyclad algae occur in the Cincinnatian (Cross et al. 1996). *Lepidolites dickhautii* Ulrich has a sausage-like shape, about 2 cm long, but is usually flattened (Figure 5.1G). Its surface has a scaly appearance, and it occurs in the Kope Formation. *Anomaloides reticulatus* Ulrich is reported from the lower Fairview Formation and has a similar scaly surface. However, it is club-shaped, and can reach several centimeters in length. *Ischadites circularis* (Emmons) has been reported from the Fairview, Corryville, and Mt. Auburn Formations (Halve 1948) but its taxonomic status has not been recently reviewed.

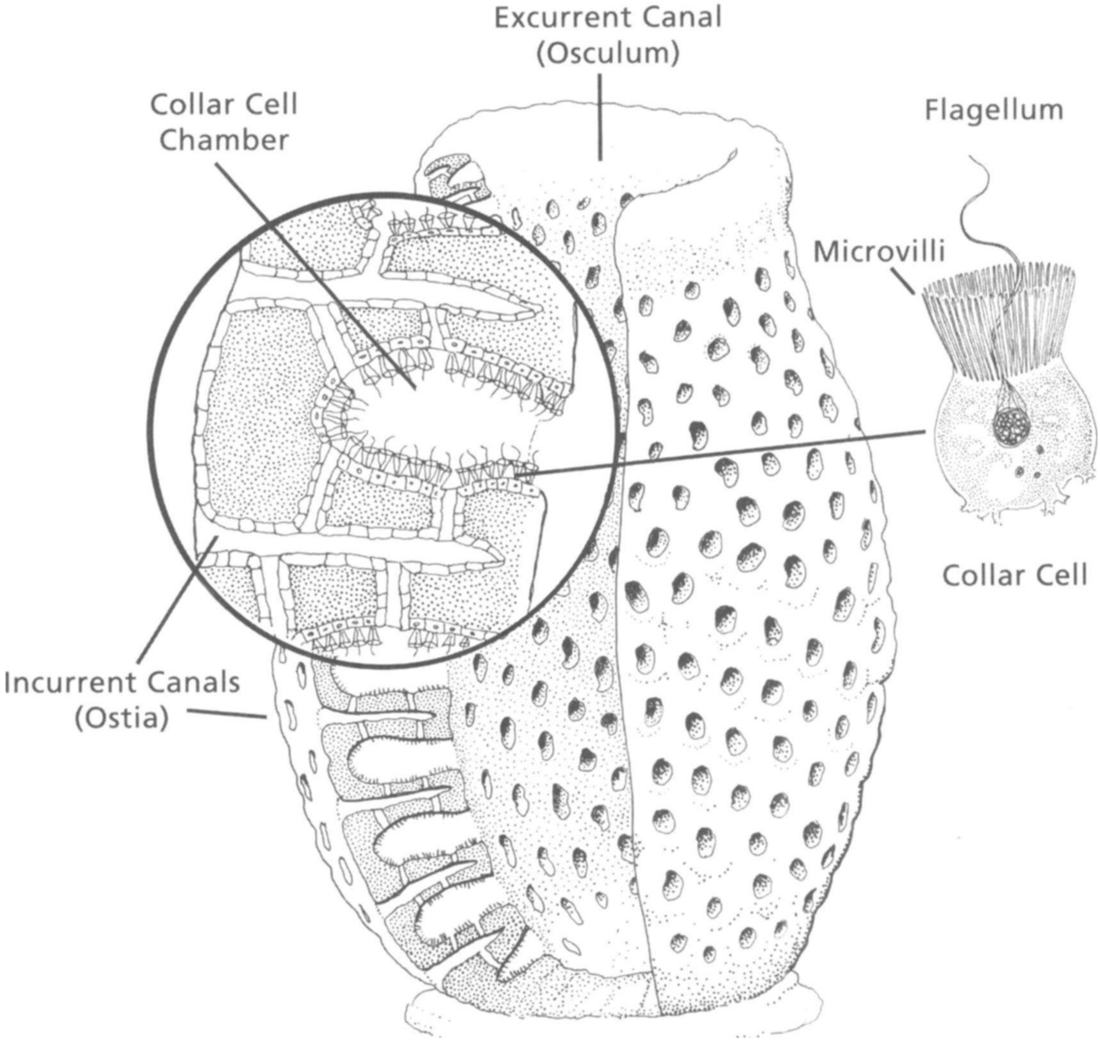
One red alga, *Solenopora richmondensis* (Miller), occurs in the Whitewater and Elkhorn Formations of the uppermost Richmond Group (Black-well et al. 198
cerium richmondense). The skeletal microstructure of this alga, with parallel laminae and vertical pillars, could easily be mistaken for a stromatoporoid (see chapter 6).

Two other algae of uncertain affinities are reported from the Cincinnatian: *Cyclindrocoelia covingtonensis* Ulrich from the upper Fairview Formation, and *Faheria anomala* Miller from the upper Fairview, Bellevue, Corryville, Mt. Auburn, Arnheim, Liberty, Whitewater, and Elkhorn Formations (Dalve 1948). Although algae are not common in the Cincinnatian, the fact that algae have been reported throughout the section, from facies regarded as deeper water as well as shallower, suggests that the entire section represents shallow depths within the photic zone. Notably, algae are most common in facies occurring at the top of the major shallow-upward cycles: the Bellevue, Mt. Auburn, and Whitewater-Elkhorn Formations, where shoaling depths have been postulated on the basis of other sedimentary evidence.

Single-celled algae occur as microfossils in the Cincinnatian and provide the only fossil evidence for the phytoplankton that must have been the basis for the marine food chain. These microfossils fall into two groups: the acritarchs and the chitinozoans. Both groups are recovered from acid-resistant residues of rock samples. Because these planktonic microfossils were widely distributed by ocean currents, they are very useful for biostratigraphic correlation.

Acritarchs (meaning "uncertain origin") include a wide variety of microscopic fossil cysts with organic (non-mineralized) walls; they may represent several different groups of algae; consequently acritarchs are not a formal taxonomic group (Williams 1978; Cross et al. 1996). Acritarchs are generally spherical in shape, less than 100 microns in diameter (micron = millionth of a meter), and have projecting spines that often branch (Figures 5.1A-C). Although acritarchs are similar to the resting stages of the dinoflagellates (division Pyrrophyta), one of the major components of the modern marine phytoplankton, they cannot be diagnostically related to any particular phytoplankton group. Acritarchs occur throughout the Cincinnatian and their diversity is considerable: fifty-two species were recorded by Colbath (1979) in a core from the Kope Formation of Indiana; Jacobson (1978) reported forty-four species from the Cincinnati region; and Loeblich and Tappan (1978) described forty new species from the Cincinnatian of Ohio, Indiana, and Kentucky. Jacobson (1979) found that fluctuations in abundance of different acritarch species corresponded to paleoenvironmental variations in relative water depth.

Despite the name, chitinozoans are neither composed of the protein chitin, nor do they definitely represent an animal group. The actual composition of the minute (50-2000 microns), bottle-shaped test is similar to chitin but is termed a pseudochitin. Chitinozoans are thought most likely to be some type of phytoplankton, but their exact biological affinities are unresolved (Jansonius and Jenkins 1978; Cross et al. 1996). Like acritarchs, chitinozoans are found throughout the Cincinnatian (Miller 1976; Jacobson 1979) and provide useful information for worldwide biostratigraphic correlation (Figures 5.1D-F).


Excurrent Canal
(Osculum)
Collar Cell
Chamber
Flagellum
Microvilli
Collar Cell
Incurrent Canals
(Ostia)

PORIFERANS AND CNIDARIANS: SPONGES, CORALS, AND JELLYFISH

6

Sponges

Although sponges are regarded as the least specialized, hence most primitive of multicelled animals, they play an essential role as "sanitary engineers" in aquatic environments, living as active suspension feeders or filter feeders (Plate 3A). By removing minute organic particles from the water, sponges prevent decay products from poisoning the environment. This is a long-running role, as sponges first appear in the fossil record during the late Precambrian, over 540 million years ago.

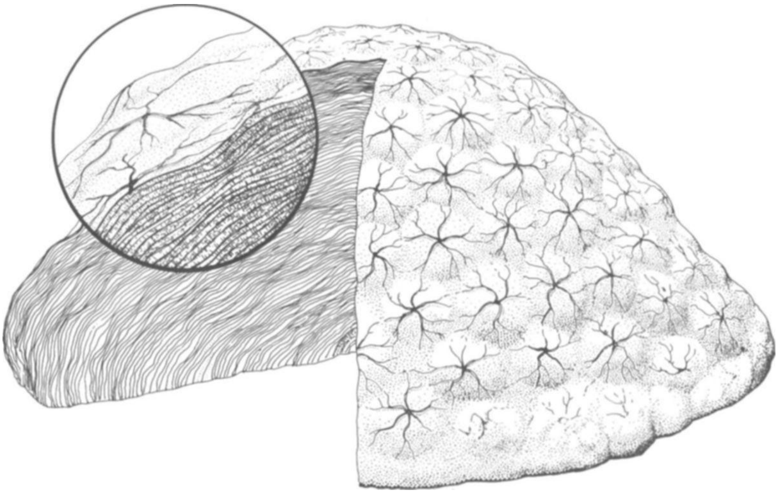
The body of a sponge lacks distinct cell layers, but is composed of different specialized types of cells that perform different life functions. The fundamental sponge cell is the collar cell, equipped with a waving flagellum that draws water into a cone formed of microvilli (Figure 6.1). The simplest sponge is a hollow tube, open at one end. Collar cells line the interior of the tube and create a feeding current that passes through the body wall via openings called ostia and tubular cells called porocytes. The collar cells remove food particles that are digested by amebocytes. The feeding current carries wastewater, depleted of nutrients, out of the sponge cavity through one or more chimney-like openings called oscula. Because sponges are fixed to the substratum and do not move about, they are often regarded as inert or nonliving. In fact they are actively circulating water and processing it for nutrients (Plate 3A).

The body of a sponge is mostly composed of a fibrous protein called spongin, which is also secreted by specialized cells. (This is what makes up a natural bath sponge.) After death, spongin readily decays, so that many sponges have little chance of becoming fossilized. Most sponges also secrete minute, mineralized spicules that are embedded within the spongin network. Spicules can be as simple in form as a single needle, but can also be very complex, burr-like, and even fused to form a basket-like lattice; their composition is either calcium carbonate or silicon dioxide. Once a sponge decays, the spicules are released into the sediment where they can be preserved as microfossils. Sponges that have dense or fused networks of spicules are more likely to be preserved intact, and it is these types that make up most of the fossil record of sponges.

In the late 1960s biologists diving on the coral reefs of Jamaica discovered a new group of living sponges that completely defied the concept of a typical sponge (Plate 3B). Moreover, these new sponges provided an important link to some fossils that had long been misclassified. Among these fossils are some found in the Cincinnatian. The new sponges are called sclcrosponges or coralline sponges because they form a massive calcareous skeleton like that of coral. The sponge body is restricted to a thin surface layer in

Figure 6.1. *A simple sponge, showing a cross-section of the body wall. Inset shows a magnified view of incurrent canals (ostia), collar cells and collar-cell chambers. Drawing by John Agnew.*

Figure 6.2. *Reconstruction of a living stromatoporoid, modeled on a living sclerosponge. A section is removed to show internal laminae of the skeleton. Living tissue occupies only the uppermost layer, with excurrent canals radiating from oscula. Magnified inset shows surface tissue and microstructure of laminae. Compare to Figure 6.3D, below. Drawing by John Agnew.*

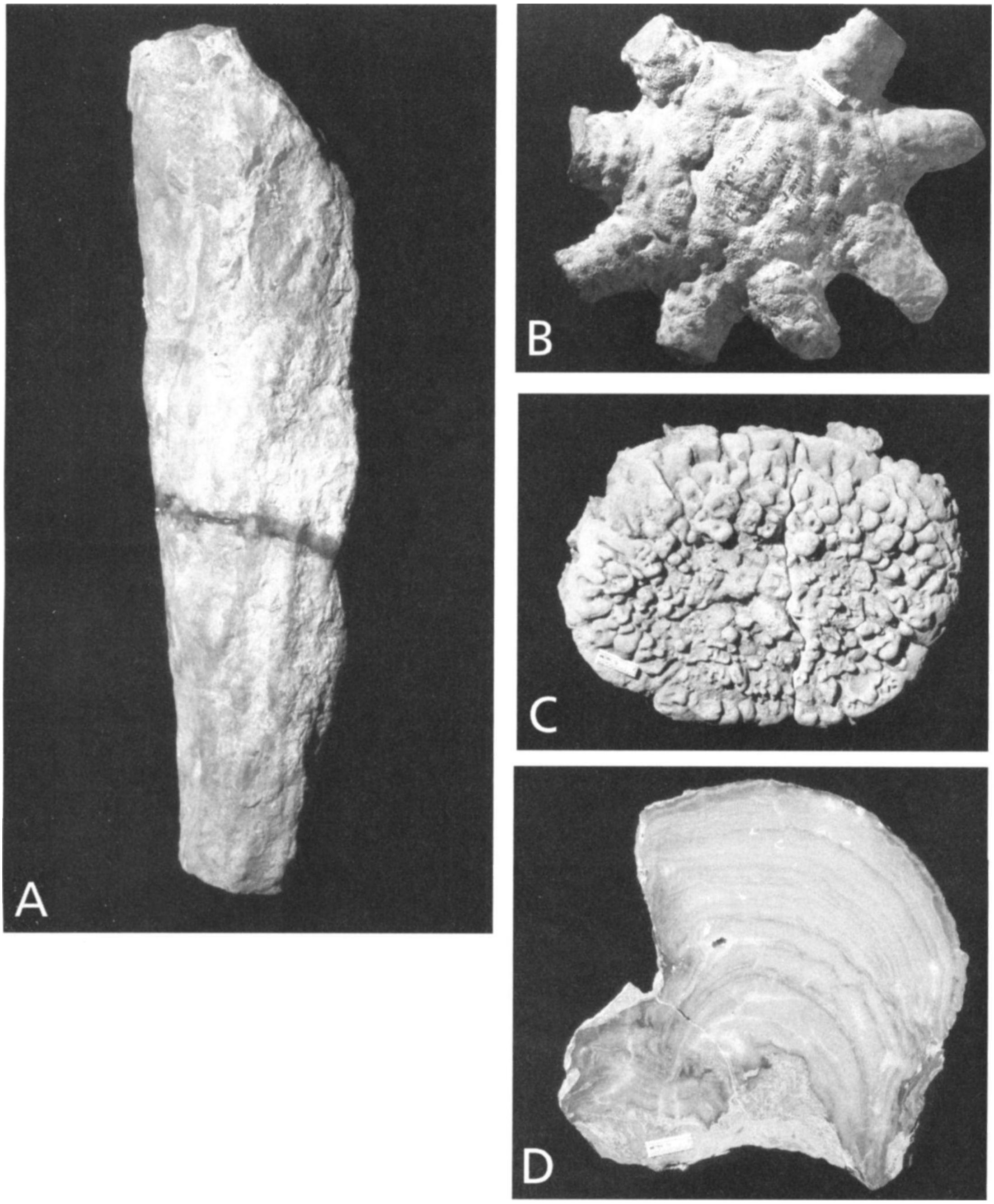


which typical sponge cells carry out filter feeding (figure 6.2). Wastewater canals that converge on the oscula leave starburst patterns of grooves in the calcareous skeleton that match with structures called astrorhizae in the fossil group known as stromatoporoids (figures 6.2, 6.3A, D). These and other similarities enabled the stromatoporoids to be recognized correctly as a new group of sponges, after they had been classified with cnidarians, bryozoans, and even protozoans. Stromatoporoids first appear in strata of Ordovician age, and were thought to have become extinct in the Cretaceous, until the living sclerosponges were found. During the Silurian and Devonian periods, stromatoporoids were major reef builders along with corals, but the modern sclerosponges (more distantly related to the Paleozoic forms) are restricted to deep reef environments and play a smaller role in reef building.

Sponges are not common fossils in the Cincinnatian, although they often may be overlooked because they can resemble bryozoans or corals, and also have a rather nondescript appearance (figure 6.3C). Five genera of sponges and three genera of stromatoporoids are recognized in the Cincinnatian (Dalve 1948; Rigby 1996). *Brachiospongia* is the largest and most striking sponge (figure 6.3B). This sponge has a hollow central cavity from which radiate 6-12 straight or curved, finger-like projections; its diameter can reach 28 cm (11 in). Other Cincinnatian sponges arc described in detail and illustrated by Rigby (1996).

Stromatoporoids are not common in the Cincinnatian and may superficially resemble bryozoans in having a mound-like or encrusting form (Figure 6.3D). They differ from bryozoans in being densely covered with tubercles. Cross-sections of Cincinnatian stromatoporoids are composed of blister-like skeletal deposits called vesicles, whereas bryozoans have a tubular structure (Figure 6.2). *Aulacera* is a very distinctive, large Cincinnatian stromatoporoid with a cylindrical shape (figure 6.3A). In life, *Aulacera* grew upright on the sea floor like a tree or a stalagmite, but they are preserved lying horizontally like fallen logs. *Aulacera* found in Ordovician strata slightly younger than the youngest Cincinnatian beds on Anticosti Island in the Gulf of St. Lawrence reached gigantic sizes, up to 28 cm in

Figure 6.3. *Cincinnatian sponges and stromatoporoids.* A. *A cylindrical stromatoporoid, Aulacera undulata (Billings), MUGM 29618, Richmondian, horizon and locality unknown,* x *0.3.* B. *A large sponge, Brachiospongia tuberculata James, holotype, CMC IP 209, Richmondian, Liberty Formation, Clinton County, Ohio,* x *0.3.* C. *A sponge, Pattersonia tuberosa (Beecher), MUGM, Maysvillian, Fleming County, Kentucky,* x *0.3.* D. *Polished cross-section of a stromatoporoid, Labechia huronensis (Billings), MUGM 634A2t, Richmondian, Montgomery County, Ohio,* x *0.3.*



diameter and 1-2 m in length (Cameron and Copper 1994). In the Cincinnati region they are restricted to the Richinondian formations, the Elkhorn formation in particular, and diameters up to 5-10 cm are known.

Cnidarians

The stony corals are the best known members of the phylum Cnidaria, which also includes jellyfish, sea anemones, and many groups like In-

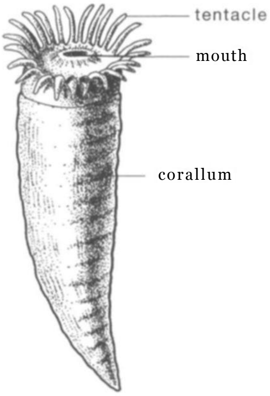


Figure 6.4. *Reconstruction of the Cincinnatian solitary rugose coral, Grewingkia canadensis, showing the polyp with extended tentacles. Drawing by Kevina Vulinec.*

droids, sea fans, sea whips, and soft corals that are often mistakenly thought to be seaweeds. Despite such a bewildering array of forms, cnidarians share several features that indicate their common relationship as members of one of the simplest multi-celled animal (metazoan) phyla. Cnidarians stand apart from other animals in having two body forms, the polyp and the medusa. The polyp, as typified by a sea anemone or stony coral (Plate 3C; Figure 6.4), is cylindrical in shape and attached at the base to a hard substratum. The body wall consists of only two cell layers (unlike the three layers found in all other metazoans), separated by a non-cellular jelly layer called the mesoglea. There is a single opening (mouth) into the body cavity through which food is ingested and waste is expelled. A ring of tentacles surrounding the mouth serves for food capture and defense. The medusa or jellyfish has the same structure as the polyp (with thicker mesoglea) but is free-living, swimming by muscular pulsations with the mouth oriented downwards. Both polyp and medusa forms arc present at different stages during the life cycle of some cnidarian species.

The three major classes of cnidarians differ in their expression of the polyp and medusa stages. Hydrozoans (including hydroids, Portuguese Man-of-War, a (true jellyfish) restrict the polyp to a larval stage and live mostly as medusae. Anthozoans (anemones, corals, "soft corals") live exclusively as polyps, and often as colonies of multiple polyps that are genetic clones of a single initial polyp. One other feature common to all cnidarians provides a clue to their mode of life. Microscopic stinging cells (cnidoblasts) are concentrated in the tentacles of all cnidarians. Upon contact with a foreign object the stinging cell releases a harpoon-like hollow thread that pierces soft tissue and injects a toxin. Small organisms are stunned or killed by the stinging cells, then grasped by the tentacles and stuffed into the mouth. Thus cnidarians live as predaceous carnivores, although polyps and weakly swimming jellyfish must rely on water motion to supply their prey. Because the prey of most cnidarians is mainly minute zooplankton, they are also considered to be passive suspension feeders.

In the Cincinnatian strata, two major groups of cnidarians arc represented: the anthozoan corals and the scyphozoan conulariids. The corals include both solitary and colonial species.

Solitary Corals

Cincinnatian solitary corals, commonly called horn corals or cup corals, and one colonial coral belong to the order Rugosa. Rugosans first appeared in the Late Ordovician and became extinct by the end of the Permian. The common name "horn coral" refers to the conical or cylindrical shape of the calcitic skeleton (corallum); these corals are commonly mistaken for a fossilized cow's horn (Figures 6.4, 6.5). The polyp occupied a depression (calice) at the wide-end of the corallum. As the coral grew, the polyp deposited successive layers of skeletal material beneath it, thereby increasing the length of the corallum. Older parts of the corallum did not contain living tissue and thus were subject to physical abrasion or encrustation and boring by other organisms.

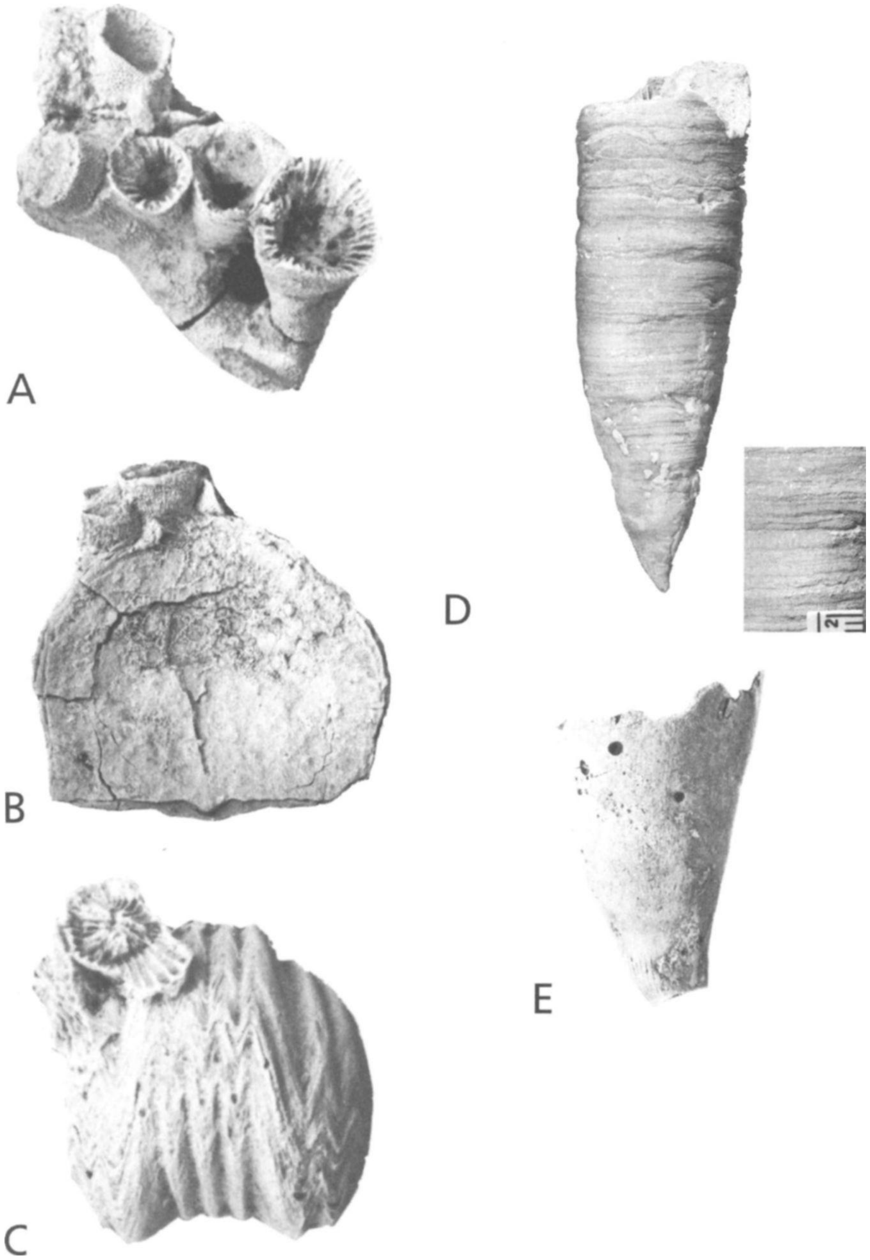
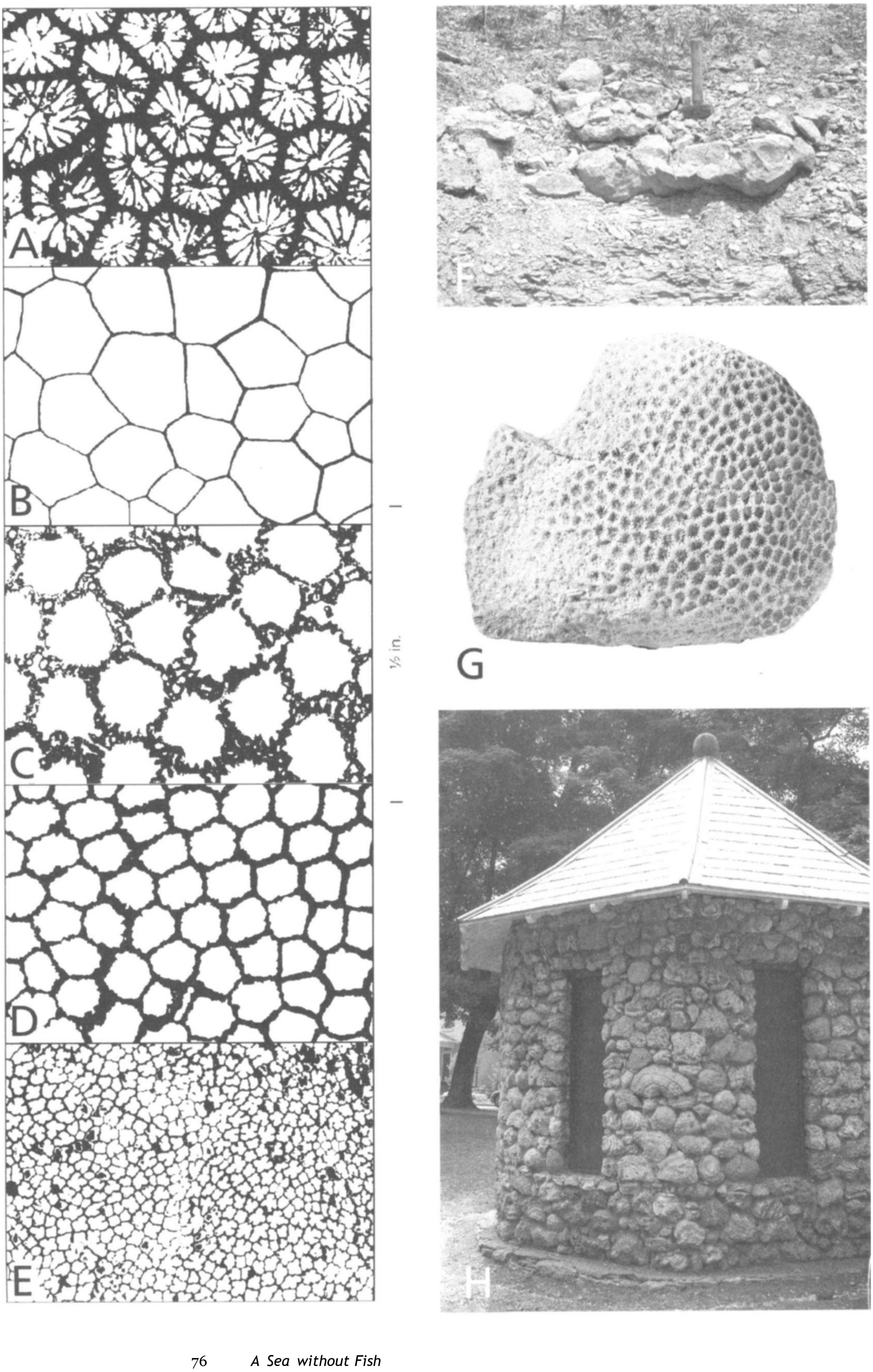


Figure **6.5.** *Cincinnatian rugose corals.* A. *Streptelasma divaricans (Nicholson), USNM 70211, several coralla attached to bryozoan, Richmondian, Waynesville Formation, Clinton County, Ohio,* x *2.0 (from Elias [1982, plate 3, figure 5]).* B. S. *divaricans, USNM 135767, three coralla attached to margin of brachiopod Rafinesquina, Richmondian, Whitewater Formation, Wayne County, Indiana,* x *1.3 (from Elias [1982, plate 3, figure 9[).* C. *S. divaricans, USNM 40086, two coralla attached to brachiopod Lepidocyclus, Richmondian, Whitewater Formation, Butler County, Ohio,* x *2.2 (from Elias [1982, plate 3, figure 8[).* D. *Grewingkia canadensis (Billings), CMC IP 50667, Weaver Collection, well-preserved corallum, Richmondian, Adams County, Ohio,* x *0.6, inset showing epithecal growth-lines, scale in mm.* E. *G. canadensis, CMC IP 45413, typical abraded corallum with broken rim, showing circular borings of Trypanites, Richmondian, Whitewater-Elkhorn Formations, Wayne County, Indiana,* x *1.0 (from Elias [1982, plate 9, figure 10]).* A - C *reprinted by permission of the Paleontological Research Institution.*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Although the soft polyp of rugosans is never preserved, rugosans are known to be corals because the calice has multiple radiating partitions called septa that are found in living corals. Septa are secreted by soft tissue partitions of the internal body cavity called mesenteries. In living anthozoans, mesenteries serve important functions in digestion and reproduction. The number and arrangement of the septa are traits used in the classification of corals. In rugosans the septa have a roughly four-fold symmetry, compared to living corals that have six-fold symmetry.

Two species of solitary rugosans occur commonly in the Cincinnatian, both in the Richmondian strata (Figure 6.5; Elias 1982, 1998). *Grewingkia canadensis* (Billings) is the largest and most common rugosan (Figures 6.5D, E). Coralla reach lengths over 13 cm (5 in) but are generally in the range 10-60 mm (0.5-2 in); the diameter ranges from 22 to 40 mm (0.9-1,6 in). Specimens are almost always found lying on their sides and appear highly abraded, encrusted, and bored (Figure 6.5E). External concentric growth lines are rarely preserved (Figure 6.5D, inset). Like some living solitary corals, *Grewingkia* probably lived upright, partly buried in soft sediment with the polyp exposed. Some encrustation and boring took place during life but continued after the coral was exhumed by storm activity and deposited on its side. Bryozoans are the most common encrusters and a worm probably formed the borings (trace fossil name *Trypanites,* see Elias 1986). Field studies demonstrate that *Grewingkia* specimens on single bedding surfaces are oriented in preferred directions that probably resulted from alignment of corals during storms.

Streptelasma divaricans (Nicholson) is the other solitary rugose coral found in the Richmondian section (Figures 6.5A-C; Elias 1982, 1998). Unlike *Grewingkia, Streptelasma* is found in growth position, on the upper surfaces of limestones. The coralla are usually 6-13 mm (0.25-0.5 in) in length, rarely exceeding 25 mm (1 in), with a diameter of 13 mm (0.5 in). Coralla occur individually and in clusters, often attached to brachiopods, bryozoans, or even coralla of *Grewingkia.* In many cases the brachiopod or host was living at the time the corals attached. The outer layer of the corallum (epitheca) shows septal grooves and interseptal ridges in contrast to the smooth, worn epitheca of *Grewingkia.*

Figure 6.6. *Cincinnatian colonial corals.* A-E. *Corallites as seen on external surface or in cross sections of corallum, at same scale* x *3.7.* A-E *from Elias (1998).* A. *Cyathophylloides, a colonial rugosan, Richmondian.* B. *Foerstephyllum, a tabulate, Richmondian.* C. *Calapoecia, a tabulate, Richmondian.* D. *Nyctopora, a tabulate, Richmondian.* E. *Tetradium, a tabulate, Richmondian.* F. *Coral bed, Richmondian, Madison County, Kentucky, length of hammer 25 cm (from Elias [1998, figure 5]).* G. *Protaraea richmondensis Foerste, MUGM 5435, a tabulate encrusting brachiopod shell, Richmondian, Liberty Formation, Preble County, Ohio,* x *1.7.* H. *Octagonal tool house built ca. 1900 in John Paul Park, Madison, Indiana, constructed entirely of colonial corals from the Richmondian coral beds exposed in the vicinity.* A-F *reprinted by permission of the Mid-America Paleontology Society.*

Colonial Corals

Most Cincinnatian colonial corals belong to another extinct coral group called the Tabulata. Tabulates are commonly called honey-comb corals because of their multiple, polygonal corallites (skeletal tubes secreted by individual polyps) (Figures 6.6, 6.7B). Tabulates originated in the Early Ordovician and became extinct by the end of the Permian. Coralla of tabulates vary in shape from sheet-like to hemispherical to spherical, reaching diameters of about 4 meters (13 ft). Individual tabulate polyps built tall, narrow corallites. Polyps periodically deposited a transverse basal plate (tabula) as they grew; thus, broken coralla or longitudinal polished sections have a characteristic ladder-like appearance (Figure 6.7B). In life, tabulate polyps were truly colonial because corallite walls are shared and have interconnecting pores. Septa are not well developed, leading some specialists

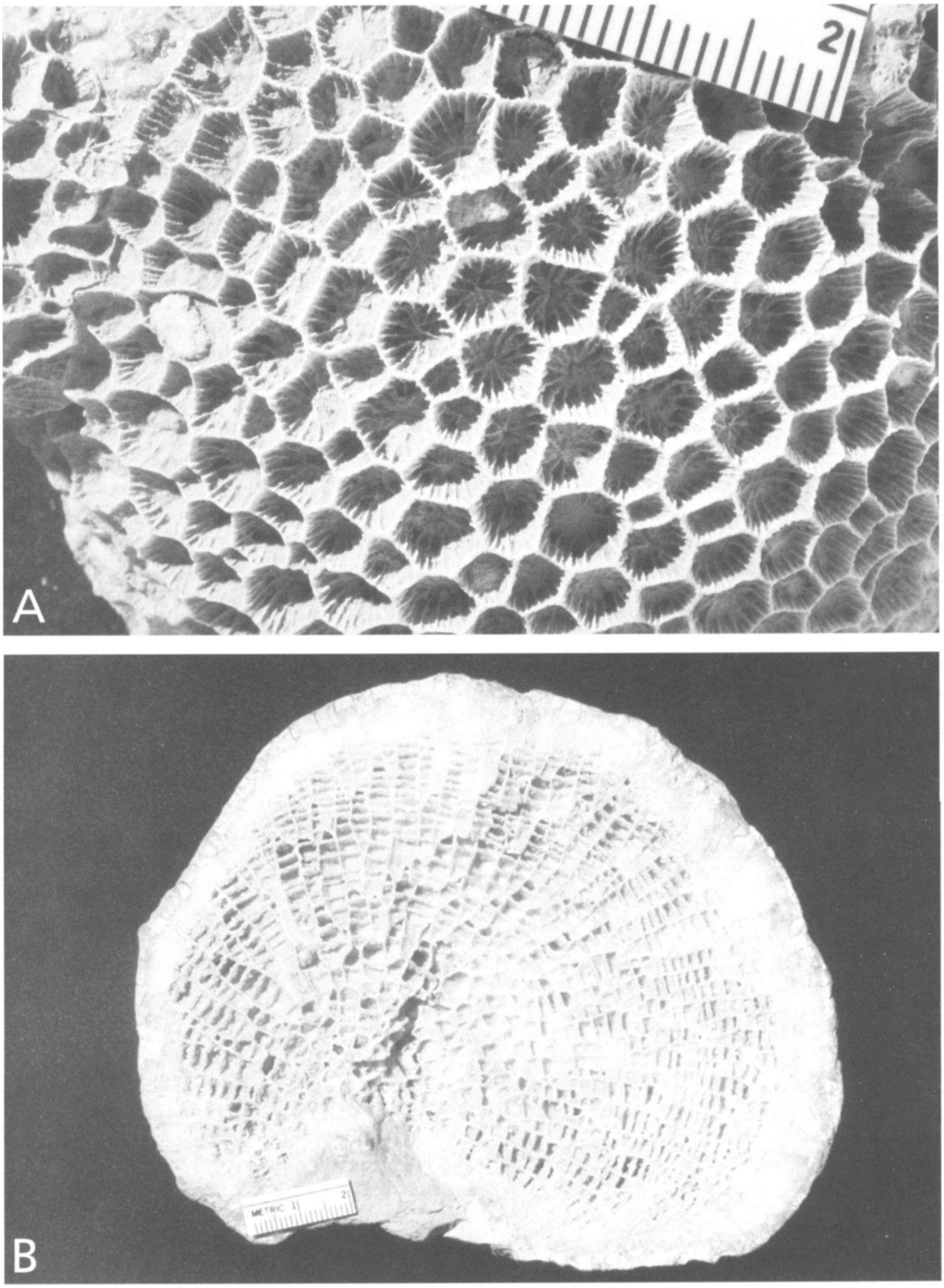


Figure 6.7. *Cincinnatian colonial corals.* A. *Cyathophylloides stellata (Hall), MUGM 5285, a colonial rugosan, Richmondian, Liberty Formation, Nelson County, Kentucky,* x *3.* B. *Foerstephyllum vacuum (Foerste), MUGM 5301, a tabulate in vertical section, showing tabulae, Richmondian, Liberty Formation, Nelson County, Kentucky,* x *0.8.*

to question whether tabulates were in fact corals. An extraordinary discovery of soft tissue polyps preserved in a Silurian tabulate (Copper 1985) settled the debate for most tabulates, although some, like the Cincinnatian *Tetradium,* are very similar to some living sponges that build a calcareous skeleton with a tabulate structure.

Colonial corals occur exclusively in the Richmondian Waynesville, Libertv, Whitewater, Saluda, and Elkhorn Formations. Within these formations, there are as many as tour distinct horizons where colonial corals are concentrated into "coral beds" up to about 4 m (12 ft) thick, traceable for great distances along the outcrop belt of the Richmondian around the Cincinnati Arch (Figure 6.6F; Browne 1964, 1965; Hatfield 1968; Elias 1998). Four genera of massive colonial tabulates *(Foerstephyllum, Calapoecia, Nyctopora,* and *Tetradium)* and one colonial rugosan *(Cyathophylloides)* are found in these beds (Figures 6.6A-F). Another tabulate, *Protaraea,* occurs in the Richmondian but did not form massive colonies. Instead, *Protaraea* exclusively encrusts the shells of brachiopods and other objects (Figure 6.6G). In John Paul Park, in Madison, Indiana, there is a unique, octagonal tool house built entirely of colonial corals gathered from the coral bed exposed north of the town (Figure 6.6H). Colonial corals are also incorporated into stonewalls beside some of the elegant houses in Madison.

Are Reefs Present in the Cincinnatian?

Although the coral beds of the Richmondian have some characteristics of reefs, they are not considered to be true reefs. Why is this so, and are there other reef-like concentrations of fossils elsewhere in the Cincinnatian? To answer the second question first, the only other reef-like structures reported in the Cincinnatian arc small mounds, only 0.3 m high by 3 in across, which were composed of trepostome bryozoans (Cuffey 1998). These mounds occur in the Maysvillian Grant Lake Limestone near Maysville, Kentucky, but unfortunately the outcrop has been destroyed.

There are three reasons why true reefs might be expected in the Cincinnatian. First, organisms with reef building potential certainly existed in abundance throughout the Cincinnatian, including corals, sponges, and bryozoans. Second, these same organisms were constructing true reefs by Early Ordovician time in other regions worldwide (Plate 2; Copper 1997). By Middle Ordovician time, bryozoans assumed a major role in reef building in regions as close to the Cincinnati Arch as Tennessee (Alberstadt et al. 1974). By Cincinnatian time, a diverse east of reef-building organisms had assembled that would dominate reef building worldwide during the ensuing Silurian and Devonian (Copper 1997). Third, the tropical to subtropical paleolatitude of the Cincinnati region during the Late Ordovician was well within the climatic range where reef building might be expected and indeed was occurring elsewhere worldwide (Plate 2; Copper 2001; Webby 2002).

The coral beds of the Richmondian, as well as the Maysvillian bryozoan mounds, have not been regarded as true reefs because they did not grow into an interconnected framework that developed significant relief in relation to the surrounding sea floor. Rather, they were restricted to low-

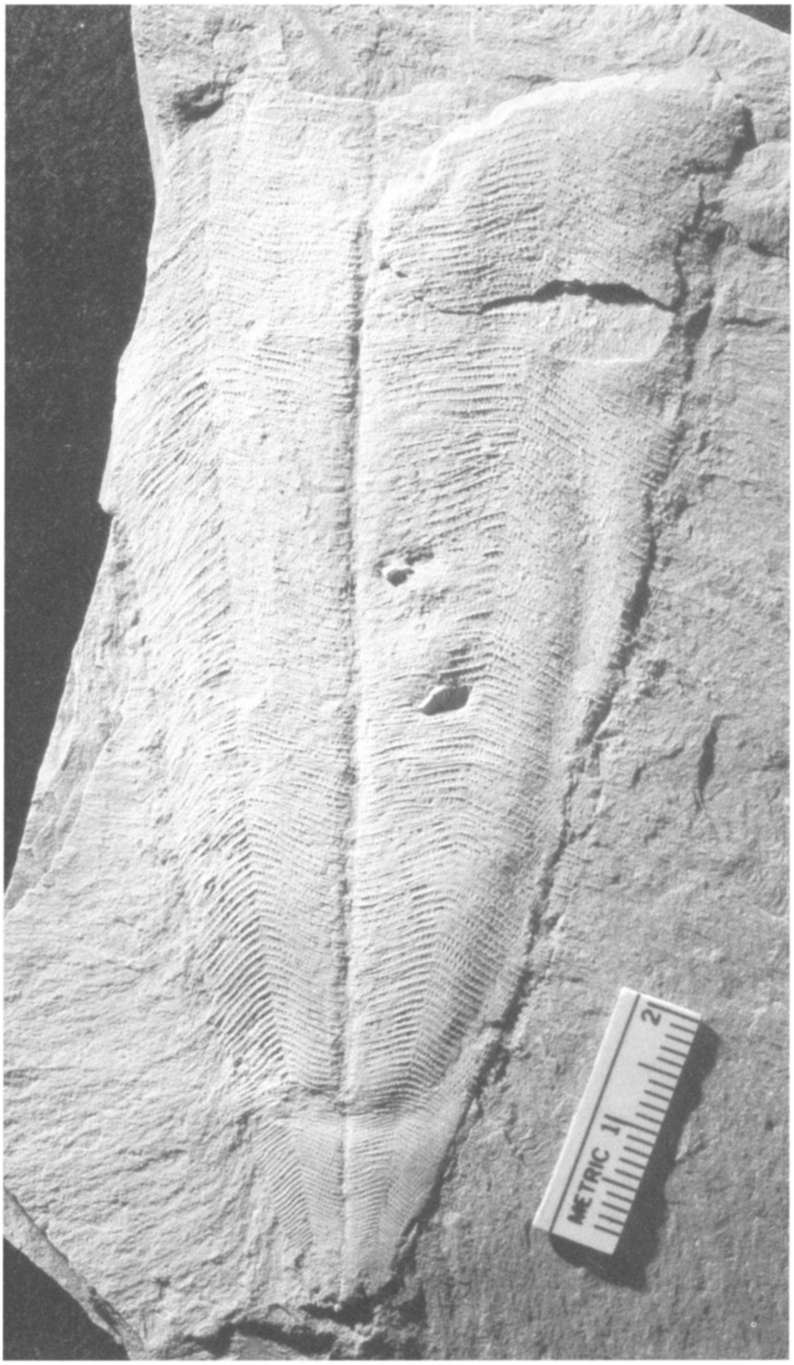


Figure 6.8. *Conulariid, Conularia formosa Miller and Dyer, University of Cincinnati collections, Maysvillian, Corryville Formation, Butler County, Ohio,* x 7.2.

relief colonies living very close to sea level (Hatfield 1968). Within the coral beds, concentrations of corals are no more than a few meters wide (Figure 6.6F). There is no differentiation of the coral cluster as a reef "core" from the beds lying adjacent to it. A reef core usually indicates the corals constructed a mound having relief greater than that of a single colony, less than one meter. Coral clusters probably existed as small patches on a level sea floor, similar to small living patch reefs. The size of some tabulate colonies is comparable to that of many living corals in patch reefs. Hatfield (1968) showed that the coral zone within the Saluda Formation acted as a low, coral barrier surrounding a central lagoon where fine-grained carbonate sediments accumulated. In this way the coral zone acted as do present-day reefs to influence water movement and sediment deposition. Application of the terms patch reefs and biostromes to the Richmondian coral beds is therefore quite reasonable.

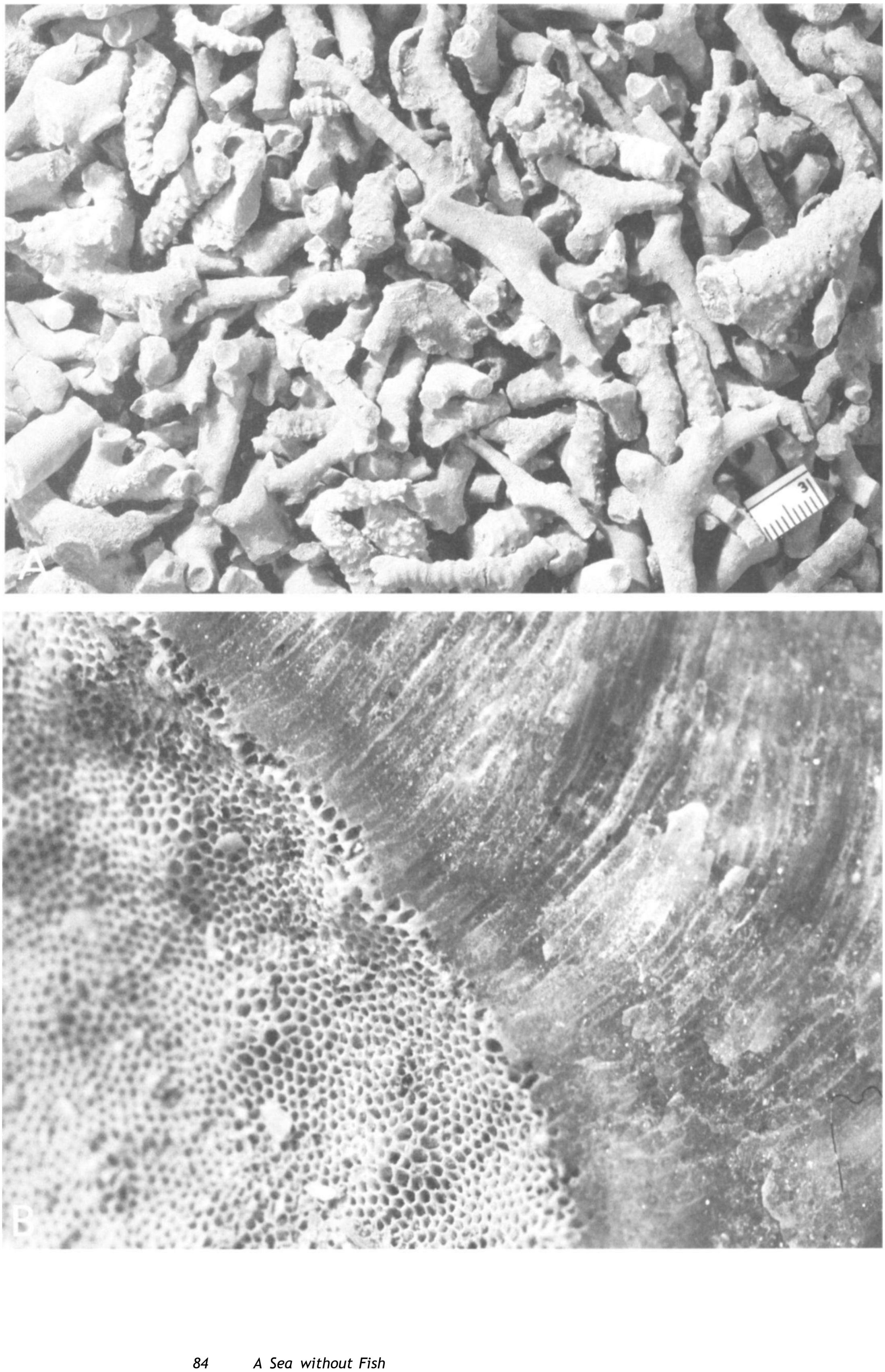
The inability of Cincinnatian corals and other potential reef builders to construct major reefs has several possible explanations. First, corals were present in the region only during Richmondian time (Webby 2002). The absence of corals during Edenian and Maysvillian time is puzzling, because of the similarity of the rest of the fauna throughout the Cincinnatian. Environmental conditions in the Cincinnati Arch region may have been unsuitable for solitary and colonial corals during the Edenian and Maysvillian, but it is difficult to identify the factors responsible. Abundance of fine-grained sediments and frequent disturbance of the sea floor by storms are two factors that might have restricted the presence of corals. However, both factors are pervasive throughout the Cincinnatian, and it is not certain that either decreased significantly during the Richmondian. According to Elias (1982) solitary corals were introduced during an early Richmondian invasion from sources to the west. Solitary corals are present in the Edenian-Maysvillian strata of the Maquoketa Group to the west.

The introduction of corals to the Cincinnati region during Richmondian time possible was related to progressive shallowing of the region during the Cincinnatian that culminated in the Richmondian (Anstey and Fowler 1969; Hay 1998). Coral beds developed on a shallow platform that was flanked by deeper water toward the west and north (Elias 1982). Present-day coral reefs develop along similar platform margins where a break in slope separates shallow from deeper water. Prior to the Richmondian, the Cincinnatian platform may have been deeper and without a break in slope toward the west that have favored coral development.

Conulariids

The conulariids are a minor group yet are among the most problematic fossils to be found in the Cincinnatian. They are usually found in a compressed condition in shales and siltstones of Maysvillian and Richmondian formations. As compressed specimens, conulariids appear to have a high triangular shape, with finely striated markings in a chevron-like pattern on a very thin integument, brown or black in color (Figure 6.8). The integument is calcium-phosphatic in composition. Uncompressed specimens are found elsewhere that show the original shape to be pyramidal and four-sided, and some have triangular flaps extending from the sides at the wide end, suggesting a means of closure. Cross-sections of uncompressed specimens reveal a bifurcating septum originating from each of the four sides. Evidence for attachment at the apical end is occasionally found, but is often lacking. Possibly conulariids lived part of their lives attached and later became free-living.

The zoological affinities of conulariids have been debated for a long time. Chiefly on the basis of their four-part structure, conulariids have been classified with the scyphozoan cnidarians, which have a tetrameral (four-fold) body plan. There are living scyphozoans with a chitinous theca and some that live attached by means of a stalk. Some have argued that conulariids should be recognized as a distinct phylum (Babcock 1996b; Babcock and Feldmann 1986), but recent work by Van Iten and others (1996), and Hughes and others (2000), confirms that the similarities between conulariids and scyphozoans are indicative of a close evolutionary relationship. Conulariids are found in marine strata of Cambrian through Triassic age. A single species, *Conularia formosa* Miller and Dyer, is recorded from the Cincinnatian of the Cincinnati Arch region.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BRYOZOANS: "TWIGS" AND "BONES"

The rocks in the Cincinnati region are loaded with fossils. Visitors to the area commonly are struck by all the "tilings" in the rock that look like small twigs, or, with a stretch of the imagination, small pieces of bones (Figure 7.1A). They are the most common fossils in the bedrock of the area. Indeed, if you were to pick up a fossil in the Cincinnati region at random, chances are that it would be one of these objects. But they are neither twigs nor bones. They are, in fact, the remains of a group of organisms called bryozoans (Plates 3D,E).

If you look at an unbroken surface of your bryozoan fossil with your trusty hand-lens, you see that it is replete with tiny holes (figure 7.1 B). If you shift your field of view to a broken surface, the tiny holes are revealed to be minute tubes. Each one of those minute tubes was once home to an equally minute animal. Thus, the fossil in your hand was constructed by a colony of tiny creatures. A bryozoan colony is reminiscent of a piece of coral found on a present-day beach in that coral reefs also are made by myriads of individual animals. Despite the superficial resemblance of bryozoan colonies and coral colonies to one another, the animals involved are very different, indeed. Corals are members of phylum Cnidaria, commonly called coelenterates. Each coral animal is basically sac-shaped with a single aperture serving as both mouth and anus.

A bryozoan animal is more complexly organized (Figure 7.2). There is an alimentary canal, with a distinct mouth on one end and a distinct anus on the other. Surrounding the mouth is a ring of tentacles called a lophophore. The lophophore serves as a food-gathering structure and for gas exchange between the animal and the surrounding water (in other words, it is also a respiratory structure). The anus is located outside of the lophophore. This is what gives the taxon of the bryozoans its technical name—phylum Ectoprocta. The "procta" part of the word means "opening," and the "ecto" means "outside of."

Frankly, most people do not call these animals ectoprocts. In former years, when the creatures were less well understood than they are today, people spoke of phylum Bryozoa. Eventually it was recognized that so-called phylum Bryozoa lumped together animals that are not-at-all closely related to one another. Hence, the name "Bryozoa" should be abandoned, in the technical sense. However, like the use of the term "glasses" to refer to items made of plastic, the term "bryozoans" persists in common parlance. Bryozoans sometimes are said to comprise phylum Polyzoa, especially in Great Britain. In some respects, "Polyzoa" is an appropriate name for the group. "Poly" means "many," and "zoa," "animals." The word "Bryozoa" literally means "moss animals," presumably because a living bryozoan

Figure 7.1. A. *Fragments of bryozoan colonies are the most abundant fossils in the type-Cincinnatian. Parvohallopora ramosa (d'Orbigny), CMC IP 27957, Bellevue Limestone, Cincinnati, Ohio. Scale in mm.* B. *Surface of bryozoan colony showing minute openings (zooecia) on the left and a cross-section through a broken surface on the right. Each of the openings leads to a tube that was home to a tiny, individual animal. Trepostome bryozoan, Monticulipora mammulata d'Orbigny, CMC IP 51107, Bellevue Limestone. Cincinnati, Ohio. Diameter of individual openings (zooecia) about 0.2 mm.*

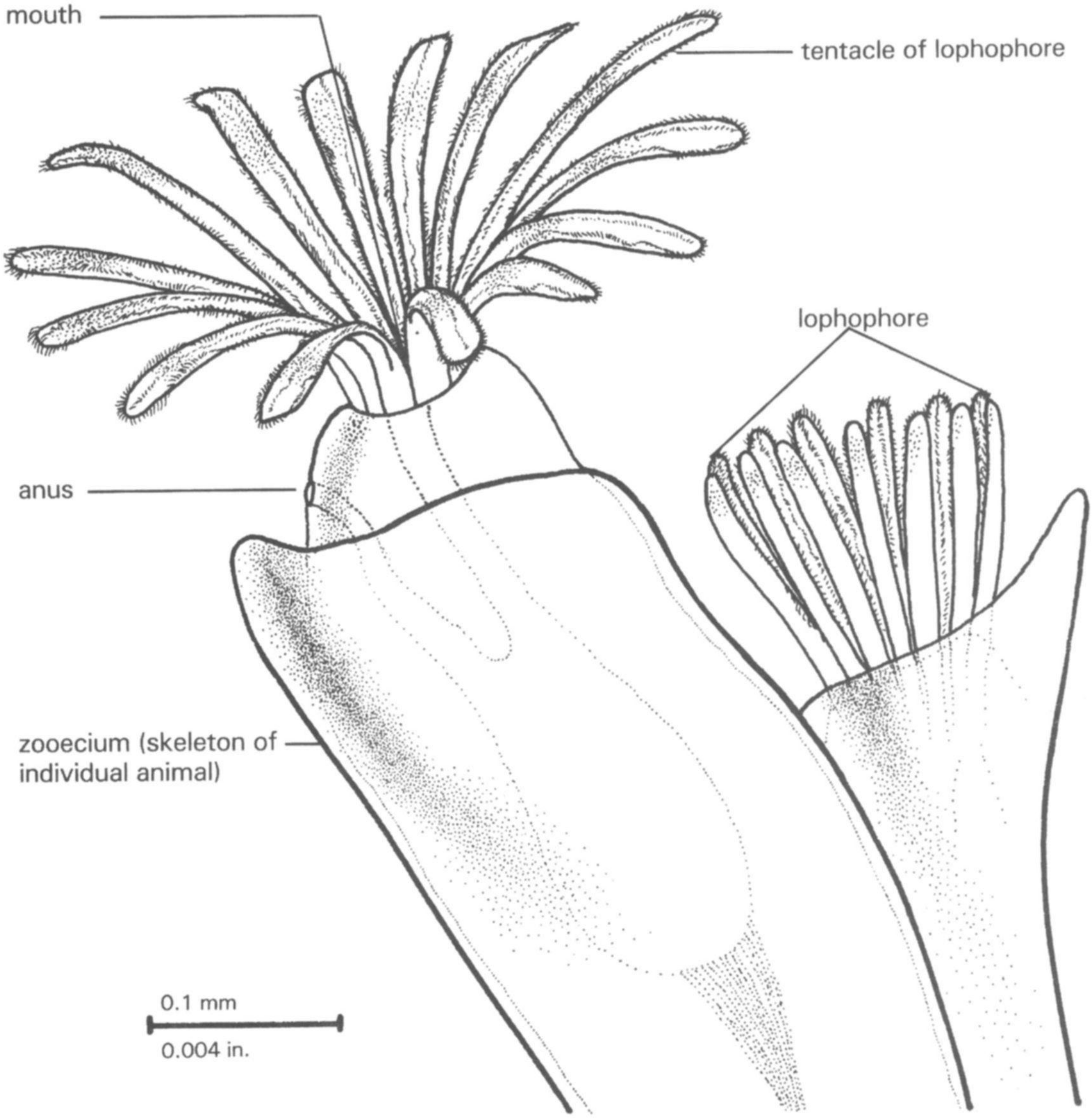


Figure 7.2. Living bryozoan, *showing one zooid with tentacles extended in feeding position (left) and the other partly retracted (right). Drawing by Kevina Vulinec.*

colony, with its surface of many minute animals, might be thought to resemble a rock coated with many of the tiny plants we call moss. Potential confusion can ensue, however, if one forgets the fact that bryozoans are decidedly animals, whereas mosses are just as decidedly plants. Regardless of the technical terms and the reasoning behind them, most people refer to fossil ectoprocts colloquially as bryozoans, and they have done so for generations. We will follow that hoary tradition here.

Bryozoans are animals. All animals derive the energy they need to grow, reproduce, and, indeed, to live, by consuming other organisms, or, at least, organic matter produced by living organisms. A parasite, for example, a tape-worm living within the alimentary canal of another animal, may absorb organic-rich fluids from within its host. A mosquito eats its victim one tiny drop of blood at a time. But bryozoans are neither parasites nor mosquito-like. So what do bryozoans eat, and how do they eat it?

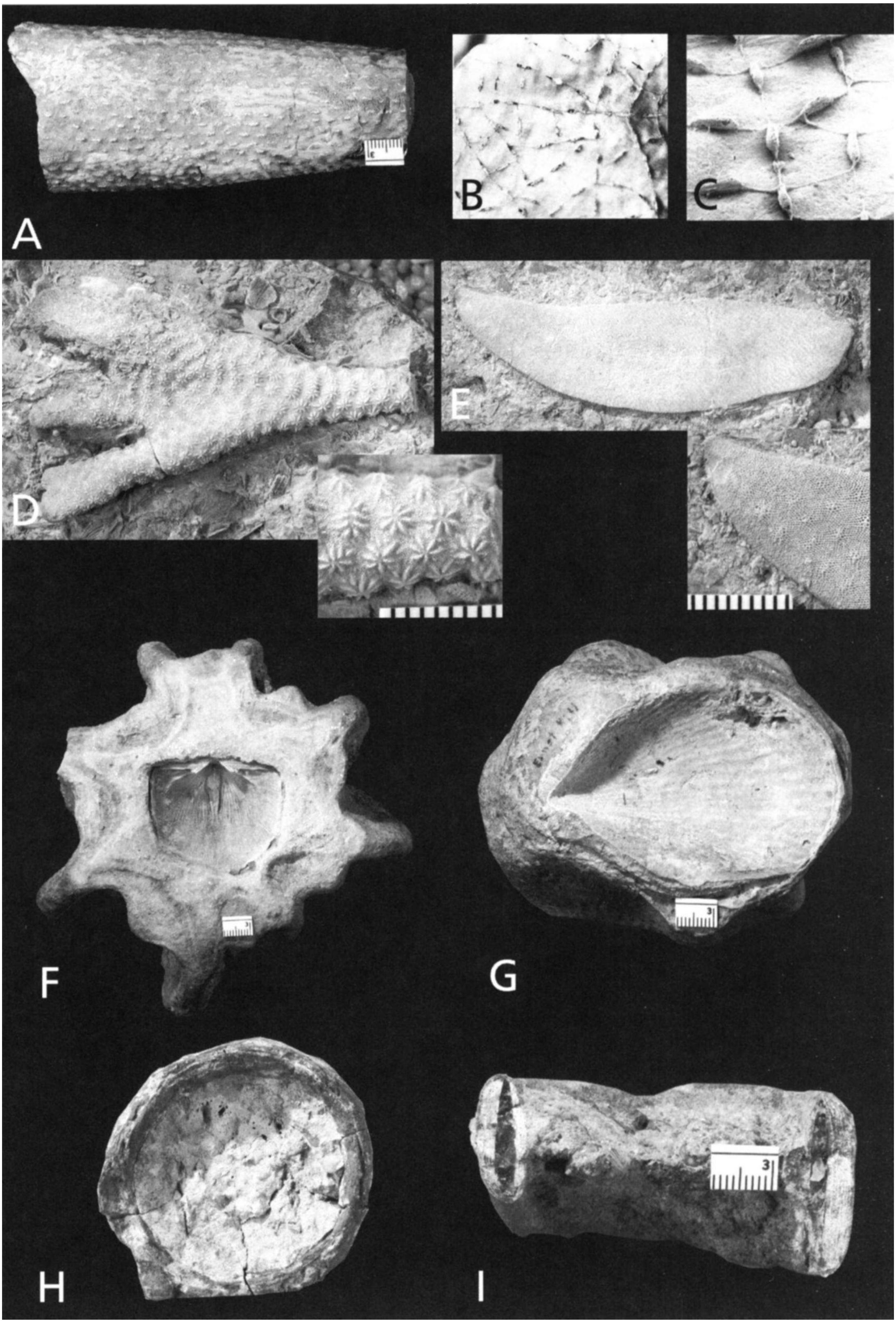
Bryozoans are aquatic. Depending on the kind, some bryozoans live in fresh water, but most live in salt water. In either case, the bryozoan subsists on minute organisms (protozoans and so on) and tiny bits of organic matter suspended in the water. The bryozoan does not just wait passively for such food to fall into its mouth; it literally filters the food from the water. Bryozoans are active filter feeders. The individual animal spreads the tentacles of its lophophore into a funnel-, bowl-, or vase-like configuration (Plate 3E; Figure 7.2), and cilia that line the tentacles move in such a way that food particles are carried down to the mouth. Not only does the individual polypide generate feeding currents for itself, but the colonies of at least some kinds of bryozoans generate currents that enhance feeding in the colony as a whole. In at least some kinds of bryozoans there are particular areas on the colony that have polypides that direct currents away from the colony. These excurrent chimney's (Plate 3F) carry water that already has been filtered by the lophophores away from the zoarium, and thereby draw unfiltered, nutrient-laden water across polypides elsewhere in the colony (McKinney and Jackson 1989). Moreover, the very topology of the colony may facilitate the passage of nutrient-filled water through the colony and across its polypide-lined, and, hence, lophophore-lined, and, hence, food-gathering surfaces.

Fossil bryozoan colonies come in a wide variety of sizes and shapes (Figures 7.3, 7.4). some are lumps the size and shape of a gum-drop. Some are stony masses larger than your fist. Some grow up from a shell or shell fragment on the sea floor as a small blade or delicately branched structure resembling a miniature version of a present-day "stag-horn coral." Such colonies can exceed the size of a basketball, although what we mostly see are twig shaped fragments. Many bryozoans grow as thin crusts on brachiopod shells or mollusc shells (see Figure 9.2D). A small number even grow within the shell matter of the brachiopod or mollusc, forming tiny dendritic or anastomosing canals (Figures 7.3B, C). Whatever its size and shape, the hard parts of a bryozoan colony comprise what is called a zoarium.

So zoaria exhibit a tremendous variety in overall shape. They also offer a tremendous variety in details. The surface of the colony may be smooth. Many, however, bear regularly spaced bumps, termed monticules, or regularly spaced depressions, called maculae. Monticules may be equidimensional in map-view, or they may be elongated, even ridge-like. They may be disposed in a seemingly random array, or they may have a distinct pattern. For example, specimens of the aptly named genus *Constellaria* are veritable constellations of star-shaped bunches of monticules (Figure 7.3D). Some students of bryozoans have concluded that monticules and maculae are simply manifestations of the same phenomenon, so do not differentiate the two from one another; they therefore call all of them, whether bumps or depressions, maculae (McKinney and Jackson 1989). Regardless of what one calls these elevations and depressions, they apparently were the places on the colony where the excurrent chimneys were generated.

All this variety would seem to offer a fertile field for the taxonomist—a new name for each morphologic variant. Indeed, a whole slew of bryozoan genera and species have been recognized by a whole slew of paleontologists. But there is a problem. Sometimes, in a single colony, the character-

Figure 7.3. *Cincinnatian bryozoans.* A. *Colonies of the bryozoan genus Spatiopora characteristically form a thin coating on shells of orthoconic cephalopods, MUGM uncatalogued, Cincinnatian, scale in mm. Note that raised lumps on colony surface (monticules) are elongated and aligned with the axis of host nautiloid shell.* B, C. *Ctenostome bryozoan, Ropalonaria venosa Ulrich.* B. *Colony on shell of brachiopod Rafinesquina, CMC IP 40061, Waynesville Formation, Butler Co., Ohio,* x 9. *Arrow indicates sac zooid.* C. *Scanning electron micrograph of polyester cast of cavities excavated by zooids into host shell, BMNH D.52264,* x *22.* B *and* C *from Pohowsky (1978, plate 1, figures 5, 7) and reprinted by permission of the Paleontological Research Institution.* D. *Cystoporid bryozoan, Constellaria florida Ulrich, CMC IP 51108, Fairview Formation, Kenton Co., Kentucky. Inset, enlargement showing characteristic star-shaped monticules, scale in mm.* E. *Cryptostome bryozoan, Escharopora sp., CMC IP 51110, Fairview Formation, Boone Co., Kentucky. Escharopora has zooecia on both sides of the thin, bladelike zoarium. Inset, enlargement showing zooecia, scale in mm.* F. *Basal surface of trepostome bryozoan*



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istics of one "species," or even "genus," give way to those of another—all in the space of a centimeter or two. Presumably, everyone in a single colony is of the same species. Thus, the conclusion is inevitable: overall colony shape and details on its surface may not always be reliable indicators as to who is related to whom. Indeed, there is ample evidence provided by present-day bryozoans that environment can play a significant role in colony shape, at least in some taxa.

Well, if the shape of the zoarium is not an incontrovertible taxonomic indicator, what, it anything, is? Is there an "inner truth" in bryozoan taxonomy? It turns out that there is just that, namely, the internal structure of the colony. Each zoarium consists of the hard parts of all of the animals that comprise the colony. An individual bryozoan animal is called a zooid, and the haul parts of that individual animal constitute a zooecium (Figure 7.2). If one examines the holes in a zoarium with a hand-lens or low-power microscope, one commonly sees that the holes are not identical (Figure 7.1B). There may be size classes of larger holes and smaller holes; there may even be spine-like projections in addition to holes. It would appear that, in at least some colonies, not all the zooids were identical. In some present-day colonial animals, there is polymorphism, with different-shaped or different-sized individuals performing different tasks, for the good of the colony, the species, or both. That seems to have been the case among at least some now-extinct bryozoans. As mentioned previously, the surface of a zoarium may be marked by regularly spaced bumps or depressions (Figures 7.3A, D). In general, these monticules and maculae, respectively, consist of zooecia of sizes and natures different from those between them, and, hence, seem to represent areas of the colon in which the zooids performed particular functions for the colony as a whole.

As we noted previously, some bryozoan colonies exceed the size of basketballs. How do we know that? The answer is painstakingly simple, with the emphasis on the word "painstaking." In general, bryozoans are found only as small fragments scattered throughout the rock. Very occasionally, however, one finds that all the fragments of a colony are lying together, as part of a single layer of rock. That's the good news: the complete colony is there! The bad news, however: although the colony may be complete, it is not whole. That's where the "painstaking" comes into the picture. One must oh-so-carefully collect each fragment, paying meticulous attention to just where the fragment was in the rock and adjacent to what other fragments. Then one must play three-dimensional bryozoan jigsaw puzzle and glue the tens, or hundreds, or thousands of pieces each in its proper place.

According to the old nursery rhyme, "All the King's horses and all the King's men couldn't put Humpty together again" (Opie and Opie 1955). As it happens, some of the local fossil collectors and other paleontologists have been more clever, or at least more persistent. For example, amateur paleontologists Jerry Rush and, more recently, Ron Fine have spent countless hours collecting and reconstructing bryozoan colonies from the type-Cincinnatian rocks. It is to the perseverance of such folk that we know that local bryozoan colonies did, in fact, sometimes exceed the size of basketballs. Indeed, one colony re-assembled by Mr. Fine is some 66 cm by 35 cm by 15 cm (Figure

that has grown on the pedicle valve of the brachiopod Rafinesquina and overgrown it, Richard Arnold Davis collection, Bellevue Limestone, Cincinnati, Ohio, scale in mm. G. *Trepostome bryozoan colony that has grown on shell of pelecypod Ambonychia and overgrown it, Richard Arnold Davis collection, Cincinnatian, horizon and locality unknown, scale in mm.* H. *Ring-shaped bryozoan zoarium* ("We*ichold donut") presumably encrusting nautiloid, CMC IP 51109, Richmondian, Hamilton Co., Ohio,* x *0.7.* I. *Cross-section of ring-shaped bryozoan zoarium ("Weichold donut") encrusting nautiloid, Richard Arnold Davis collection, Upper Maysvillian-Lower Richmondian, Butler Co., Ohio, scale in mm. Dark, elliptical zone on right and left sides of ring are calcitic replacement of nautiloid shell.*

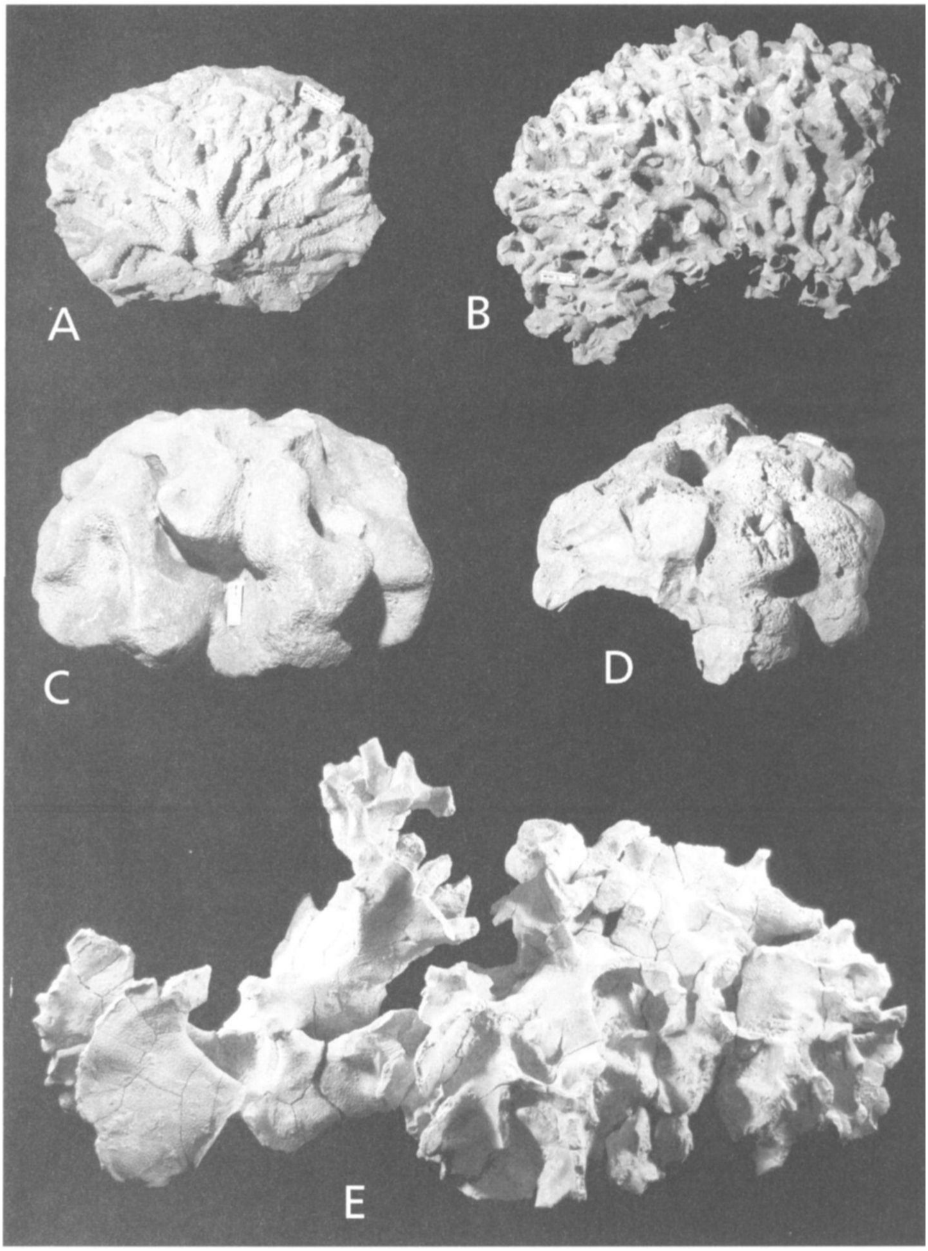


Figure 7.4. *Large bryozoan colonies from the type-Cincinnatian.* A. *Intact colony of a branching trepostome bryozoan, Parvohallopora ramosa d'Orbigny, University of Cincinnati collections, Corryville Member of Grant Lake Limestone, Hamilton Co., Ohio. Scale in mm.* B. *Intact colony of an unidentified branching trepostome bryozoan. CMC IP uncatalogued, Cincinnatian, no horizon or locality data. Scale in mm.* C. *Intact colony of trepostome bryozoan, Monticulipora mammulata d'Orbigny, CMC IP uncatalogued, Cincinnatian, no horizon or locality data. Scale in mm.* D. *Trepostome bryozoan encrusted on probable nautiloid shell that has disappeared, Monticulipora mammulata d'Orbigny, University of Cincinnati collections, Corryville Member of Grant Lake Limestone, Hamilton Co., Ohio. Scale 2 cm in length. Note borings into bryozoan.* E. *Intact colony of trepostome bryozoan, Heterotrypa frondosa d'Orbigny, CMC IP, Corryville Member of Grant Lake Limestone, Kenton Co., Kentucky. Colony about 65 cm in width. This colony was excavated and reassembled by Ron Fine. See Cuffey and Fine (2005).*

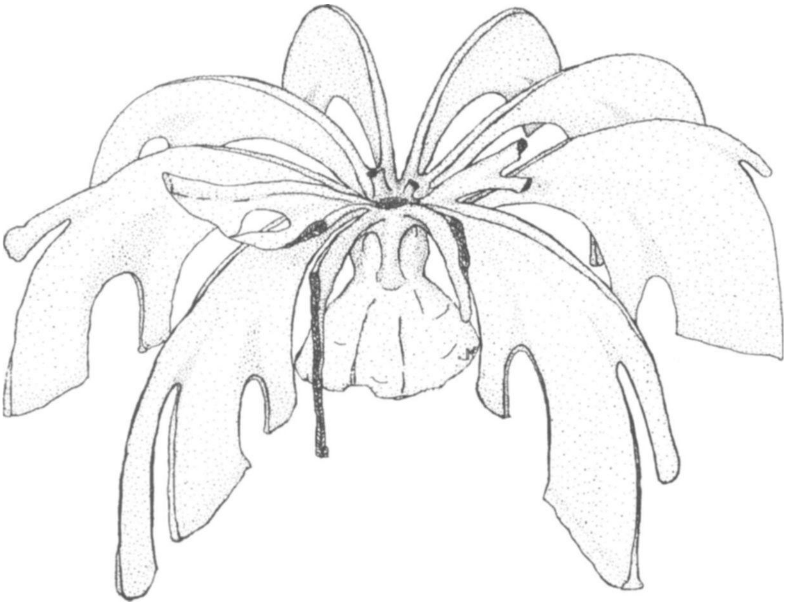


Figure 7.5. *Reconstruction of the lower part of the zoarium of Heterotrypa sp., diameter about 28 cm. From Waugh et al. (2004). The open structure of the zoarium would provide exposure of interior feeding surfaces to water flow, while the downward-arching fronds would provide stabilization and attachment to the substratum. Reprinted by permission of Sigma Gamma Epsilon.*

741,). a whopping 26 inches by 14 inches by 6 inches (Cuffey and Fine 2005). Similar efforts by Erickson and Waugh (2002), Waugh and Erickson (2002), and by Waugh et al. (2004) provided new information about the form and patterns of water flow through complete colonies (Figure 7.5).

Another spectacular growth of bryozoans was found in a roadcut several miles south of Maysville, Kentucky. Here were discovered two broad mounds of bryozoans, each between three and three and a half meters wide by about one-third meter tall (10 feet by 1 foot). Like Mr. Fine's specimen, these mounds grew on the sea floor, but, unlike his, each of the Maysville mounds consists of numerous individual colonies and may have taken a thousand years to grow to that size (Cuffey 1998).

When organisms produce elevations on the sea floor, such constructs are technically termed bioherms ("bio" means "life," and "herm" means "mound"). The Great Barrier Reef is the most spectacular example of this phenomenon in today's oceans. It must be admitted that in comparison to the string of coral reefs that stretch more than 2000 km (1260 statute miles) parallel to the east coast of Australia, the mounds in Northern Kentucky are less than miniscule. However, to the fossil collector used to bryozoan fragments much smaller than pieces of blackboard chalk, the bryozoan mounds are gargantuan. On a jocular note, Roger Cuffey, one of the most productive bryozoan workers alive today, long has referred to the Maysville mounds and such as "bryoherms." Alas! This paragraph must close on a sad note: sometime during the 1990s, road widening destroyed the Maysville mounds. There is, of course, some solace in the possibility that even bigger bryoherms still may be buried somewhere in the local rocks, awaiting discovery.

Associations

In most localities and in most strata, bryozoans are the most common fossils one encounters. In sheer abundance alone, they must be reckoned to have been truly important denizens of the Cincinnatian sea floor. This impression is nothing but enhanced when one focuses in on the details of just where and with whom they occur.

At many times and in many places, the Cincinnatian sea bottom appears to have been soft mud. Most of the kinds of animals that we generally find preserved as fossils do not seem to have "liked" soft, muddy bottoms, presumably because the mud did not provide solid footings upon which to build a stable life. It was all too easy to be engulfed by the ooze. Moreover, the fine sediment was too easily swirled up into the water and clogged respiratory and food-gathering apparati. liven a centimeter or two above the mud was more hospitable. Bryozoans ordinarily did not grow their colonies directly on the surface of the mud. But let a storm drop a few shells or fragments of shells onto the goo, and the sea floor was open for colonization. So often, when one is able to examine the actual base of a colony—where growth commenced—one discovers that the colony was founded on a fragment of a shell of a brachiopod or pelecypod, if not a complete or nearly complete shell (Figures 7.3F, G, 7.4D). Once the sea floor was a bit stabilized, the bryozoans colonized and grew in earnest.

Once established, the bryozoans themselves added to the stability of the sea floor in their immediate vicinity. First, as colonies grew, a certain proportion of them toppled over, and their skeletal material became incorporated as part of the sea floor, thus increasing the stability of the bottom and making it more hospitable for other creatures. Moreover, the little "thickets" of bryozoan colonies provided places for other organisms to hide from potential predators or, in the case of the predators, places from which to orchestrate ambushes of potential prey. In addition, some animals scrambled up the stalks and branches of bryozoan colonies to avoid the muddy water immediately adjacent to the sea floor. And larvae that happened to attach up in a bryozoan "thicket" would not only have escaped the worst of the turbid water, but also might have had a better chance of latching onto minute particles of food suspended in the water. Moreover, even as trees ameliorate the effects of wind on the land, bryozoan colonies must have moderated the currents on the sea floor. This would not only have made life easier for some organisms, but would have resulted in entrapping sediment, thereby further helping to stabilize the sea floor.

One particularly intriguing example of how bryozoan colonies were used by other creatures was documented by Douglas Shrake of the Ohio Division of Geological Survey in his master's thesis. Trilobites, like other arthropods, are enclosed within a hard exoskeleton. Because this "suit of armor" cannot expand as the animal grows, the trilobite periodically must shed its exoskeleton, expand in size, and harden up a new protective shield. This is an especially trying time for the trilobite, first because it can be difficult to wriggle and squirm out of the old armor, and, second, because until the new suit hardens, the animal is "naked"—a soft, tempting morsel for any passing predator. Shrake found evidence that individuals of the trilobite genus *Primaspis* resorted to lowly bryozoans to make the time of trial a bit less trying (Shrake 1987, 1989).

When the time for shedding was at hand, the trilobite apparently climbed its way up into a suitable part of a bryozoan colony and wedged the projections of its exoskeleton into the bryozoan (see Figures 11.6E, F) This enabled the trilobite to pull itself out of the old exoskeleton and commence the hardening of the new one, all the while being hidden amongst the bryozoan fronds from the eyes of would-be predators. Although this must have been a convenient arrangement for the trilobite, it may have been less so for the bryozoans. Shrake found that, in some instances, there-was pathologic growth in the colony as the bryozoans grew up and around the trilobite exoskeleton they had no way to dislodge.

The trilobite/bryozoan association described by Doug Shrake is just one of a host of examples of the interactions of bryozoans and myriad other creatures. On the one hand, a bryozoan larva would attach to almost anyone, given suitable circumstances, and a colony would sprout. Bryozoan colonies have been documented as attached to, encrusting, overgrowing, or etched into articulate brachiopods, inarticulate brachiopods, cephalopods, corals, cornulitids, crinoids, foraminifers, hydrozoans, monoplacophoran molluscs, pelecypods, trilobites, and, of course, other bryozoans, both of the same and of different species (see chapter 16, Table 3). On the other hand, a number of other organisms have been found attached to or bored into bryozoans: corals, articulate brachiopods, inarticulate brachiopods, cornulitids, and pelecypods, along with a number of organisms of uncertain affinities, including ***Catellocaula. Sanctum, Sphenothallus,*** and ***Trypanites*** (see chapter 16, Table 3).

In some cases, it is obvious that both the "guest" and the "host" were alive at the time of the association. In other cases, the "guest" was merely using a dead shell, exoskeleton, or whatever as a handy site for attachment on the sea floor. In other words, it commonly is a tough task to unravel in-life association from post-mortem happenstance. Nonetheless, it is abundantly obvious that the Cincinnatian sea floor of the ancient past, and, hence, the Cincinnatian rocks and fossils we find today would have been drastically different without the bryozoans.

Ordovician Doughnuts

Occasionally a lucky collector will find in the rocks of the Cincinnati area a stone object that looks rather like a doughnut (Figures 7.3H, I). Closer examination reveals that this toroid fossil consists of bryozoan zooecia; indeed, it is a ring-shaped zoarium.

The bryozoan rings have been known for a long time. Years ago, when Kenneth F. Caster, the eminent paleontologist at the University of Cincinnati, was shown one of them by a local fossil collector, he quipped, "Ah! Yes! A Weichold Doughnut." He then went on to explain that Weichold was one of the old-time collectors in the Cincinnati region, and that these unusual fossils had been dubbed "Weichold doughnuts" or "Weichold rings," although he did not know the specific connection between Weichold and the rings.

So why would a bryozoan zoarium grow in the shape of a ring? Weichold doughnuts tend to be some 5 or 6 cm in diameter (2–*2 1/2* in). As it happens, that diameter is comparable to that of the shells of some of the orthoconic cephalopods in the local rocks. Could there be a connection? Within some of the Weichold doughnuts, there is a ring of what might be recrystallized cephalopod shell (Figure 7.31). Perhaps the apertural part of the tube that comprises the shell of an orthoconic nautiloid cephalopod broke off and came to rest on the sea floor. Then, one or more bryozoan larvae settled on this hard object protruding above the ooze. As the zoarium grew, it assumed the ring-shape of the "segment" of cephalopod shell.

Such rings of cephalopod shells have been described and figured in the scientific literature (Teeter 1978), and similar things have been found in the local rocks. However, the story may not be quite so straightforward. The problem is that some of the Weichold doughnuts seem to be bryozoan hard parts all the way through—with no obvious remnants of cephalopod shell.

Frank McKinney, the well-known bryozoan worker, has seen a ring-shaped colony of the bryozoan genus ***Constellaria,*** with mud in the center. His interpretation was that the colony had slowed the water and caused mud to precipitate to such an extent that growth of the colony was able to proceed only at the periphery (McKinney, pers. comm.). However, this colony was some 8 to 10 inches across (20-25 cm)—more than twice as big as the largest Weichold rings. Obviously, the phenomenon needs some serious scientific study.

Ordovician Hitch-Hikers

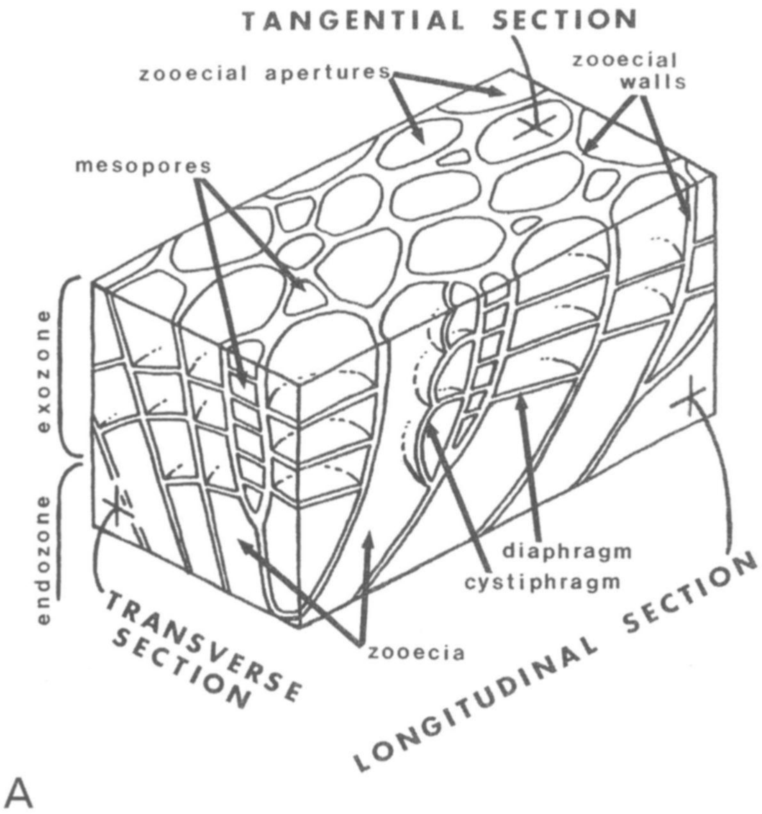
As mentioned above, many bryozoan colonics in the rocks of the Cincinnati region originally grew on shells on the sea floor. In some cases, the shell no longer sheltered its maker, but was merely a lifeless, hard object lying on the mud. In other cases, both the bryozoans and the organisms on which the zoarium grew were alive. In these instances, the attachers are called epizoa, and the attachee is the host (Davis et al. 1999).

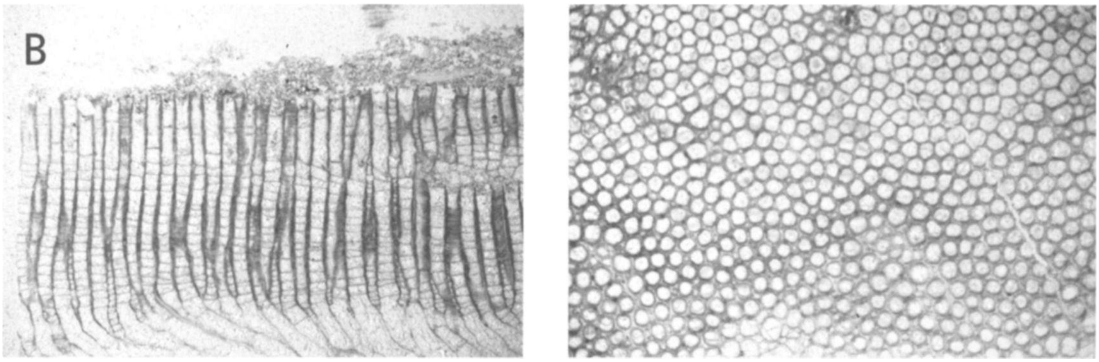
Some bryozoans carried epizoism to a higher level.

Not too uncommonly, an observant fossil collector will find a fossil that has the size and shape of an orthoconic cephalopod. However, unlike the case of an ordinary nautiloid, the surface bears the tell-tale apertures of zooecia (Figure 7.3A)—and looks are not deceiving. The specimen is an orthoconic nautiloid, but one that bears a thin coating that consists of a bryozoan colony. It is obvious that the cephalopod shell was not just lying around on the sea floor dead and empty, because its entire exterior is covered by the encruster—with neither gaps nor seams. Moreover, the picture is enhanced by the surface features of the zoarium. Instead of being equidimensional bumps, the monticules are decidedly elongate, and their longest dimension is aligned with the length of the orthoconic shell. It is almost as though the bryozoan colony was carried through the Cincinnatian sea on the swimming cephalopod. The whole cephalopod/bryozoan assemblage looks so streamlined that even the monticules are disposed so as to minimize the friction of slipping through the water.

This bryozoan/cephalopod association has been known for well over a century (Ulrich 1883). In fact, at least one taxon of bryozoans, *Spatiopora,* seems to be known only as encrustations on cephalopods (Baird et al. 1989). Early on, the association was interpreted as a parasite/host relationship. However, in parasitism, the parasite consumes part of the host. In the

Figure 7.6. A. *Detailed studies of bryozoans require carefully oriented thin-sections or acetate-peels. Diagram shows orientation of sections and terminology of internal skeletal structures used to identify species. From Arens and Cuffey (1989, figure 5), reproduced by courtesy of Roger J. Cuffey, with permission of the Pennsylvania Academy of Science.* B. *Left, longitudinal thin section of Heterotrypa frondosa (d'Orbigny), CMC IP 40336, Bellevue Limestone, Cincinnati, Ohio, R. J. Singh Collection. Right, tangential thin section of same. Both approx.* x *10.*





bryozoan/cephalopod association, it is not likely that the bryozoans were "eating" the cephalopod. It is possible that they were deriving nutrition from leftovers and organic debris generated when the cephalopod, itself, fed. It could be that the bryozoans picked up suspended matter from the sea water as the cephalopod swam from place to place.

At first glance, one might worry that the weight of a "stony bryozoan" would have impeded significantly the swimming of the cephalopod. However, the bryozoan colony is just one zooecium thick and would have been mostly soft parts. Moreover, like present-day Nautilus, the Ordovician cephalopod may have been able to compensate for the extra weight of the bryozoans by means of the gas in its camerae (see chapter 9). In addition, the bryozoan coating might have increased the hydrodynamic drag on the cephalopod.

There even may have been sonic advantages to havning a coating of bryozoans. Present-day "decorator crabs" are camouflaged by the load of anemones and such like that they carry. Indeed, the crabs deliberately "plant" other creatures on their dorsal surfaces. Perhaps the bryozoan epizoa helped conceal the Cincinnatian cephalopods that bore them. (Of course, the zoarium would have covered, and thereby made visually useless, any color patterns that the cephalopods had; but that is a story that does not belong in the chapter about phylum Bryozoa.)

Studying Bryozoans

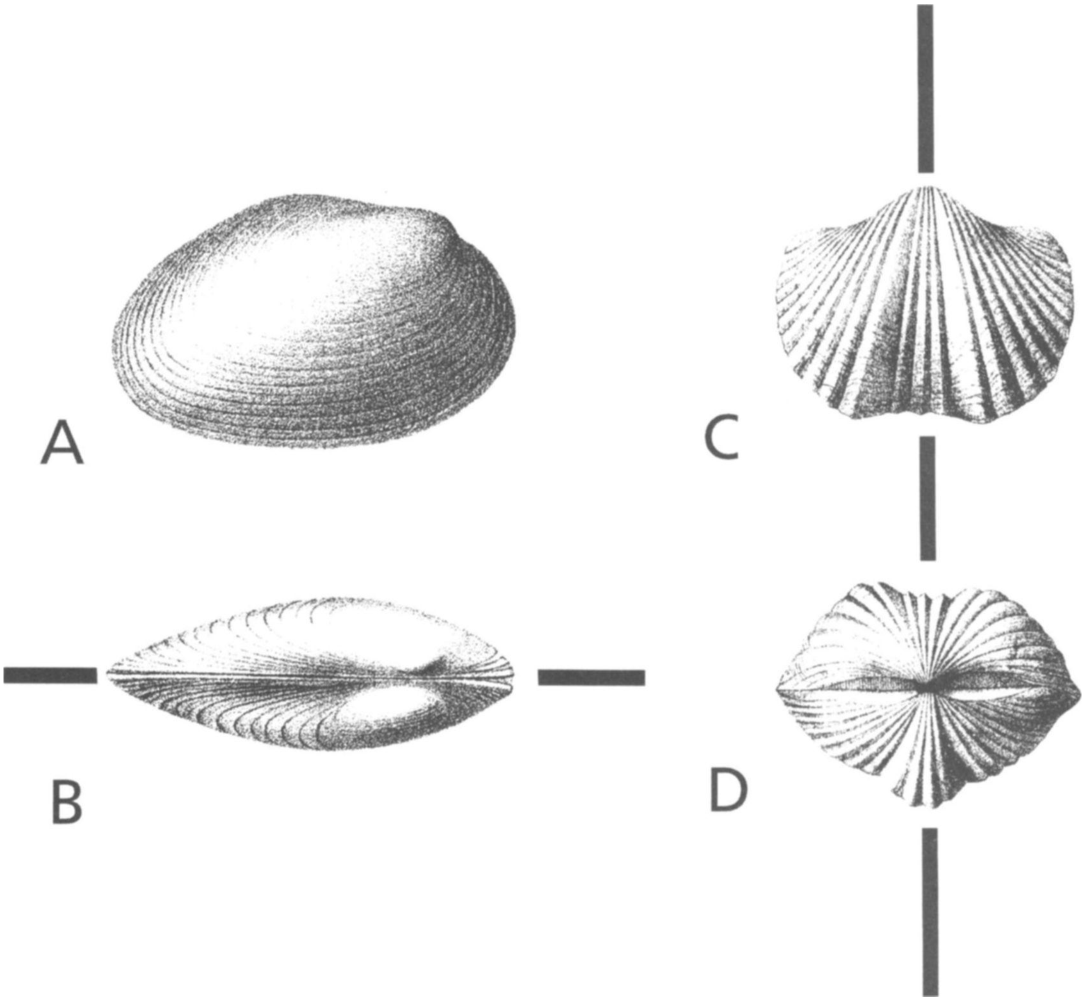
Most bryozoan specimens can be identified only on the basis of internal structures, at least definitively so. This means that, except for Superman, it is necessary to cut them open—no small feat for the ordinary fossil collector. It is necessary to use a rock saw to make precisely oriented cuts through an individual specimen. Because the bryozoan colony is preserved as part of the rock, it will not let enough light through to see internal details. This can be overcome in two ways. The zealous and well-equipped paleontologist can cut and grind the specimen into slices so thin that they become transparent. These are called thin-sections, and they are what generally are used in studying bryozoans.

Depending on the nature of the specimen, alternatively, it may be possible to use what are called acetate peels. Like a thin-section, a peel starts with a carefully oriented cut through the specimen. The cut surface is then carefully ground flat and then etched in an appropriate acid of appropriate "strength." If the specimen is suitably preserved, certain of its features will be a bit more resistant to dissolution by the acid. Hence, they will stand out slightly from the surface. If one takes a thin sheet of plastic (the acetate) and uses acetone to allow the acetate to adhere to the etched surface, it may be possible to pull away the sheet, along with enough of the specimen, to reveal internal details.

The use of thin-sections is generally considered to be "industry standard," but, regardless of which study technique is used, both require equipment that may be beyond the budget, or desire, of the ordinary fossil collector. Moreover, both require definite safety precautions and safety equipment; for example, acids can etch more than just rock, and acetone not only is flammable, but its vapor is unhealthy to breathe.

As indicated, both thin-sections and peels must be carefully oriented within the zoarium. This is to maximize the information that may be derived about the internal structure of the colony. Because there are different kinds of zooids in a colony, it is important to be able to study the different sizes, shapes, and natures of the zooecia as viewed in a plane perpendicular to the individual tubes. This is best done in a tangential section, which is cut parallel to the surface of the colony and near its surface (as opposed to near its center, or axis) (figure 7.6). On the other hand, a longitudinal section is cut parallel to the length of the individual tubes and can provide important information on both the growth of the zoarium and of the zooecia of which it consists. A transverse section is oriented at right angles to the other two, for example, across a branch of a given colony. In short, one needs longitudinal, tangential, and transverse sections of a colony to get a complete picture of its internal structure, and this complete picture is essential to an understanding of just what kind of bryozoan is at hand and how it grew and was constituted.

After the properly oriented thin-sections or peels are made, the only way they can be studied adequately is under the microscope. This, again, is a piece of equipment that may challenge one's budget.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BRACHIOPODS: THE OTHER BIVALVES

8

Brachiopods are among the most common fossils in the Ordovician rocks of the Cincinnati area. Only fossils of bryozoans are more numerous to the naked eye. In a study of type-Cincinnatian limestones, Martin (1975) reported that brachiopods and bryozoans together constitute about 60 percent of the fossil fragments comprising the limestones. There even are some layers, for example, in the Bellevue Limestone, in which the rock is a veritable coquina, in this case consisting of complete and nearly complete shells of large, flat brachiopods of a single genus. These aptly named "shingled *Rafinesquina* beds" commonly are thought of as remains of very shallow-water deposits reminiscent of the shingled beaches of today. Although they have been living on Earth since the Cambrian Period, brachiopods are not well-known animals to most of us. In fact, many folks confuse them with that group of molluscs that includes the clams. Members of the phylum Brachiopoda and those of the molluscan class Pelecypoda are bivalved animals, that is, each has a shell that consists of two valves. But there the resemblance ends. The brachiopods and pelecypods are otherwise strikingly different animals.

First, the orientations of pelecypods and brachiopods are different (Figure 8.1). The two valves of a clam are anatomically left and right in position, with the hinge connecting the valves located at the top of the animal (technically called dorsal). However, the two valves of a brachiopod are dorsal and ventral, respectively, and the hinge is at the rear of the animal (posterior). Thus, although both pelecypods and brachiopods are bilaterally symmetrical animals, the planes of symmetry of the two are at a right angle to one another (Figure 8.1). We can conclude from this that, although animals of both groups each have two valves, "bivalvedness" in each group evolved independently; the two groups are not at all closely related, and neither evolved from the other.

From a practical point of view, however, it happens that the difference in orientation generally provides a convenient way to tell fossil brachiopods from fossil pelecypods. Each valve of most brachiopods can be divided into two halves that are mirror images of one another (Figure 8.1C). On the other hand, it is the two valves of most fossil pelecypods that are the mirror images of one another (Figure 8.1 B). In other words, the plane of symmetry of an ordinary pelecypod is between the valves; in an ordinary brachiopod, it is down the middle of each valve.

Moreover, in general, the two valves of a brachiopod shell are NOT mirror images of one another (figure 8.1D). For example, one valve maybe decidedly deeper than its opposite. In addition (or instead), one valve may have a portion along the midline that is distinctly convex toward the

Figure 8.1. *Comparison of a brachiopod with a pelecypod.* A *and* B, *pelecypod.* C *and* D, *Platystrophia ponderosa showing sulcus and fold. Drawings from Meek (1873), courtesy of the Ohio Department of Natural Resources Division of Geological Survey.*

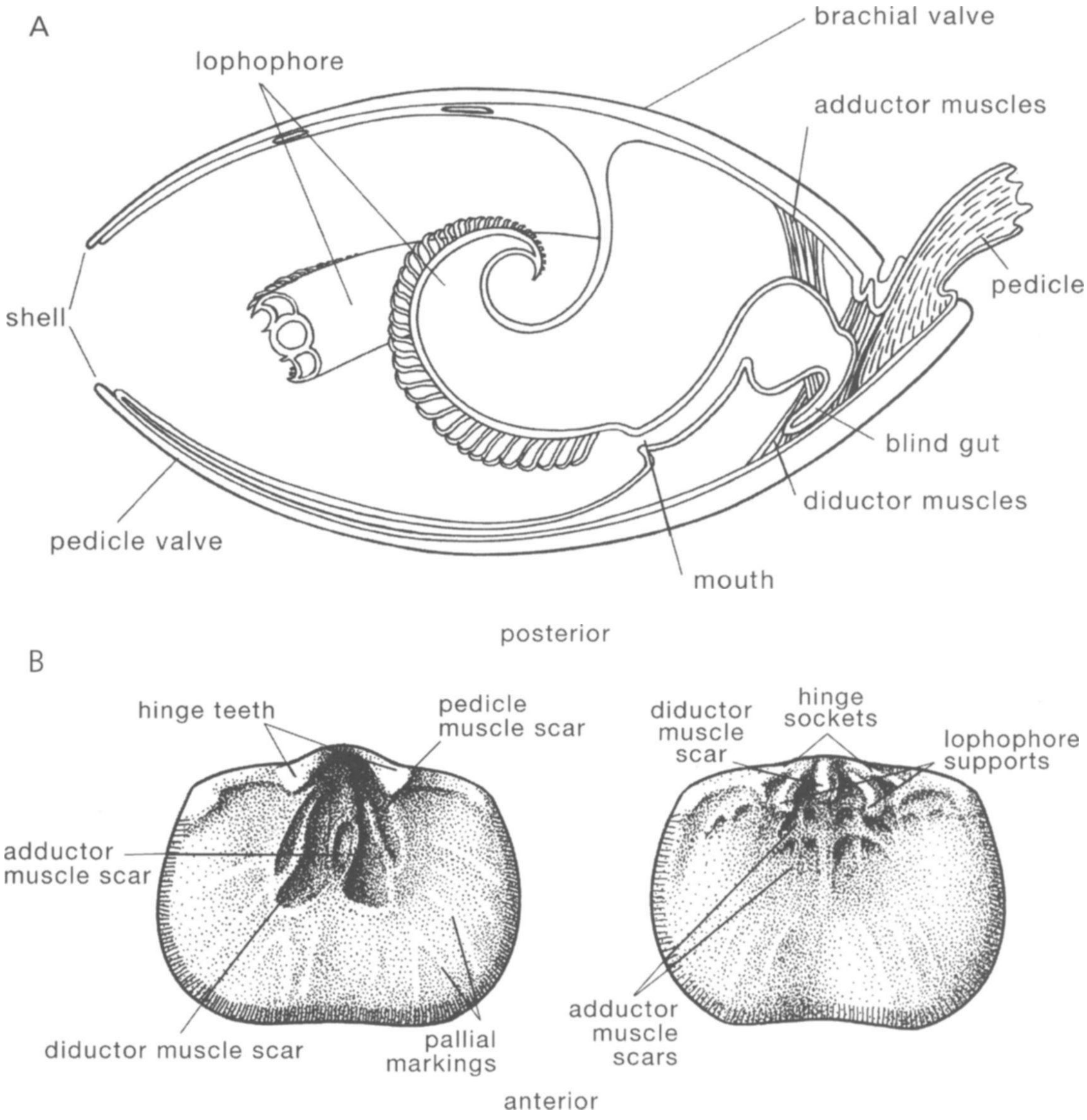


Figure 8.2. A. *Cross-section of an articulate brachiopod.* B. *Interior views of pedicle valve (left) and brachial valve (right) of the Cincinnatian orthid brachiopod Hebertella. Drawings by Kevina Vulinec.*

outside of the animal (this structure is called a fold), and the other valve may have a distinct concavity in the same position (called a sulcus).

As the overall symmetry of pelecypods and brachiopods differs, so too does the operation of the shells. In a pelecypod, the two valves are joined at the hinge by an elastic pad or ligament. When the shell is held closed, the ligament is stretched, so that when the animal relaxes the two valves gape apart from one another. To close the shell, the pelecypod animal must contract one or two adductor muscles (the number depends on the type of clam).

In brachiopods, however, there is no ligament. The animal must contract what are called diductor muscles to open the shell (Figure 8.2A). It uses adductor muscles to close the shell; these adductors are stretched when the shell is open.

Thus, when a pelecypod relaxes, its shell opens. by way of contrast, when a brachiopod relaxes, its shell tends to close. This has important implications for how one finds pelecypods and brachiopods as fossils. Upon death (the ultimate relaxation), the individual valves of a pelecypod tend to get separated from one another, because they gape apart, allowing currents, for example, to tear them asunder. On the other hand, the two valves of a brachiopod shell more commonly remain together, and are found that way by the intrepid fossil collector.

Brachiopod shells tend to be better preserved than are pelecypod shells for another reason, too. Most brachiopod shells consist of calcium carbonate, but so do pelecypod shells. How ever, calcium carbonate exists in more than one form. Most brachiopod shells arc of the mineral calcite, whereas pelecypods consist of or include aragonite. The atoms of calcium, carbon, and oxygen are arranged differently in aragonite and calcite, and the two substances have different properties. Because of this, pelecypods tend not to be preserved as well as brachiopods. The practical result is that you may find main well-preserved brachiopods In the rocks of the Cincinnati area, but pelecypods, with few exceptions, are preserved as internal molds.

Brachiopods are filter feeders. They extract small particles of organic matter from the sea water. These particles are captured by a ciliated structure called the lophophore (Plate 3F; Figure 8.2A). 'The lophophore occupies much of the space between the valves, forming a pair of tubular "arms" that extend on each side of the plane of symmetry. A gutter-like food groove runs along the arms from which ciliated tentacles extend to form a filter (Plate 3F; Figure 8.2A). The beating of the cilia causes water to flow into the shell, along or through the tentacles, and then out of the shell again. The food particles stick to the cilia and are transported by them to the food groove and mouth, which is located on the centerline of the animal. As with all animals, food is metabolized, and waste is expelled.

In at least some brachiopods, the lophophores arc supported by projections from the interior surface of one valve. This so-called brachial valve is the one that is anatomically dorsal in position. In some instances, each branch of the lophophore is complexly coiled; in such cases, the lophophore support may be coiled, too. It is the two "arms" of the lophophore that give the brachiopods their name; the ancient Creek word "brachion" means "arm." The "pod" part of the name comes from "podos," one of the parts of speech of the ancient Greek word "pous." which means "toot"; it recalls a time when brachiopods were thought to be close relatives of the molluscs, which include the gastropods, pelecypods, and cephalopods, among others.

Inarticulates vs. Articulates

Before proceeding further, it must be admitted that the picture of brachiopods painted above is a bit over-simplified. The brachiopods do not comprise a single, homogeneous lineage of animals. The brachiopods portrayed above mostly fall into a group called articulate brachiopods. They are called articulates, because the two valves of the shell are articulated—they are connected together by way of a well-developed hinge (Figure S.2B). Along the hinge of one valve arc projections, called teeth, that fit into sockets in the hinge area of the opposing valve. Because of the interlocking teeth and sockets, the so-called dentition, it would be difficult for a would-be devourer of brachiopod flesh to twist the valves apart to get at supper.

Animals of the other major group of brachiopods, not surprisingly, are termed inarticulates. In these animals, there are neither teeth nor sockets. Not having a real hinge, the task of keeping the valves together is a greater challenge for an inarticulate. The musculature is a good deal more complicated in inarticulates than in articulates—to keep the two valves from being twisted apart from one another.

In an articulate, there is a hinge, which serves as a fulcrum. The diductor muscles and the adductor muscles, in order to open and close the shell, operate against one another about the fulcrum (Figure 8.2A). But an inarticulate has no such fulcrum. The animal opens its shell, not by contracting diductors, but by pulling the body back toward the rear of the shell, thereby causing the valves to gape sufficiently for the animal to feed, respire, and perform other necessary activities.

Another common difference between articulates and inarticulates involves the composition of the shell. In most inarticulates the shell consists, not of calcium carbonate, but, rather, of calcium phosphate. (Note, however, that this is not a universal rule, for the shells of some of the animals traditionally called inarticulates are calcium carbonate, like those of the articulates.)

Studies of present-day forms have been taken to suggest that the articulate and inarticulate brachiopods may, in fact, not be particularly closely related. An inarticulate brachiopod has both mouth and anus, whereas an articulate has no anus. The early life histories of the animals of the two groups are different, too; for example, the pedicle of an inarticulate has a different origin than does the pedicle of an articulate. Detailed studies of the genetics of present-day animals are beginning to throw light on the issue of the relationships of the various groups of brachiopods (Cohen and Gawthrop 1997). However, pending the amassing of further information, we will follow the usual tradition of considering the Articulata and the Inarticulata to be two subphyla of the phylum Brachiopoda. One alternative scheme would be to recognize those two groups as separate phyla. On the third hand, some experts on brachiopods prefer to do away with the formal taxa Articulata and Inarticulata altogether and recognize instead three subphyla (Williams et al. 2000); followers of that scheme retain the concepts of articulated brachiopods and inarticulated brachiopods, but only as descriptive terms.

Brachiopod Life Habits

Regardless of such taxonomic issues, the brachiopods as a whole are benthic creatures. Some of them simply lie on the sea floor, whereas others each are physically attached to the sea floor by means of a fleshy stalk called a pedicle. In 1972 Peter Richards published a study that explored the relationship between shell form and life habits of many characteristic Cincinnatian brachiopods. His research demonstrated that Cincinnatian brachiopods have a variety of life habits and that careful attention to morphological features of the shell as well as preservational evidence helps to explain the diversity seen in this important group. His work has guided and inspired much subsequent research and the discussion that follows

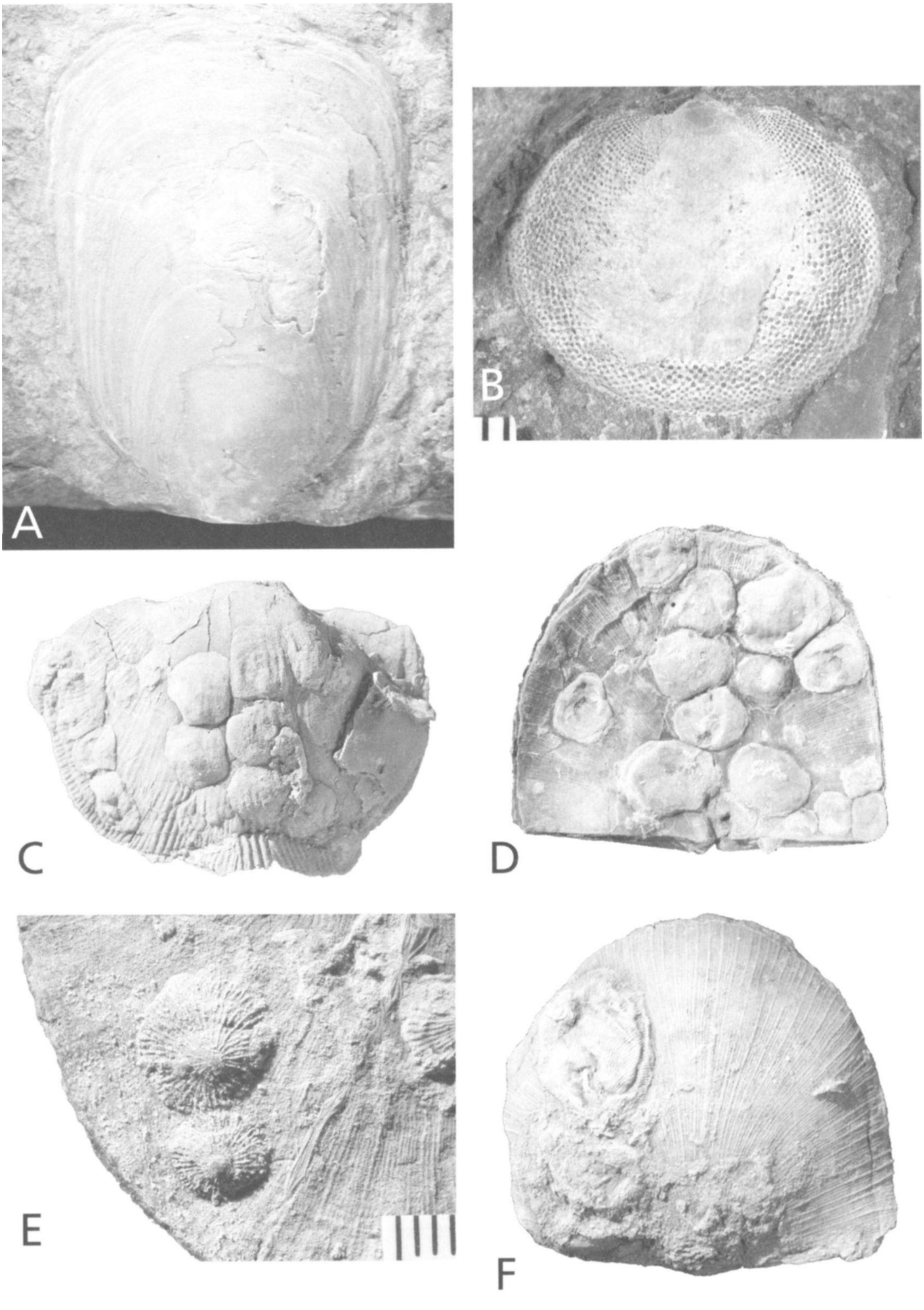
Inarticulates

Some present-day inarticulates (genus *Lingula* and its relatives) spend much of their time in a burrow. When it comes time to feed, the pedicle extends so that at least the anterior part of the shell projects up into the water. In some brachiopods, there is an opening in the shell through which the pedicle extends. In general, this pedicle foramen is in the anatomically lower valve, which, hence, is called the pedicle valve. The pedicle of some brachiopods may be attached to another shell on the sea floor; this may result in pedicle attachment scars which consist of tiny, characteristic pits in the other shell. In an inarticulate brachiopod, as in you, there is a mouth, esophagus, stomach, intestine, and anus. In an articulate brachiopod, however, there is no anus (figure 8.2A). What might have been a complete digestive tract is, in fact, a cul de sac. Thus, the only egress for waste material is back out the mouth. In present-day animals that have been studied, solid waste is regurgitated as small pellets; these are then expelled from the shell by rapid snapping of the valves.

Although the articulates are more readily noticed, inarticulates are not rare. Most of them, however, grew on the shells of other animals and, hence, are relatively small and easily overlooked (Figure 8.3). Presumably, the other shells provided a solid substrate to which to attach; it could well be that the little "hangers-on" (technically called epizoa) made their living by consuming the waste matter expelled by their "hosts." In any case, the shells of these inarticulates commonly look a bit like scabs, blisters, or little volcanoes on the shells of articulate brachiopods. Some of them grew so tightly affixed to their larger cousins that the ribbing of the shells of the latter deform or show through the shells of the inarticulates.

Another kind of inarticulate may be found in the rocks of the Cincinnati region by the sharp-eyed collector. Given the moniker "inarticulate," it is ironic that this other group comprises animals that have tongue-shaped shells. Luckily for paleontologists, these so-called lingulides are represented in present-day oceans, so that we readily can see them. An individual member of genus *Lingula* (Latin for "tongue"), from which the group gets its name, has a way of life reminiscent of that of some burrowing worms. The animal anchors the distal end of its long pedicle to the sea floor and uses its shell to dig vertically down into the sediment front end foremost. In due course, the burrower veers to the horizontal and then back up to the sea floor. Most of the U-shaped burrow collapses from behind, so that only the one vertical tube remains, with the opening of the shell at or near the sea floor and the pedicle pointing down into the sediment. When necessary (or desired?), the gape between the valves can be raised above the sea floor by extension of the pedicle, and the animal can feed, or whatever. In times of danger, the animal can retreat into its burrow by contracting the pedicle.

Lingulides are not particularly common in the type-Cincinnatian. Very occasionally a specimen is found with its shell oriented perpendicular


A
B
C
D
E
F

to the stratification, in what appears to be its life position, that is, the animal's orientation in space during its life. The individual in Figure 8.3A is a case in point.

It is only by great good fortune that that particular individual made it into a museum. Ralph Dury was a Cincinnati entomologist of some considerable repute. However, his actual livelihood was in real estate. According to Charles Dury, Charles's son and director of the Cincinnati Museum of Natural History for more than five decades, the specimen in figure 8.3A started its museum career in a real estate project. Charles Dury was having a stone wall built. Being a meticulous fellow, he visited his sites on a regular and frequent basis. He happened to make one of these visits to the building site shortly after a load of stone had been delivered. In the course of examining the stone to be certain that it was up to his standards, he saw the chunk with the lingulide in its life position. So, instead of ending up as part of a wall, the piece of rock ended up as part of the collections of the Cincinnati Museum of Natural History, along with Charles Dury's insect collection—but that is another story (Vulinec and Davis 1984).

Figure 8.3. A. *Pseudolingula sp., CMC IP 51994, Cincinnatian, horizon and locality unknown,* x *1.9. Specimen oriented perpendicular to bedding, presumably in life position with beak downward.* B. *Trematis millepunctata Hall, CMC PT 585, brachial valve interior, Cincinnatian, horizon and locality unknown,* x *3.* C. *Petrocrania scabiosa (Hall) encrusting on Hebertellasp., MUGM 29461, Arnheim, Oxford, Ohio,* x *1.3.* D. *Petrocrania scabiosa (Hall) encrusting on brachial valve of Rafinesquina sp., Bruce and Charlotte Gibson Collection, no. 1042, Richmondian, Franklin Co., Indiana, approx.* x *1.5.* E. *Philhedra laelia (Hall), MUGM 26219, two specimens encrusted on Rafinesquina brachial valve exterior, Liberty Formation, Preble Co., Ohio,* x *3.* F. *Schizocrania filosa Hall, CMC IP 36, encrusted on Rafinesquina pedicle valve exterior, Corryville Formation, Warren Co., Ohio, x 1.8.*

Articulates

The vast majority of the brachiopods that one sees in the Ordovician rocks of the Cincinnati area are articulates. There is a tremendous variety of them (figures 8.4-8.9). Some have an external shape that makes them easy to identify to genus or, even, species. On the other hand, there are some that are beastly difficult to tell apart. The problem is that brachiopods that are only distantly related may look alike externally (Figure 8.6). It is only when one carefully studies the various features on the inner surface of each valve that their true relationships may become apparent. Useful features include the scars where muscles attached to the valves, the structures that supported the lophophores, and so on. One even may need to examine the internal structure of the shell material that makes up the valves. It seems that the environment in which the brachiopods lived led different lineages to evolve similar external shapes. The phenomenon is called convergent evolution, and the result is homeomorphy—the existence of two or more kinds of animals that are not closely related but that nonetheless look alike. This is a common enough occurrence that it is an old saving: "Homeomorphy is rife amongst the brachiopods." This, of course, presents a problem to the collecfor of fossil brachiopods. It means that he or she must make a real effort to obtain loose valves that have been naturally cleaned over time so as to reveal their internal features, hailing that, the collector must break, cut, or grind specimens open and clean them meticulously to reveal the inner truth.

Some of the articulate brachiopods must have spent much of their lives anchored by their pedicles to shells, hardgrounds, or other solid objects on the sea floor (Figure 8.9E). They were not frozen in position, though, because they apparently had adjustor muscles that allowed the individual animal to move its shell with respect to the pedicle. We know this because present-day articulates have such adjustor muscles, and where these adjusters attach to the insides of the valves, there are muscle scars

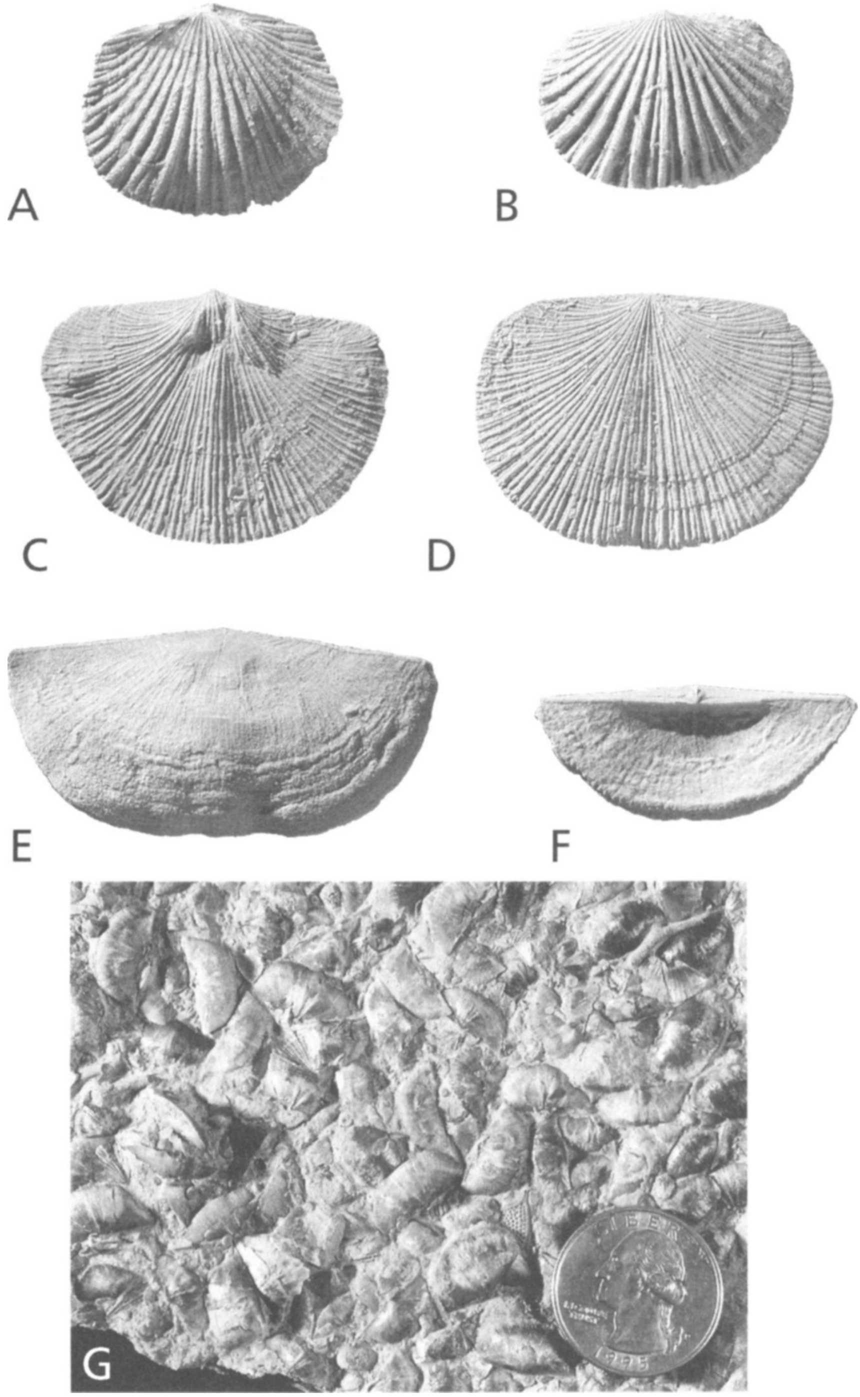


Figure 8.4. A, B. *Plectorthis neglecta (James), MUGM uncatalogued. Fairview Formation, Hamilton Co., Ohio.* A. *Brachial valve exterior.* B. *Pedicle valve exterior, both* x *1.8.* C, D. *Dalmanella emacerata (Hall), MUGM 24362, Kope Formation, Hamilton Co., Ohio.* C. *Pedicle valve exterior.* D. *Brachial valve exterior, both* x *2.4.* E, F. *Sowerbyella rugosa (Meek), MUGM 24564, Kope Formation, Cincinnati, Ohio.* E. *Pedicle valve exterior.* F. *Brachial valve exterior, both* x *2.2.* G. *Slab covered with Sowerbyella rugosa, Kope Formation. Courtesy of Paul E. Potter.*

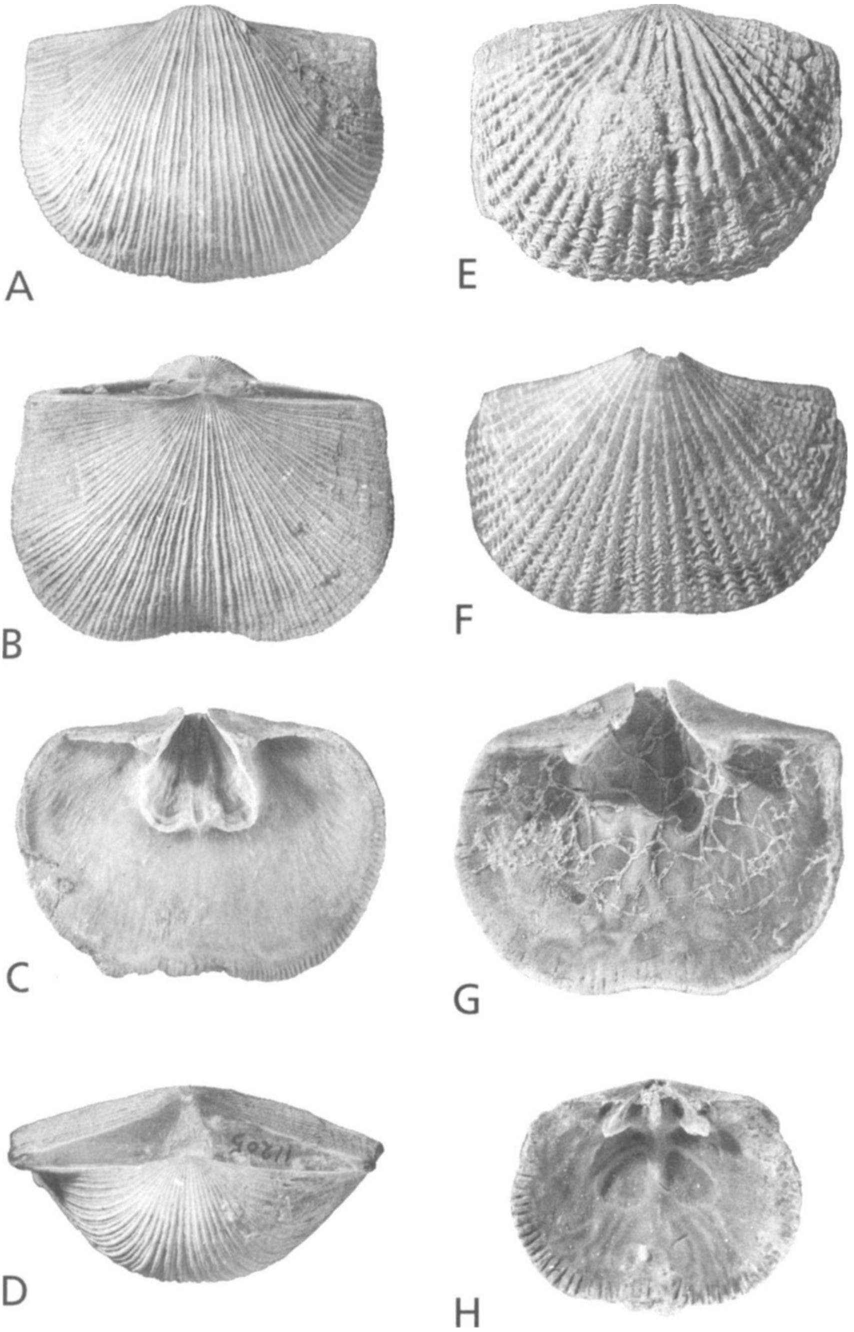


Figure 8.5. A-D. *Hebertella occidentalis (Hall), MUGM 11205, Waynesville Formation, Franklin Co., Indiana.* A. *Brachial valve exterior.* B. *Pedicle valve exterior.* C. *Pedicle valve interior, showing muscle scars and triangular pedicle opening.* D. *Posterior view of articulated valves and triangular pedicle opening, all* x *1.2.* E-H. *Glyptorthis insculpta (Hall);* E-F, *MUGM 22450, Liberty Formation, Preble Co., Ohio.* E. *Brachial valve exterior.* F. *Pedicle valve exterior,* x *2.8.* G-H, *MUGM 29458, Arnheim Formation, Butler Co., Ohio.* G. *Pedicle valve interior, showing muscle scars, triangular pedicle opening, and encrusting cyclostome bryozoans,* x *2.2.* H. *Brachial valve interior, showing muscle scars and cardinal processes,* x *1.8.*

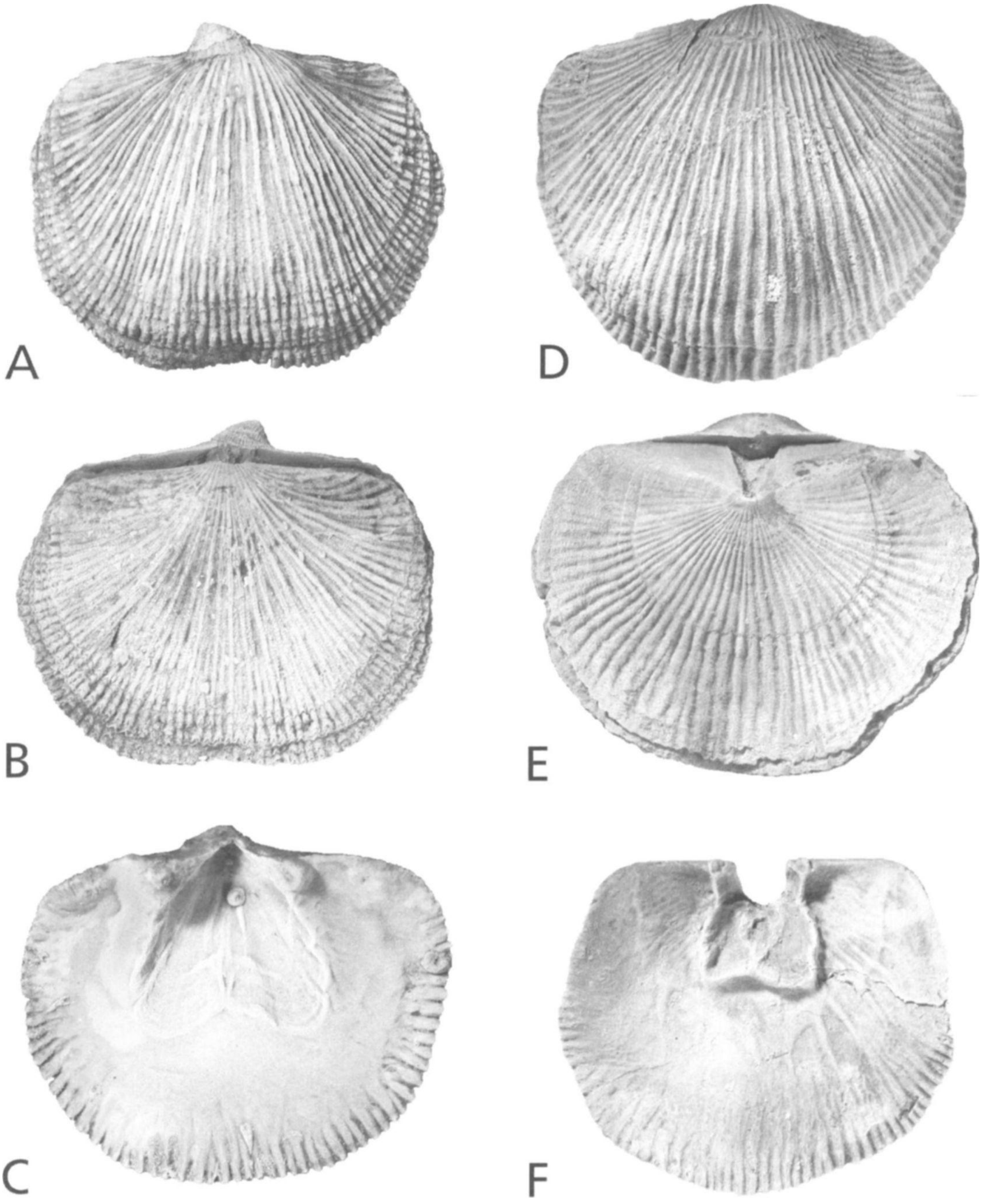


Figure 8.6. A-C. *Plaesiomys subquadrata (Hall), MUGM 22933 Liberty Formation, Preble Co., Ohio.* A. *Brachial valve exterior, inarticulate brachiopod Philhedra laelia on beak,* x *2.1.* B. *Pedicle valve exterior, x.2.1.* C. *Pedicle valve interior, showing muscle scars,* x *2.4.* D-F. *Retrorsirostra carleyi (Hall), MUGM 23037, Arnheim Formation, Butler Co., Ohio.* D. *Brachial valve exterior.* E. *Pedicle valve exterior, note triangular pedicle opening and flanking inter-area.* F. *Pedicle valve interior, showing muscle scars,* x *2.*

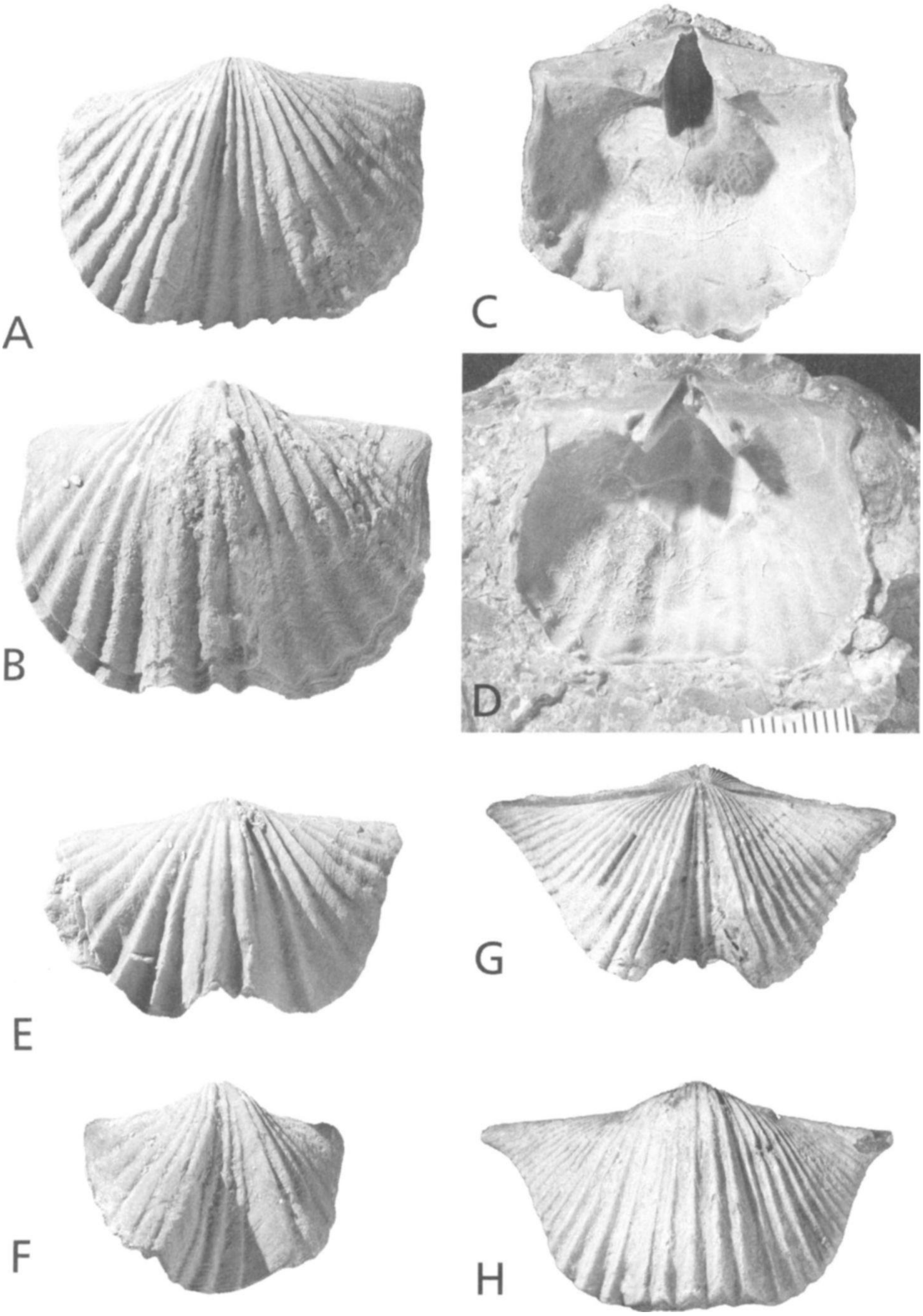


Figure 8.7. *Three of the many described species of Platystrophia.* A-D. *Platystrophia ponderosa Foerste, MUGM 24060, Maysvillian, Campbell Co., Kentucky* A. *Pedicle valve exterior,* x 7.5. B. *Brachial valve exterior,* x 7.5. C. *Pedicle valve interior, showing pedicle opening and deep muscle scar,* x *1.0.* D. *Brachial valve interior, showing muscle scars,* x *1.3. Early collectors of Cincinnatian fossils referred to this large, robust brachiopod as the "double-headed Dutchman."* E, F. *Platystrophia laticosta (Meek), MUGM 11315, Maysvillian, Cincinnati, Ohio.* E. *Brachial valve exterior.* F. *Pedicle valve exterior, both* x 7.5. G, H *Platystrophia acutilirata (Conrad), MUGM 23360.* G. *Pedicle valve exterior.,* H. *Brachial valve exterior, Whitewater Formation, Preble Co., Ohio, both* x *1.4.*

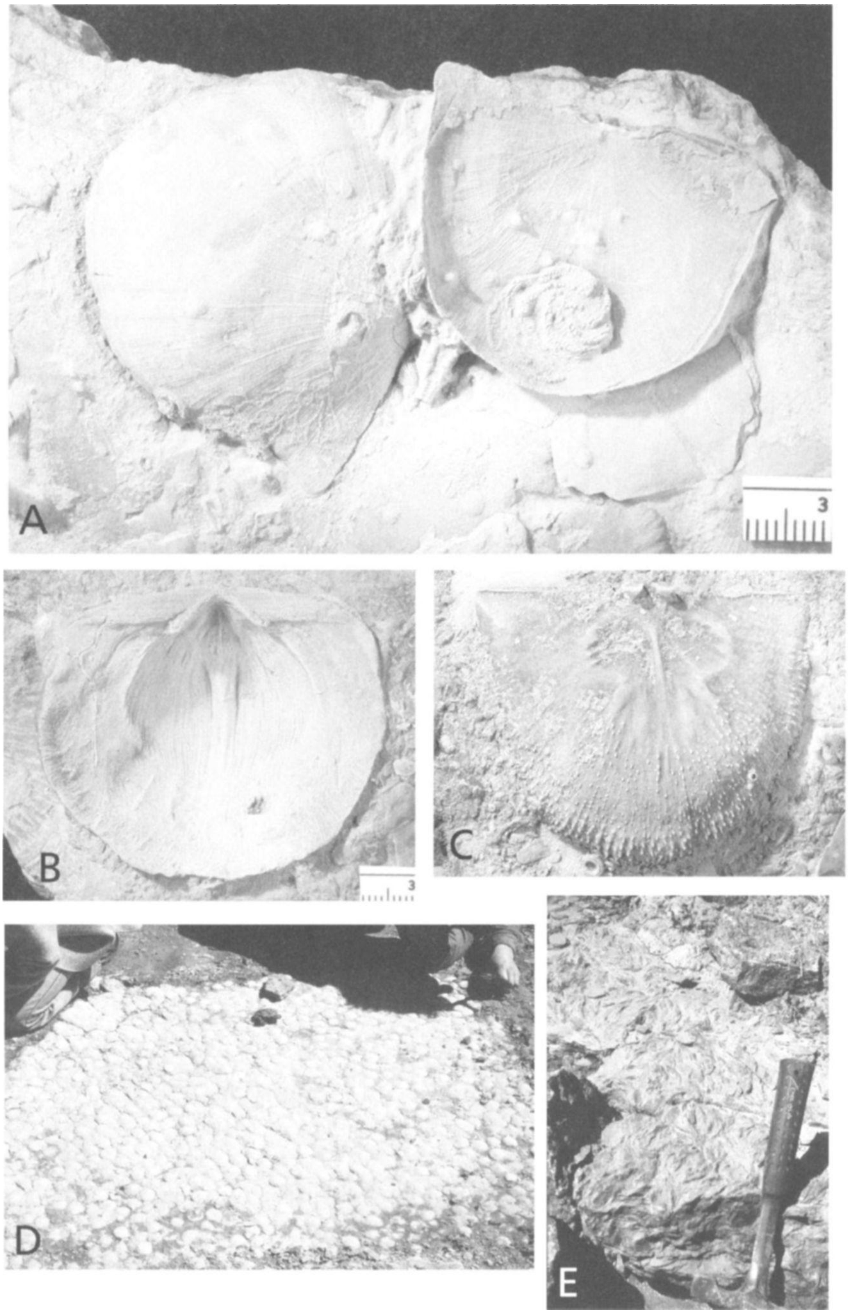


Figure 8.8. *The many faces of Rafinesquina: Rafinesquina alternata (Conrad).* A. *University of Cincinnati collections, left, pedicle valve up, with encrusting edriasteroids and cyclostome bryozoans, right, brachial valve up, with encrusting edrioasteroid Streptaster vorticellatus and crinoid locrinus subcrassus wedged beneath lower left edge, Corryville Formation, Boone Co., Kentucky, scale in mm.* B. *Pedicle valve interior, CMC IP 51111, showing muscle scars, scale in mm.* C. *Brachial valve interior, University of Cincinnati collections, showing muscle scars and pair of cardinal processes along hinge at top, Corryville Formation, Boone Co., Kentucky, size about same as in* B. D. *Rafinesquina pavement, with pedicle valves up, Fairview Formation, Kenton Co., Kentucky.* E. *Shingled Rafinesquina bed, with valves perpendicular to bedding, Fairview Formation, Kenton Co., Kentucky.*

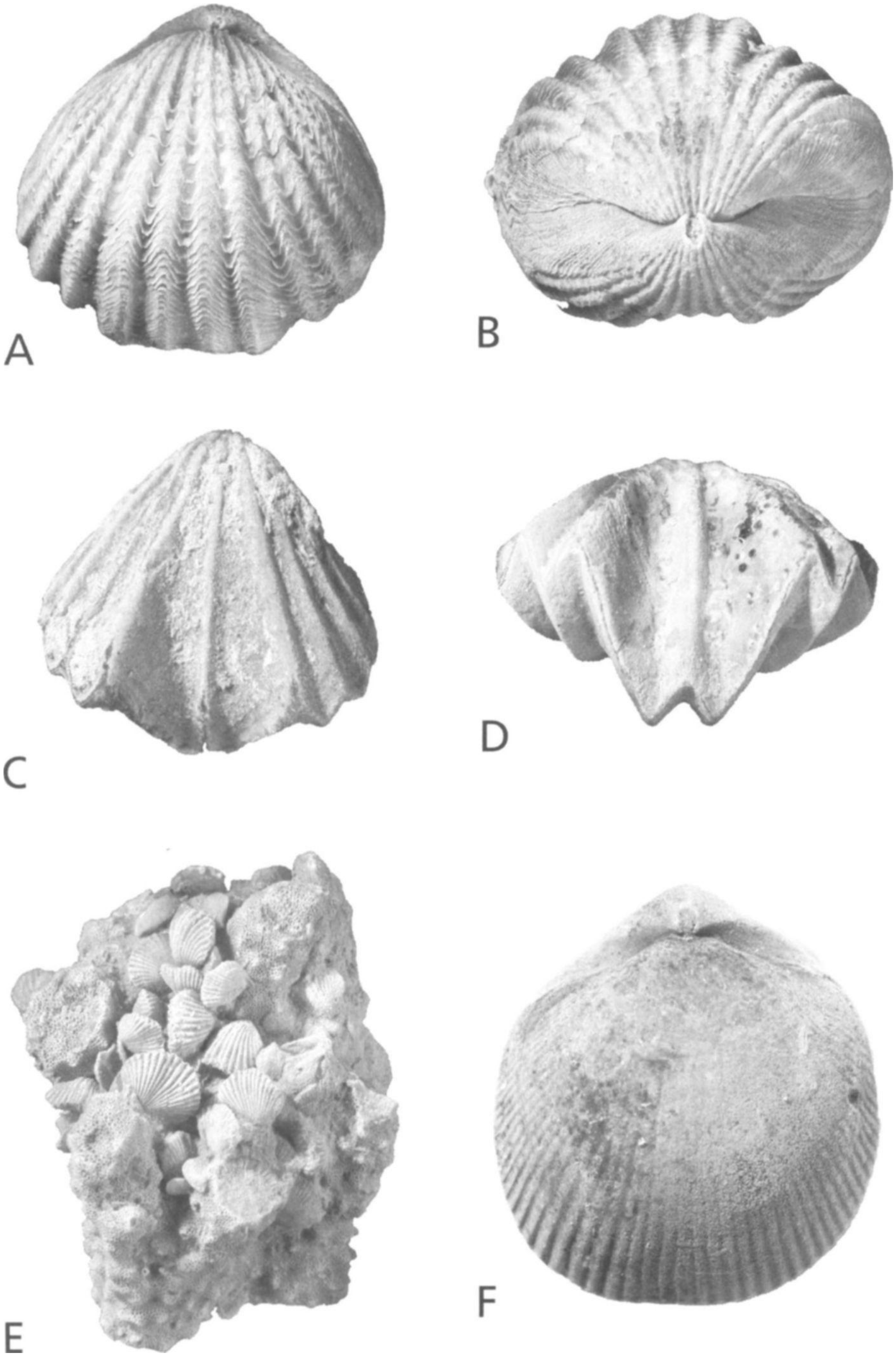


Figure 8.9. A, B. *Hiscobeccus capax (Conrad), MUGM 25490, Liberty Formation, Preble Co., Ohio.* A. *Brachial valve exterior.* B. *Posterior view of articulated valves showing small pedicle opening,* x *2.2.* C, D. R*hynchotrema dentatum (Hall), MUGM 25933, Whitewater Formation, Preble Co., Ohio. C. Pedicle valve exterior.* D. *Anterior view of articulated valves showing pronounced sulcus,* x *3.4.* **E.** *Zygospira modesta (Say), CMC IP 51112, Corryville Formation, Boone Co., Kentucky, attached in life position to bryozoan Parvohallopora sp.,* x *1.9.* F. *Catazyga schuchertana (Ulrich), MUGM 7614, Waynesville Formation, Jefferson Co., Indiana, brachial valve exterior,* x *3.4.*

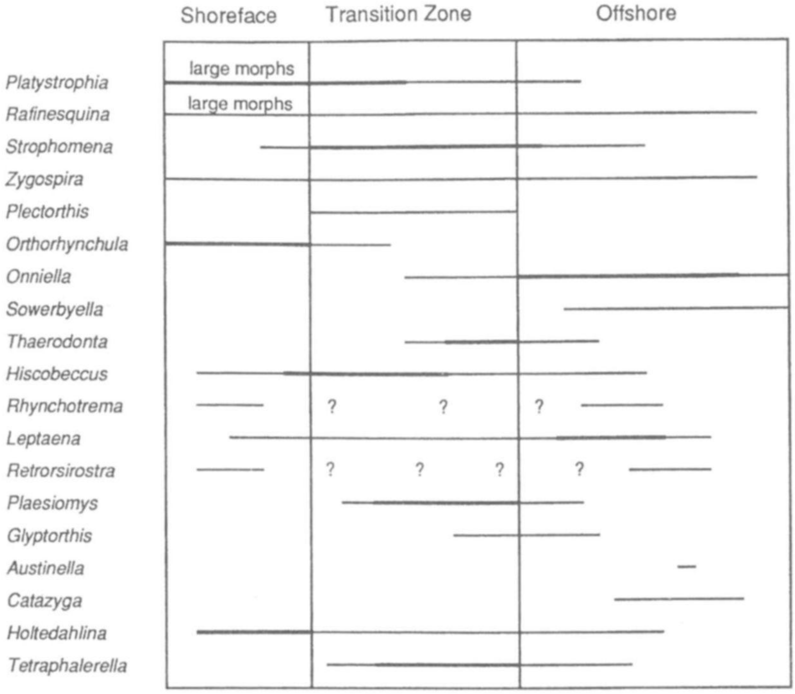


Figure 8.10. *Environmental distribution of brachiopods in the Cincinnatian Series. Shoreface environments are equivalent to the shallow subtidal (1-2 m or 3-6 ft); transition zone environments are deeper subtidal (3-6 m or 10-20 ft), and offshore environments are deeper water, with a maximum depth of about 30 m (100 ft). The heavy lines indicate the environments where each genus is most abundant and thin lines indicate environments where a genus is present at lower abundance. From Holland (1997), in Paleontological Events. Copyright 1997 Columbia University Press. Reprinted with permission of the publisher.*

that occur in particular positions. Many fossil brachiopods have comparable muscle scars.

On the other hand, some kinds of fossil articulates have no pedicle foramen, the opening through which the pedicle extends beyond the hinge area of the shell. There has been a great deal of discussion as to how these creatures survived in areas where the sea floor was soft mud.

Brachiopods of genus ***Rafinesquina*** (figure 8.8) are, perhaps, the most common of the larger articulates in the rocks of the Cincinnati area. The overall shape of the shell is described as "concavo-convex"; the brachial valve (anatomically dorsal) is concave to the exterior, and the other valve (anatomically ventral) is convex to the outside. The whole shell, then, is saucer- or bowl-shaped. The adult animal does not seem to have had a pedicle—no pedicle foramen. Hence, it must have been free on the sea floor. But imagine a saucer-shaped shell in a current; all too easily, it would have been flipped so that the convex side was uppermost. The result would have been that the commissure, the opening between the valves, would have been against the sea floor. If that sea floor were soft mud, the animal would have had considerable difficulty generating sufficient currents with the cilia of its lophophore so as to bring life-giving nutrients and oxygen between the valves. Thus, there seems to be a conflict between hydrodynamics and biology.

The bleak picture of the brachiopod. upside down with its opening in the mud, may be misleading. It portrays the animal as an immobile lump unable to right itself. True, there was no pedicle on which the animal, using adjuster muscles, could twist and turn itself back into a viable position. But, what if the animal were less like an inanimate saucer and more like a living scallop of today? A scallop is a kind of bivalved mollusc. The "scallop" you enjoy in your favorite seafood restaurant is an adductor muscle of one of those pelecypods. The adductor of a scallop is powerful enough, in life, to snap the animal's valves together so swiftly that the creature can be lifted above the sea floor. Some scallops can even swim for some distance, although rather jerkily and in decidedly irregular trajectories.

Dattilo (2004) has found evidence that one Cincinnatian brachiopod with a concavo-convex shell, Sowerbyella*,* was capable of escaping from burial beneath sediments stirred up by storms, presumable by snapping its valves. Individuals of *Rafinesquina* may have had similar capabilities, because convex-up specimens are found with a moat-like furrow around the commissure that formed while the brachiopod was alive (Meyer 2006). These recent findings suggest that these brachiopods without pedicle attachment might have led much more active lives than previously realized.

Distribution of Type — Cincinnatian Brachiopods in Time and Space

Despite the high diversity of type-Cincinnatian brachiopods, the distribution of species is not uniform throughout the stratigraphic succession. There are distinct associations of species and shell types that characterize different stratigraphic intervals and even individual beds. Recent research In Steven Holland, in collaboration with Arnold Miller, David Meyer, and Benjamin Dattilo (Holland et al. 2001) showed that the relative abundance ofbrachiopods and other fossils changes within the Kope Formation, a unit generally regarded as having a uniform shaley lithology. In the lower Kope, fossil assemblages as found on characteristic limestone bedding surfaces are dominated by the small, thin-shelled ***Sowerbyella,*** along with branching bryozoans, small, slender crinoids like ***Cincinnaticrinus*** and ***Ectenocrimis,*** and the trilobite ***Cryptolithus.*** Higher in the Kope, another thin-shelled but larger brachiopod, ***Dalmanella,*** becomes more abundant. In the highest sections of the Kope, the large thin-shelled brachiopods ***Rafinesquina*** and ***Strophomena*** and the large, rather thick-shelled ***Platystrophia*** become the dominant brachiopods. In conjunction with changes in the lithology, bedding, and other characteristic fossils, Holland. Miller, Meyer, and Dattilo (2001) interpreted the changes in the Kope Formation as a paleobathymetric gradient reflecting transition from deeper to shallower water.

Throughout all type-Cincinnatian depositional sequences the nature of the brachiopod assemblages provides one of the most reliable and abundant indicators of paleoenvironmental conditions such as depth and level of water movement energy (see chapter 15). The relationship between brachiopod morphology and depth reflects both the type of substratum and the level of water movement energy. In the deeper water, muddy environments, brachiopods with small, thin, flat shells acted like snowshoes
In shallower water, larger, concavo-convex brachiopods like ***Rafinesquina*** and ***Hebertella*** were better adapted to stronger wave energy. Other larger brachiopods like ***Platystrophia,*** with thicker shells and well-developed plications (ribs radiating from the beak), characterize some of the shallowest, highest wave-disturbed environments. Figure 8.10 shows the environmental distribution of other brachiopods within the type-Cincinnatian.

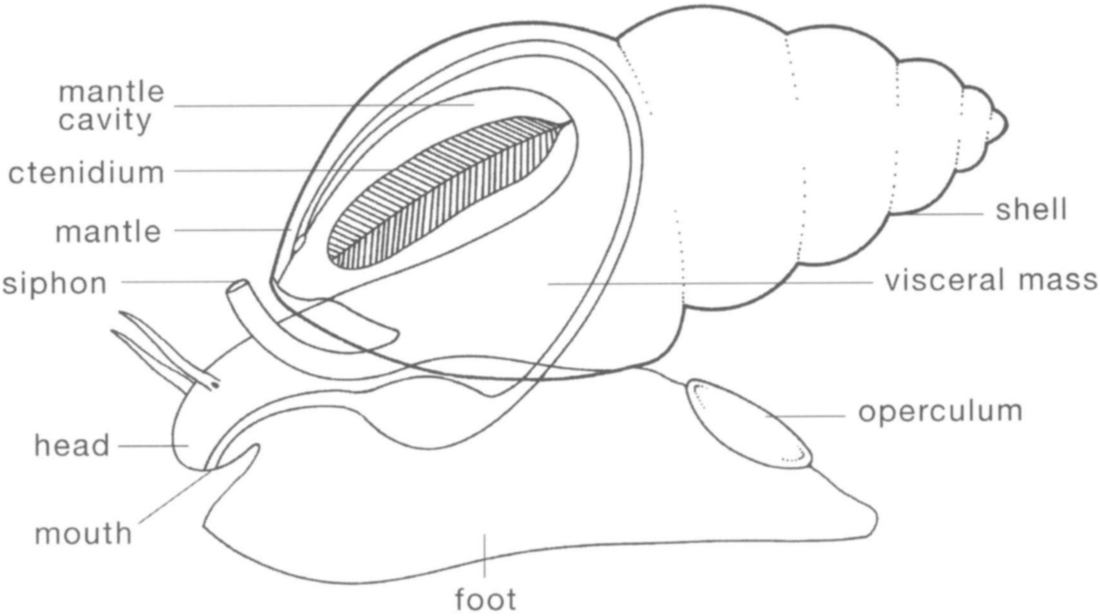
Even on a smaller scale, brachiopods reveal some very basic aspects of life on the Late Ordovician sea floor. Very densely populated limestone beds, featuring brachiopods like *Rafinesquina, Strophomena,* and ***Dalmanella,*** are very common throughout the type-Cincinnatian and are called shell pavements (also called shingled beds as noted above). In such shell pavements, the brachiopods are usually preserved with convex valves upward, sometimes covering the entire bed surface (Figures 8.4G, 8.8D, 8.8E). Shell pavements can be as thin as a single layer of shells, or thicker, with the entire thickness up to a few tens of centimeters consisting of stacked brachiopods. In some cases, the valves are vertical or tilted at various angles and packed closely together in an edgewise shell bed. The edgewise shell pavements are good evidence of water movement in the form of wave oscillations because there are present-day examples of edgewise shell beds and shale fragments formed in very shallow water by wave oscillations. II the hingelines or beaks of the brachiopods were always directed downward in an edgewise bed, it might be possible that the densely packed shells actually had lived in a manner similar to an oyster bed. However, analysis of valve orientation within edgewise shell beds shows that valves do not show such a pattern and even can be predominantly hingeline-upward (Seilacher 1973, pers. comm.).

There has been considerable debate as to how shell pavements could have formed. Many workers felt that the thin, concavo-convex shells of the characteristic brachiopods like *Rafinesquina* and *Strophomena* initially lived on a soft, muddy sea floor, with the convex valve downward. During a storm, the fine-grained muds could have been swept away, leaving a concentration of shells (called a lag deposit) to form the shell pavement. Possibly the shells were even carried some distance by storm currents to be deposited later. In cases where pavements form edgewise beds, storms could very well have been involved, but not all pavements are edgewise.

It is also possible that shell pavements accumulated by abundant production of shells of a single species over some time span in one place. In one shell pavement from the Corryville Member of the Grant Lake Formation in northern Kentucky, mostly convex-upward shells of *Rafinesquina* form a kind of imbricated or shingled bed, but the spaces between the shells are mud-filled, forming a type of limestone known as packstone (Meyer 1990). If the mud had been removed by a storm, the remaining shell bed could have formed a grainstone. Shells in the upper surface of the bed are a mixture of articulated shells with good preservation of fine surface features and disarticulated shells that are abraded and broken. Both abraded and unabraded shells are encrusted with bryozoans and edrioasteroid echinoderms. Some articulated brachiopods have the moat-like feature mentioned above that suggests activity of the living brachiopod. All these features are evidence that the shell bed accumulated gradually without significant transportation. Ultimately the entire bed was smothered by an influx of mud, probably produced by a storm.

Characteristically, a stratigraphic section with the type of shell pavement described above will contain repetitions of thin shell-pavements smothered by shales. Harris and Martin (1979) described this pattern in the

Waynesville Formation as a form of paleoecologic succession (see Figure 4.S). In present-day settings, ecologic succession occurs when one assemblage of animals or plants alters the habitat IN such a way that other species can replace the so-called pioneer species. Harris and Martin (1979) suggested that thin-shelled brachiopods were pioneer species that first colonized soft muddy patches of the sea floor and provided a pavement on which encrusting animals like bryozoans and inarticulate brachiopods could settle. Eventually other species could take advantage of the shell pavement and thickets of bryozoans, so that the diversity of the assemblage increased upward from the bottom of a pavement bed. Storms frequently smothered the shelly patches with mud, thus interrupting the succession until brachiopod larvae once again could colonize the barren muds. some paleoecologists have questioned whether paleoecologic succession comparable to present-day succession can be detected in the fossil record because most stratigraphic changes in fossil assemblages represent a much longer time scale than the scale of years to decades over which present-day succession occurs. Although we still do not know how much time was required for the formation of characteristic, thin type-Cincinnatian shell pavements, it is possible that they formed over a short time scale. It also seems correct to view the brachiopods as having a pivotal role in providing a hard substratum onto which encrusting animals could settle, thus altering the habitat in the manner of successional pioneers. Clearly, succession at the scale of individual shell pavements was an important act on the stage of the Cincinnatian sea floor, and brachiopods played a major role in that evolutionary play.


mantle cavity
ctenidium
mantle
siphon
head
mouth
foot
shell
visceral mass
operculum

MOLLUSCS: HARD, BUT WITH A SOFT CENTER

9

Everyone knows molluscs—the oh-so-familiar snails and slugs, the clams, mussels, scallops, and oysters, the octopus, and the squid. But the mollusc story is not a simple one. There are more kinds of molluscs than of any other group of animals, save the arthropods. So what links all the molluscs together?

The word "mollusc" is derived from the Latin word "molluscus," meaning "soft." This refers to the fact that every mollusc has a soft, fleshy body. But that, of course, is not the image conjured up in the mind's eye at the mention of snails, clams, and oysters. In most of the molluscs, the soft parts are enclosed within a hard shell. And it is on the basis of differences in the shells that the molluscs of the type-Cincinnatian are differentiated from one another.

One might be tempted to sort the shelled molluscs into three groups, at least with respect to their shells. The animals of one group have basically a single shell; take, for example, the coiled cone of most snails or that of the pearly nautilus. In contrast to these univalved molluscs are those in which the soft parts are enclosed between two "shells" (strictly speaking, each of the two is called a "valve"). The bivalved molluscs that leap most readily to mind are the clams, mussels, oysters, and their kin. In a third group, and a relatively small one at that, the shell consists of a number of plates arranged so that the animal, at first glance, appears to be segmented. (In this case, looks are deceiving, because, unlike the annelid worms and the arthropods, molluscs are not truly segmented.) The present-day chitons exemplify the polyplacophoran group (literally, "many plate bearing").

Figure 9.1. *Gastropod mollusc, showing internal features. Drawing by Kevina Vulinec.*

Regardless of whether the animal has a shell that is a single valve or one consisting of two valves or many plates, the material of the shell is primarily calcium carbonate in the mineral form of either calcite or aragonite. Because aragonite is less stable than calcite, aragonitic shells usually dissolve after death, leaving just external and internal molds to record where the shell once had been (see chapter 5). This, of course, can greatly affect what we find as fossils.

As a mollusc progresses through its life, it generally adds shell material at the periphery of its shell or of each valve of its shell. Thus, the life history of that shell or valve is recorded in a series of concentric growth-lines visible on the exterior of the shell. This allows us to decipher the changes in the size and shape that the shell or valve went through during the life of the individual animal. (This stands in strong contrast to animals that shed their exoskeletons as they grow. An individual adult trilobite, for example, does not present to even the careful observer its life history in its hard parts.)

Of course, even in molluscs that have shells, the hard parts are merely a part of the whole animal. In general, the body of a mollusc incorporates five of what commonly are called body regions: the head, the foot, the visceral mass, the mantle-complex, and the gills (technically termed ctenidia, from their comb-like shape). The mantle, the shell, and the mantle-cavity together comprise the mantle-complex. The mantle is a sheet of tissue that hangs down on each side of the bulk of the animal or otherwise encloses it. The shell, if present, is attached to the outside of the mantle and is secreted by it. To the inside of the mantle is the mantle-cavity, in which are located the gills, if they are present.

The last phrase of the previous paragraph is an important tip-off. Not all kinds of molluscs have all five body regions developed to the same extent. Snails, for example, each have an obvious head, whereas clams do not. Squids have well-developed gills; however, in terrestrial snails, there are no ctenidia, and the mantle-cavity serves, in effect, as a lung.

It is only fair to admit that there is so much morphologic and anatomical variation among the molluscs as a whole that it is difficult to point to any trait that occurs in all molluscs. Some have shells, and some do not. In most, the shell is external, but in some it is internal. Some have gills, and some do not. Some have heads, and some do not. And so on.

Regardless of whether one is convinced that form follows function, or vice versa, the tremendous morphological spectrum exhibited by the molluscs as a whole is coincident with tremendous ecological and behavioral spectra. Save for the fact that molluscs have not mastered in-air flight, virtually any terrestrial or aquatic environment on Earth will have a representative suite of molluscs.

This tremendous array of sizes, shapes, behaviors, and ways of life among the molluscs is the result of millions of centuries of organic evolution. Included in this almost incredible diversity of animals are, to brag a bit, not only the largest of all invertebrates, but also the most intelligent of all invertebrates (both, it happens, being cephalopods). Moreover, the largest individual nerve cells are said to occur in molluscs (again, cephalopods are the champions).

Who's Who among the Molluscs

In the introduction to this chapter, molluscs were separated into univalved molluscs, bivalved molluscs, and polyplacophoran molluscs. Although perhaps convenient to introduce the notion of morphological variation among the molluscs as a phylum, those three "groups" are a gross over-simplification. Malacologists, those who study molluscs, use the shape of the shell to sort molluscs into true biological groups—into groups whose members are evolutionary related to one another. However, unlike conchologists, those who study shells, malacologists use all sorts of traits. In addition to those of the shell. Of course, in most fossils, only the hard parts are preserved. Nonetheless, it is the goal of the paleontologist to put the living animal back into its shell and to recognize the real, biological groups of fossils.

In the Ordovician rocks of the Cincinnati region, fossils of the following biological groups of phylum Mollusca are found (recall that a phylum consists of a number of smaller groups of organisms called classes): class Cephalopoda, class Gastropoda, class Monoplacophora, class Pelecypoda, class Rostroconchia, class Polyplacophora, and class Scaphopoda. There are some groups of molluscs of which no specimens are known from the local rocks. For example, the class Aplacophora includes certain present-day animals that are devoid of preservable hard parts; hence, their name, which means "no plate bearing."

Class Gastropoda—The Snails

Snails, with their characteristic coiled shells, are probably the easiest to recognize of the molluscs in the rocks of the Cincinnati region. Snails are very common in main environments of today's world, along with their relatives, the so-called slugs and sea-slugs. (Animals of the latter two groups either have no shell at all, or a small, internal one; thus, they are unlikely to he preserved as fossils.)

Snails are the quintessential univalved mollusc (Figure 9.1). Each snail has a single prominent valve. In most snails, this is a long, narrow, conical tube that is coiled off to one side, so that it resembles a screw. Of course, by now, you have come to expect that the story is bound to be far more complicated.

First, in some snails, the shell is so flared open that it resembles a cap or a shield, rather than a screw; take, for example, the limpets and the abalones of today. Then, there are the snails in which the coiling is not to the side; rather, each whorl lies directly in line with the one next to it, so that the coil is more like a garden hose coiled flat on the ground (this is called planispiral coiling).

Although basically univalved, some snails have a hard structure that serves to block the aperture of the shell when the animal withdraws for protection. Depending on the kind of snail, this operculum, as it is called, may be made of calcium carbonate, like the shell, or of a substance called conchiolin, which is rather like the chitin of an insect's exoskeleton. Not all snails have opercula, and no operculate gastropods have been reported from the rocks of the Cincinnati region.

The name "gastropod" literally means "stomach foot," and the body region of a gastropod called the "foot" generally is a broad, flat, creeping organ (Figure 9.1). The living animal has a prominent head, generally complete with one or two pairs of stalks or tentacles.

You may well have encountered a snail or a slug in your garden, but most gastropods are aquatic. The snail or slug in your garden probably was (or had been) devouring your plants; many gastropods are herbivores. Gastropods have a structure associated with the mouth that looks rather like a carpenter's rasp. The radula, as it is called, works like a rasp, too; the animal protrudes the radula from its mouth and scrapes bits of plant matter into the mouth.

But not all snails are herbivores. Indeed, some subsist on the flesh of others. An especially striking example from the local rocks is provided by brachiopod shells or other shells that each have a tidy, circular hole. In such cases, a snail used its radula to drill a hole in the shell of another animal-object: dinner.

Figure 9.2. *Cincinnatian monoplacophorans and a bellerophontid gastropod.* A. *Archinacella area Wahlman, USNM 40615, a monoplacophoran, Waynesville Formation, Waynesville, Ohio, a, dorsal, b, lateral, c, anterior, all* x *1.6. From Wahlman (1992, plate 3, figures 7, 9, 10).* B. *Helcionopsis striata Ulrich and Scofield, USNM 45827, a monoplacophoran, Richmondian, Marion Co., Kentucky, a, dorsal, b, oblique-lateral, c, lateral, all* x *1.7. From Wahlman (1992, plate 2, figures 1, 2, 3).* C. *Cyrtolites ornatus Conrad, USNM 265906, composite mold of a monoplacophoran, Corryville Formation, Cincinnati, Ohio, a, lateral, b, dorsal,* x *1.7. From Wahlman (1992, plate 6, figures 6, 7).* D. *Cyrtolites ornatus, MUGM 18120, two individuals somehow preserved with opposing apertures, each encrusted by bryozoan Leptotrypa clavacoidea. Cincinnatian.* x *1.7.* E. *Sinuites cancellatus (Hall), CMC IP 44304, a calcitic specimen of a monoplacophoran. Cincinnatian, Cincinnati, Ohio, a, anterior, b, anterolateral,* x *1.5. From Wahlman (1992, plate 11, figures 7, 9).* F. *Salpingostoma richmondensis Ulrich, USNM 45983, an internal mold of a bellerophontid gastropod. Whitewater Formation, Richmond, Indiana,* x *1.4. From Wahlman, 1992, plate 26, figure 2.*

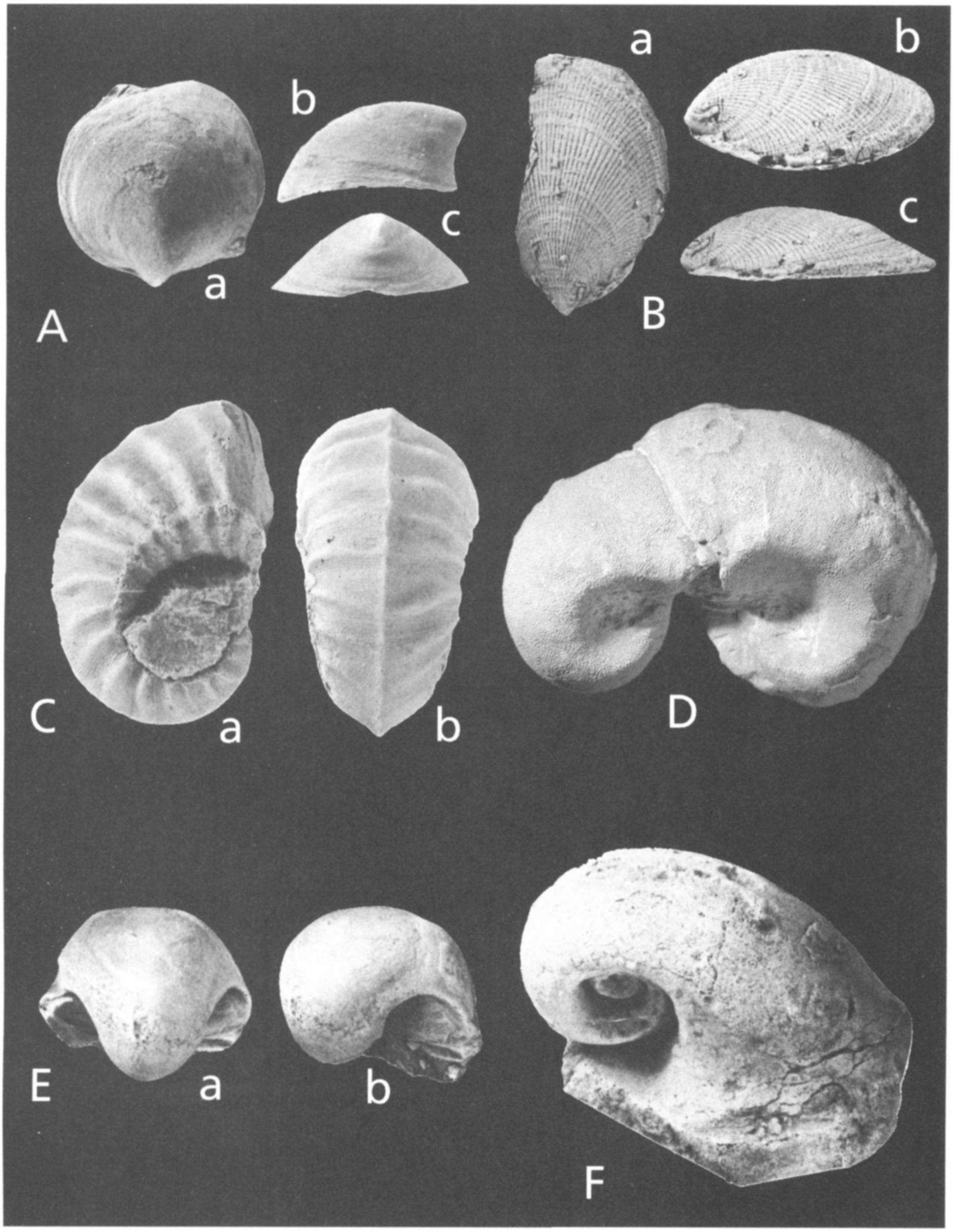
Most of the snail fossils in the rocks of the Cincinnati region consist of molds. The actual shell matter has been dissolved away, and all that is left is the sediment that originally filled or that surrounded the buried shell, or both. Exceptions to this generality are the snails of the genus *Cyclonema;* here, shell matter, not uncommonly, is present.

Gastropods of the type-Cincinnatian

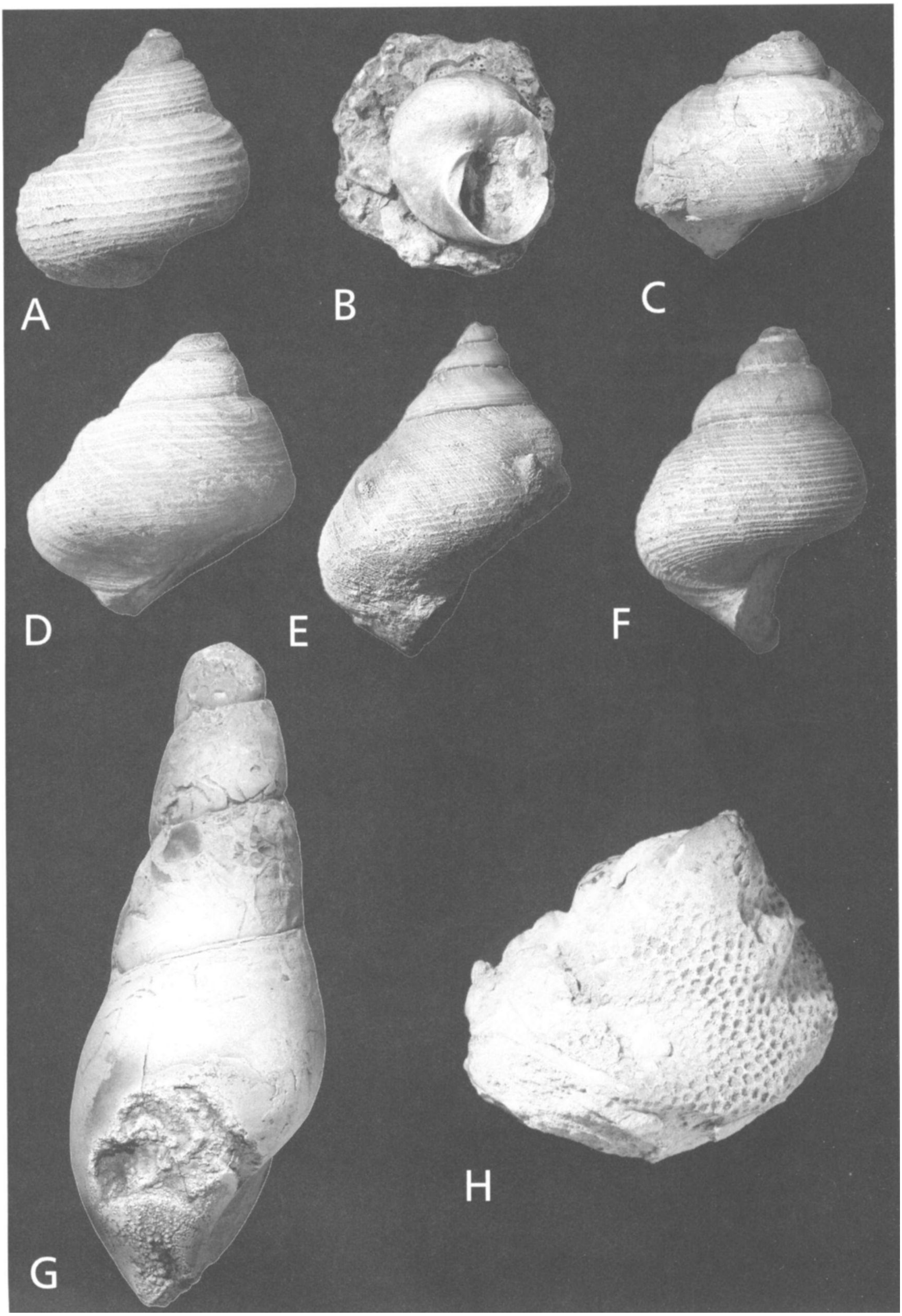
Snails (Figures 9.2, 9.3) are very common fossils throughout the Cincinnatian Series in its type area, but, because they generally are preserved only as internal molds, then- can be overlooked, and precise identification can be difficult. Nevertheless, snails undoubtedly placed an important role in the ecology of the Cincinnatian sea, especially in some environments where they were very abundant. Holland's compilation of Cincinnatian fossils lists sixty-three species of snails in twenty-three genera as occurring above the base of the Kope Formation (Holland 2005). Of these, sixteen species in nine genera belong to the planispirally coiled bellerophontids that were revised taxonomically by Wahlman (1992). of the other fourteen genera and forty-seven species, the genus *Cyclonema* accounts for eleven species, based on the 1970 study by Thompson (1970). Specimens of an additional platyceratid, which belong in *Naticonema,* occur in the type-Cincinnatian, but these have not been described in the scientific literature (Felton, pers. comm.; Bowsher 1955, plate 1). The remaining thirteen genera, including thirty-six species, have not been thoroughly revised in recent years, and, consequently, a conclusive statement about the total taxonomic diversity of Cincinnatian gastropods would be premature. Some of the most common gastropods are illustrated in Figure 9.3.

Specimens of *Cyclonema* are by far the best-preserved and most easily recognized Cincinnatian snails because their shells were calcitic rather than aragonitic in composition (Figures 9.3A-F). Individuals of *Cyclonema* are found in every formation of the type-Cincinnatian. Some species, such as C. *humerosum,* range from the Fairview through the Waynesville Formations (Thompson 1970), but others are more restricted within that range (Felton, pers. comm.) Thompson differentiated species of *Cyclonema* on the basis of shell shape, nature of the aperture, and ornament (for example, up to three sets of spiral ridges). Growth-lines parallel to the apertural margin cut across the spiral ornament to create a reticulate pattern. A quantitative study of variation in shell form and ornament within and among the many species and forms of *Cyclonema* would help to clarify the recognition of species and to determine how variation is related to depositional environment.

Specimens of *Cyclonema* are sometimes found attached to the upper surface or tegmen of crinoid calyces. This association between gastropods and crinoids is one of the best-known cases of interaction between species in the fossil record. In the type-Cincinnatian, specimens of both *Cyclonema* and *Naticonema* are found attached to the tegmens of crinoids, usually of *Glyptocrinus* and *Pycnocrinus* (see chapter 12). Because, in most specimens, the snail is positioned directly over the anal opening of the



crinoid, most workers have concluded that the snail led upon the partly digested feces of the crinoid. Bowsher interpreted this association as one of coprophagy and illustrated examples from the Cincinnatian (Bowsher 1955). Similar associations between related snails and crinoids are found from younger Paleozoic strata through the Permian, but those from the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Cincinnatian are among the oldest-known cases. Specimens of *Cyclonema varicosum* attached to *Pycnocrinus* are known from the Lexington Limestone, just below the Cincinnatian (Felton, pers. comm.). Whether all cases of snails attached to Paleozoic crinoids are instances of coprophagy has been debated; other possibilities include parasitism, predation, and commensalism (Baumiller 1990; Morris and Felton 1993). (In commensalism, individuals of the associated species gain some advantage while the host is unaffected. Given the size and location of the snails on the crinoid host, it is difficult to see how the host could remain unaffected.) A more complex association between Cincinnatian gastropods, crinoids, and tubes of *Cornulites* encrusting the snails was investigated by Morris and Felton (1993, 2003). These authors suggested that *Cornulites* gained an advantage by encrusting the snails that lived on the elevated crowns of the crinoids, either by sharing in the fecal feast or simply by virtue of the elevated position provided by the crinoid.

Most individuals of *Cyclonema* that are found are not attached to crinoids, suggesting that the association with crinoids was not obligate, and that specimens of *Cyclonema* were able to make their living in other ways. We lack direct evidence for the feeding habits of free-living specimens of *Cyclonema,* but the feeding habits of present-day gastropods may provide some clues. *Cyclonema.* along with the majority of taxa of Cincinnatian gastropods, is placed in the order Archaeogastropoda. Living archaeogastropods include many familiar forms, for example, limpets, abalones, and periwinkles. Most present-day archaeogastropods are herbivores that live by grazing on algal or bacterial coatings on the substratum, but some are predatory- on sponges or on microorganisms and organic detritus either by deposit feeding or suspension feeding (Wahlman 1992). There is no reason to suppose that type-Cincinnatian archaeogastropods could not have had a similar range of feeding habits.

One subgenus of Cincinnatian snails, *Subulites (Fusispira),* belongs to the order Neogastropoda; individuals of this taxon are notable each for having a high spire and large size (figure 9.3G). Present-day neogastropods include many familiar marine snails, for example, the whelks, the spiny murexes, and the venomous cones. Because most neogastropods are predatory, it is possible that the snails of *Subulites (Fusispira)* were predators.

Additional evidence that some type-Cincinnatian snails were predatory comes from circular holes found in brachiopods, as well as other fossils. Many present-day predatory snails attack their prey by "drilling" through the shell of the prey (usually a clam) and then inserting a proboscis that secretes digestive enzymes. The drilling is a combination of dissolution of the shell by acidic secretions and rasping by the radula. The resulting holes generally are perfectly circular, commonly with a beveled edge sloping inward, but there is much variation in size and form of the holes. Circular holes in type-Cincinnatian shells, chiefly brachiopods, have attracted the attention of many workers over the years, Fenton and Fenton (1931) first favored the interpretation that predatory snails were responsible for the borings. Bucher (1938) pointed out that bored brachiopods and pelecypods are very rare in the type-Cincinnatian, but described a thin bed

Figure 9.3. *Cincinnatian gastropods.* A. *Cyclonema varicosum Hall, CMC IP 51118, Cynthiana Formation, Lexington, Kentucky,* x *1.7.* B. *Cyclonema humerosum, Steven Felton collection, showing aperture. Grant Lake Formation, Brown Co., Ohio,* x *1.2.* C. *Cyclonema humerosum Ulrich, CMC IP 51117, Maysvillian, Cincinnati, Ohio,* x *1.6.* D. *Cyclonema bilix lata (Conrad), CMC IP 51116, Arnheim Formation, Cincinnati, Ohio,* x *1.7.* E. *Cyclonema sublaeve Ulrich, CMC IP 51114, Fairview Formation, Cincinnati, Ohio,* x *2.1.* F. *Cyclonema gracile striatulum Ulrich, CMC IP 51113, Kope Formation, Cincinnati, Ohio,* x *3.2.* G. *Subulites (Fusispira) Ulrich, CMC IP 51115, internal mold, Kope Formation, Kenton Co., Kentucky,* x *1.3. H. Paupospira moorei (Safford), MUGM 23292, encrusted by tabulate coral Protaraea richmondensis, Whitewater Formation, Preble Co., Ohio,* x *1.5. Note slit in aperture.*

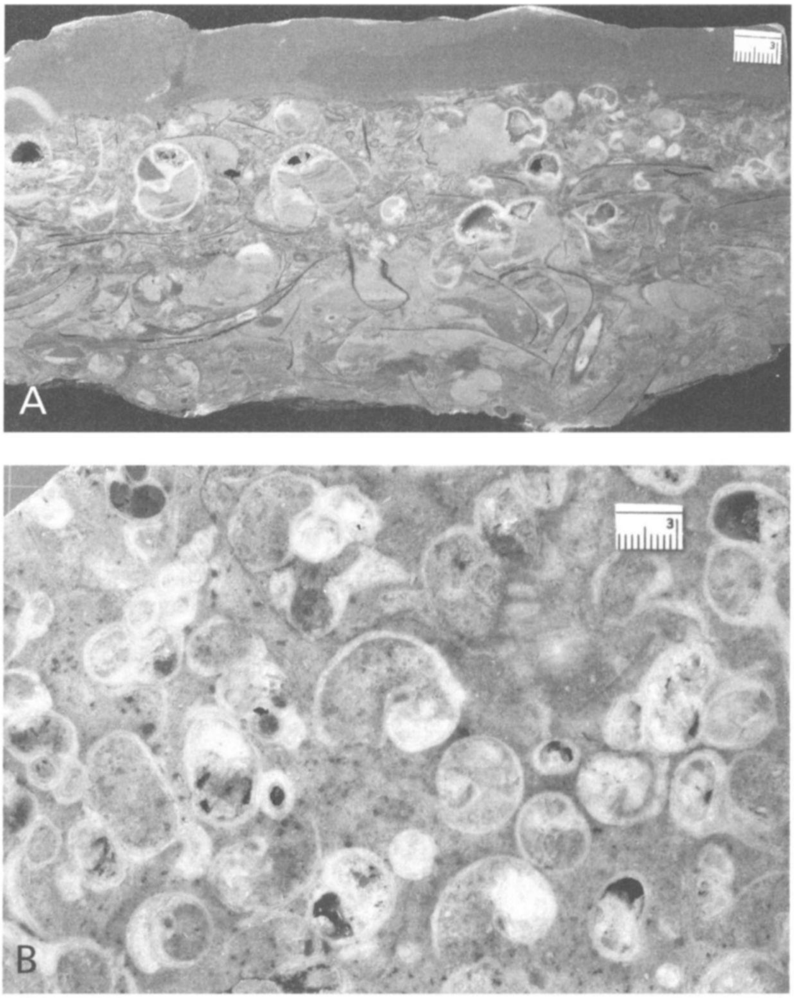


Figure 9.4. *Gastropod-rich beds.* A. *Miamitown Shale, Trammel Fossil Park, Sharonville, Ohio. Note shells with geopetal cavities (lower part filled with sediment, upper part filled with calcite crystals).* B. *Marble Hill Bed, Waynesville Formation, Trimble Co., Kentucky. Scale in mm.*

rich in individuals of the brachiopod *Onniella* from the Richmondian in which the frequency of bored shells is closer to the frequencies of bored shells in present-day settings. Carriker and Yochelson (1968) compared borings in Middle and Upper Ordovician brachiopods from Kentucky with present-day borings made by gastropods. Although they found many similarities between Ordovician and present-day borings, they concluded that gastropods were not necessarily responsible for the Ordovician borings. Kaplan and Baumiller (2000) suggested that the variations in borings found in Ordovician shells could result from many different borers. Their analysis of the *Onniella* shell bed revealed a preference in boring for the convex pedicle valve. However, controversy continues to rage over the interpretation of these borings. Wilson and Palmer (2001) pointed out that, in the same *Onniella* shell bed, some borings were drilled outward from the interior of disarticulated valves, and others penetrate not only the margins of valves but also the adjacent substratum. Their interpretation was that these borings are not predatory borings at all, but rather were drilled into the shells cemented into a hardground surface as dwellings of unknown organ-

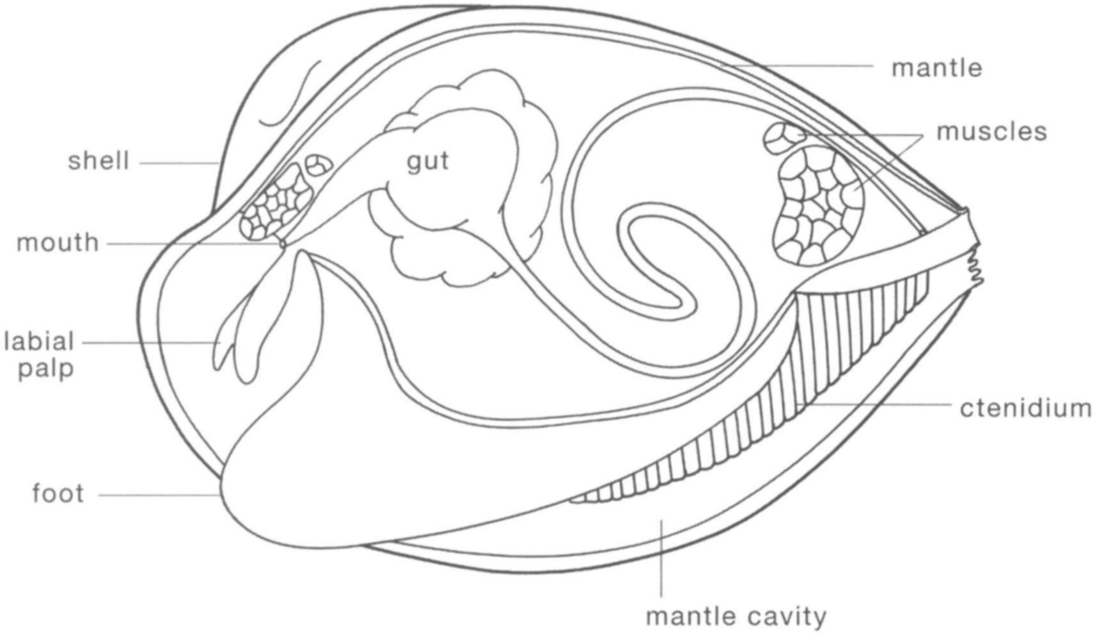


Figure 9.5. *Pelecypod mollusc, showing internal features. Drawing by Kevina Vulinec.*

isms. In a reply, Kaplan and Baumiller (2001) stated that their samples are not from hardgrounds, and they continued to regard borings as predatory in nature. The ongoing arguments show that borings in the type-Cincinnatian are probably the result of many types of behavior by different organisms, and, although not all can be assumed to be predatory, nevertheless some were very likely produced by drilling predation very similar to gastropod drilling in present-day environments.

Cincinnatian gastropods sometimes are found in great abundance in thin beds—almost to the exclusion of other fossils. Although such beds occur in many units in the section, two occurrences deserve special note. One is within the Miamitown Shale, which is Maysvillian in age, and the other is the Marble Hill Bed (Richmondian) (Figure 9.4). The Miamitown Shale is a thin, shale-dominated formation that attains a maximum thickness of five meters at Miamitown, near the Great Miami River, and thins to less than one meter near Cincinnati (Dattilo 1996). Within the Mianiitown is a layer, nicknamed the "gastropod shale," about 1.5-2 meters thick, characterized by abundant molluscs, including pelecypods, the monoplacophoran *Cyrtolites,* and gastropods (Figure 9.4A). Near the top of this interval is a thin limestone that is packed with gastropods, mostly of ***Paupospira bowdeni*** (referred to ***Loxoplocus*** in older literature), preserved as internal molds. The so-called "gastropod shale," along with the thin limestone, can be traced from Miamitown, in Ohio, to northern Kentucky, a distance of 20 km. The paleoenvironmental significance of the snail-rich Miamitown bed is not entirely clear. The overlying Bellevue Limestone, with its thin, wavy beds containing large brachiopods and bryozoans, indicates very shallow water, shoaling conditions. Thus the Miamitown could represent a slightly deeper environment, perhaps lagoons sheltered between shell-rich shoals of the Bellevue. Organic-rich muds that accuniu-

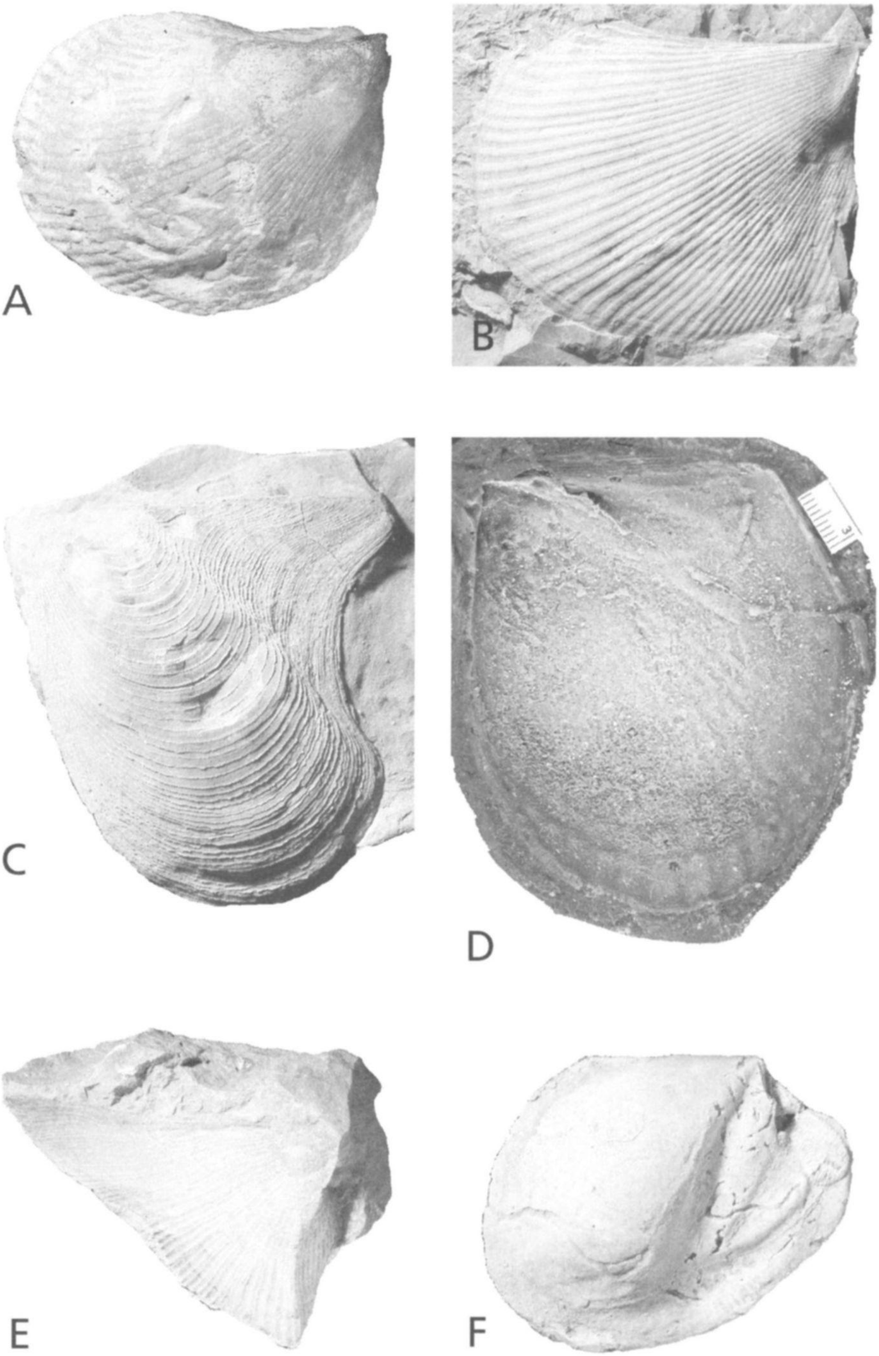


Figure 9.6. *Cincinnatian pelecypods.* A. *Ambonychia sp., MUGM De549A, right valve, Cincinnatian, no locality information,* x *0.6.* B. *Ambonychia cultrata (Ulrich), MUGM 29546, right valve, Waynesville Formation, Butler Co., Ohio,* x *0.8.* C. *Carotidens demissa (Conrad), MUGM 29431, left valve, Corryville Formation, Clermont Co., Ohio,* x *1.1.* D. *Anomalodonta gigantea Miller, CMC IP 35898, internal mold of right valve, Waynesville Formation, Warren Co., Ohio,* x *0.8.* E. *Opisthoptera casei (Meek and Worthen), MUGM 23392, right valve, Whitewater Formation, Preble Co., Ohio,* x *0.9.* F. *Ischyrodonta truncata Ulrich, MUGM 15066, internal mold of right valve, Whitewater Formation, Butler Co., Ohio,* x *1.1.*

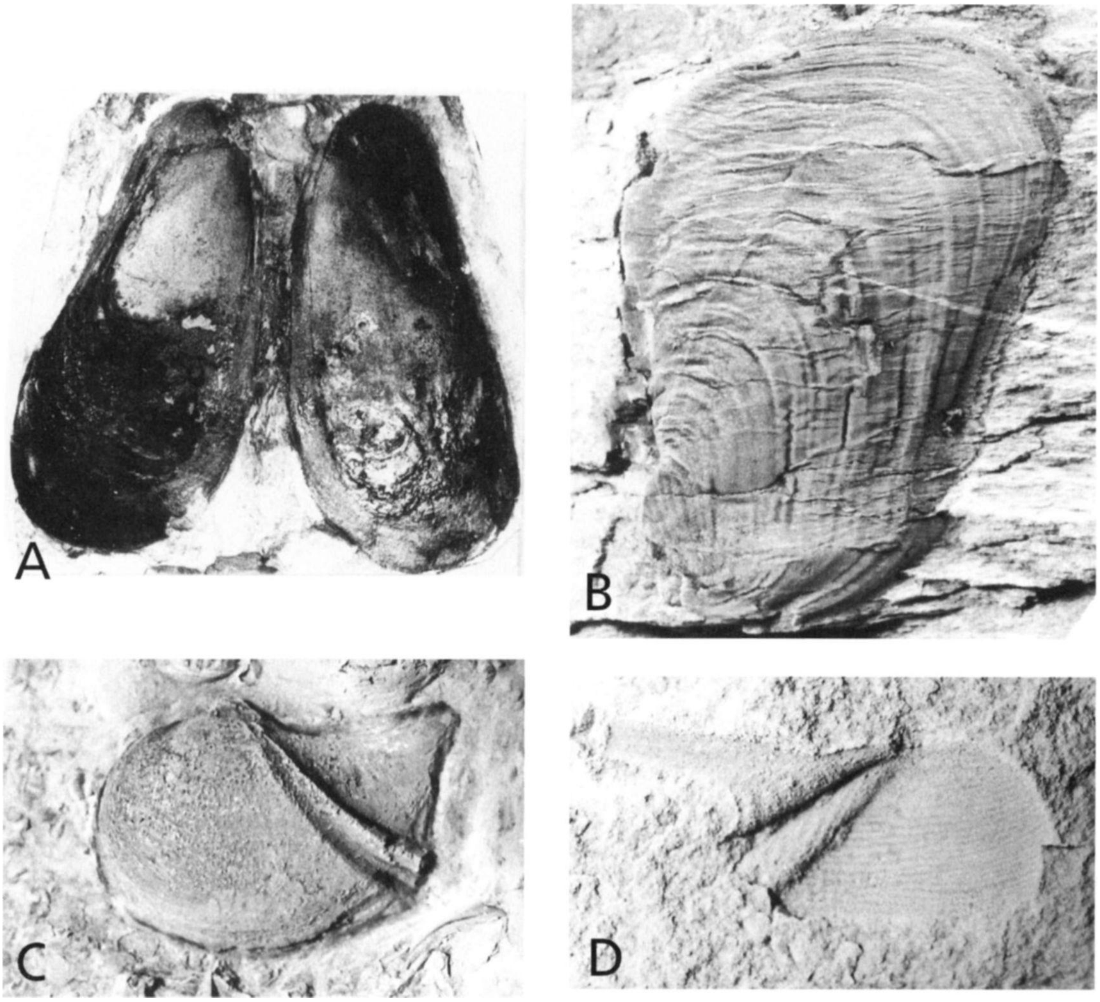


Figure 9.7. *Cincinnatian pelecypods and rostroconchs.* A. *Modiolopsis sp. cf. M. modiolaris (Conrad), USNM 46230, "butterflied" specimen with black organic film and remnants of ligament, Fairview Formation, Covington, Kentucky,* x *0.85. From Pojeta (1971, plate 15, figure 6).* B. *Modiolopsis modiolaris (Conrad), USNM 46719, internal mold preserved at right angles to bedding and highly foreshortened, Fairview Formation, Cincinnati, Ohio,* x *2.4. From Pojeta et al. (1986, plate 17, figure5).* C. *Technophorus faberi Miller, USNM 07219, left-lateral view, Kope Formation, Covington, Kentucky,* x *3. From Pojeta and Runnegar (1976, plate 11, figure 3).* D. *Technophorus milleri Pojeta and Runnegar, MUGM 6848, right-lateral view, Whitewater Formation, Butler Co., Ohio,* x 5*.1. From Pojeta and Runnegar (1976, plate 14, figure 7).*

lated in the lagoons could have provided a habitat favorable for snails, but hostile to filter-feeding brachiopods and bryozoans.

The Marble Hill Bed is another remarkable occurrence of gastropods, in which limestone lenses up to about one meter thick are packed with specimens of three species of gastropods, *Paupospira bowdeni, P. tropidophora* (Meek), and P. *moorei* (Ulrich) (Felton, pers. comm.; figure 9.4B). This bed occurs near the top of the Cincinnatian in the Rowland Member of the Drakes formation (following stratigraphic nomenclature adopted in Ken-

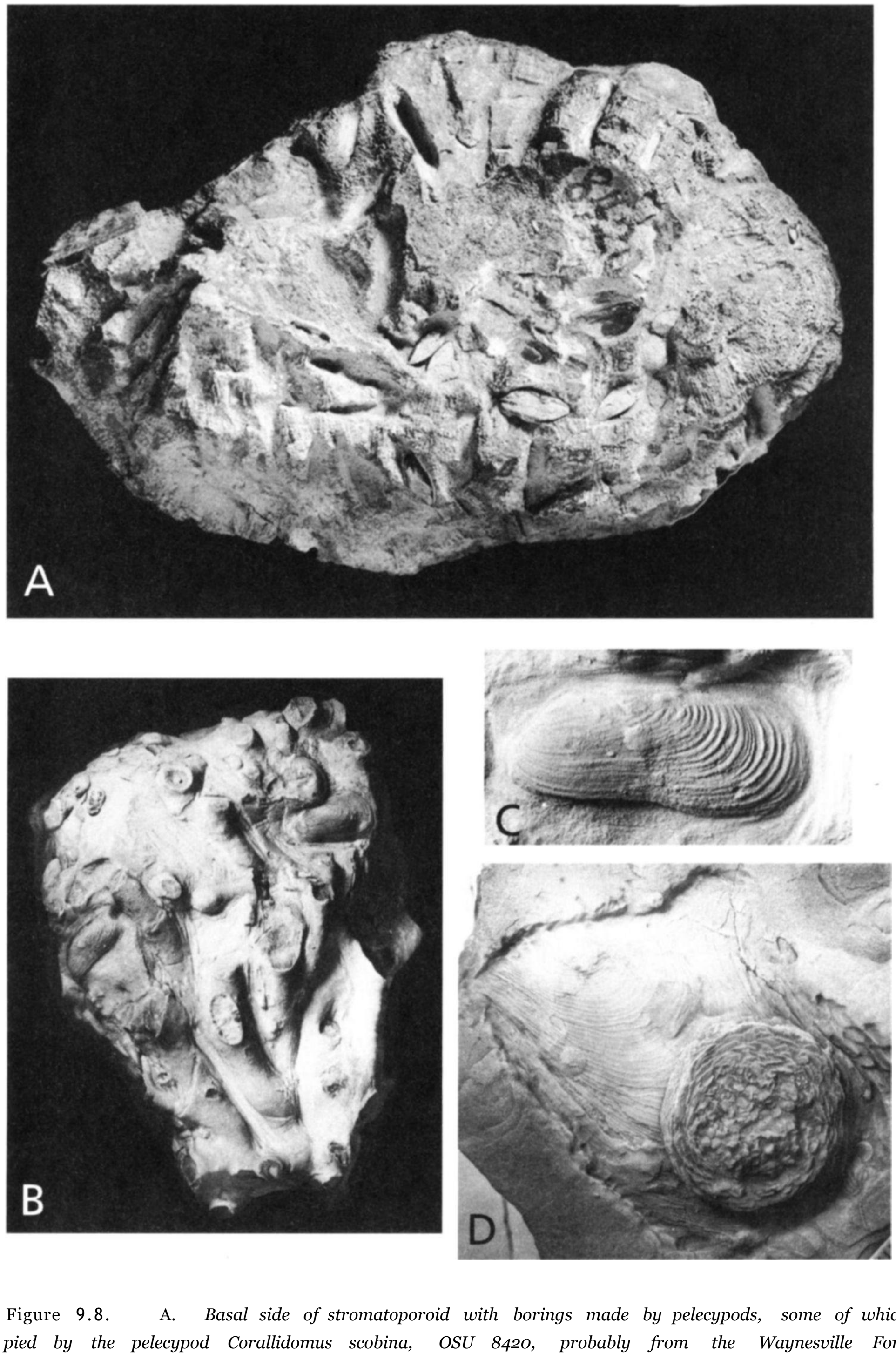


Figure 9.8. A. *Basal side of stromatoporoid with borings made by pelecypods, some of which are occupied by the pelecypod Corallidomus scobina, OSU 8420, probably from the Waynesville Formation, Brown Co., Ohio, x 0.6.* B. *Corallidomus scobina, USNM 70458, bryozoan colony with pelecypods and inarticulate brachiopod, Trematis sp., in life position among bryozoan branches, Waynesville Formation, Clinton Co., Ohio, x 0.7. From Pojeta (1971, plate 16, figure 5).* C. *Corallidomus scobina, USNM 70458, left valve of specimen attached to bryozoan colony shown in* B, x *2.8.* D. *Carotidens sp., USNM 162734, left valve with edrioasteroid Isorophus cincinnatiensis and encrusting bryozoans, Corryville Formation, Clermont Co., Ohio, x 1.4. From Pojeta (1971, plate 10, figure 15).* A *and* C, *courtesy of John Pojeta, Jr.*

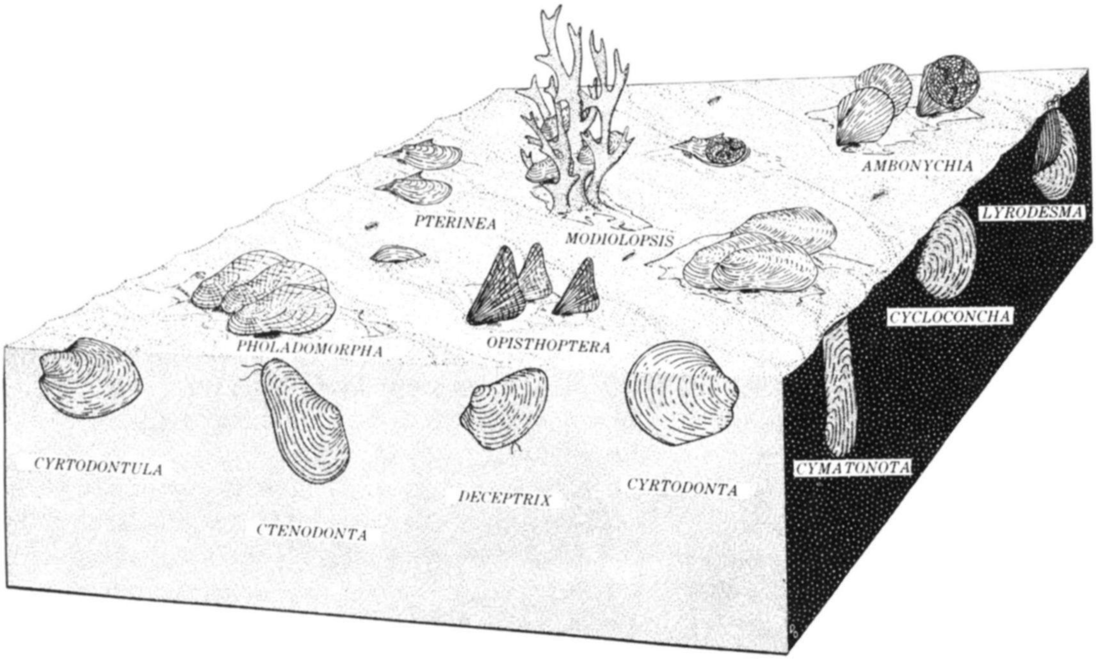


Figure 9.9. *Life habits of Late Ordovician pelecypods. From Pojeta (1971, figure 9).*

tucky; this is approximately equivalent to the top of the Waynesville Formation as used in other literature). The Marble Hill Bed is exposed near Bedford, in Trimble County, Kentucky, and adjacent southeastern Indiana (Hattin et al. 1961; Swadley 1979). Like the Miamitown snail bed, the Marble Hill Bed lies in close stratigraphic proximity to rocks of very shallow water depositional environments. Swadley (1979) interpreted the Marble Hill Bed as a complex of offshore shoals and tidal-channel deposits along the margin of a shallow lagoonal area adjacent to intertidal mudflats.

Pelecypods: a.k.a., The Bivalves

This is the group that, today, is represented by clams, mussels, scallops, cockles, oysters, and their relatives (Figures 9.5,9.6). These are all bivalved molluscs—each shell consists of two valves. (For that reason, some folks use a different name for the class, *viz.,* Bivalvia. Although such usage may be logical, it belies the fact that there are other bivalved animals that are not at all closely related to the molluscs. Examples include the members of phylum Brachiopoda and the ostracods, of phylum Arthropoda.)

This, of course, brings up the question: how does one tell the remains of the several major groups of bivalved organisms from one another? From our perspective, in the type-Cincinnatian, it is important to be able to differentiate pelecypods from brachiopods. These latter are very common in the local rocks, and their shells fall into the same size range as do those of pelecypods. One clue commonly is provided by the state of preservation. Generally, in the Cincinnati region, pelecypods are more poorly preserved than are brachiopods (see chapter 8) and occur as molds. One of the not-uncommon modes of preservation is one called a composite mold. Here, the aragonite shell is gone, and the external and internal molds are superimposed onto one another, so that the features of the exterior of a valve and those of the interior are visible in essentially a single surface. The shell matter of the living pelecypod so represented must have been fairly high in organic material, because the composite mold commonly includes a carbon film where the shell substance once was (Figure 9.7A).

Although preservation may provide a clue, the real way to identify the pelecypods is by reference to the morphology of the shell. The plane of symmetry in a type-Cincinnatian pelecypod is between the valves, whereas, in an ordinary articulate brachiopod, the plane of symmetry runs across each valve perpendicular to the hinge (see Figure 8.1).

Of course, the fossils in the rocks in and near Cincinnati have been there for hundreds of millions of years. Many things might have happened during that span of time. Sometimes, for example, the dead shell was buried in other than a living position. As soft sediments built up ever deeper on the sea floor, they became compressed into rock. In some instances, the original bilateral symmetry of the once-living animal (and, hence, of the shell) was distorted by the pressure, so that the shell appears skewed. In such instances, the original symmetry may not be immediately obvious.

Pelecypods of the Type — Cincinnatian

Because pelecypods are commonly preserved as molds in the type-Cincinnatian, they are easily overlooked and can be difficult to identify. Indeed, many specimens are nothing more than clam-shaped blobs. One exception is individuals of the pterioid genus *Carotidens* that are preserved as calcitic shells throughout the type-Cincinnatian (Figure 9.6C). Forms preserved as molds that are very common are of the genus *Ambonychia* (Figures 9.6A, B) and the genus *Modiolopsis* (Figures 9.7A, B). Occasionally, pelecypods are preserved in life position, as in the case of the burrowing *Modiolopsis* (Figure 9.7B), or *Corallidomus,* the earliest-known case of pelecypod boring into a hard substratum (Figures 9.8A, B; Pojeta and Palmer 1976). Epizoa attached to one valve of an articulated pelecypod may also indicate the preferred life orientation of the pelecypod (Figure 9.8D).

Including the commonly encountered forms, a considerable diversity of pelecypods has been documented in the type-Cincinnatian. Holland (2005) listed 164 species of pelecypods, in thirty-eight genera, for the Ordovician rocks of the Cincinnati region. However, the originally described specimens of several genera and numerous species are either poorly pieserved, of uncertain taxonomic status, or both, so that the actual diversity is surely lower. Robert Frey (1987a) traced the diversity and abundance of pelecypods in the formations of the Cincinnati region. In the shales, siltstones, and thin limestones of the Edenian (Kope Formation), he recorded fourteen genera. In Maysvillian through early Richmondian shales and limestones, he found sixteen genera. In one shale bed of the Waynesville Formation he found twenty-two species of pelecypods. In Mavsvillian limestones, pelecypods are generally less abundant than brachiopods and bryozoans, but in the Richmondian rocks, they occur in higher diversity. In Richmondian limestones, Frey recorded twenty genera of pelecypods.

Thus. Frey's work documented the spread of pelecypods from mainly clastic (shale-rich) sedimentary environments in early and middle Cincinnatian time into carbonate environments in the late Cincinnatian. The abundance and diversity of pelecypods in the type-Cincinnatian demonstrate that, even early in their evolutionary history, pelecypods occupied marine environments in a variety of offshore settings, heralding their subsequent diversification and increasing abundance in the late Paleozoic and Mesozoic (A. I. Miller 1989).

By Late Ordovician time, pelecypods had exploited almost the full range of living habits found in present-day forms (Figure 9.9). Most commonly, Late Ordovician pelecypods used byssal threads for attachment to objects on or within the sediment—similar to present-day mytilids (mussels). Epibyssate forms, such as *Ambonychia,* attached at the sediment surface or nestled within the branches of bryozoans. Endobyssate forms, such as *Modiolopsis* and *Pseudocolpomya,* attached to shell fragments or sediment grains just below the sediment surface and extended the shell for filter feeding. Free-burrowing forms included deposit feeders (who fed on organic particles within the sediment), such *as Ctenodonta,* and shallow infaunal filter feeders, such as *Ischyrodonta.* As mentioned above, the ability to bore into hard substrata was first seen in the Late Ordovician *Corallidomus* (Figures 9.8A-C). Ordovician pelecypods had not yet developed the elongate siphons and more muscular foot that enabled members of the class to exploit deeper and more rapid burrowing after the end of the Paleozoic. Likewise, Ordovician pelecypods had not acquired the habit of cementing the shell to a hard substrate, as seen in present-day oysters and other pelecypods that inhabit coral reels. It is also interesting to note that Ordovician pelecypods lacked the development of thick, corrugated shells and projecting spines found in present-day forms such as the "giant clam" (of genus *Tridaena)* or "spiny oysters" (of genus *Spondylus).* Selective pressure for the evolution of these kinds of protective morphologies possibly was absent in the Ordovician sea because shell-crushing (durophagous) predators had not yet evolved.

Cephalopods

The squids, cuttlefish, and octopi are the most familiar cephalopods in today's world, and they certainly are not heavily armored. For example, members of genus *Octopus* have no shells at all, and those of the squid and cuttlefish are internal. This is in strong contrast to the fossil cephalopods of the Cincinnati region—all known kinds had their soft parts protected by an external shell. (It happens that there is a single genus of present-day cephalopods that each has an external shell, namely, *Nautilus,* shown in Plate 4. This is the sole remnant of the vast hordes of externally shelled cephalopods that once coursed through the seas of our planet.)

The word "cephalopod" literally means "head-foot," which seems singularly appropriate for a creature that is characterized by a prominent head and a number of highly flexible tentacles. Although such soft parts have not been found preserved in the rocks of the Cincinnati region, the cephalopods probably had prominent heads and tentacles during life. What remain of the local fossil cephalopods are their external shells.

In the majority, the shell is a long, straight, conical tube closed at the narrow end. (Straight shells are said to be orthoconic.) There are, however, some in which the shell is curved or even coiled. In most of the kinds of cephalopods present, there are partitions that go across the tube for part of its length; these are called septa (singular, septum). The chambers that are separated by the septa are called camerae (singular, camera). At the larger end of the conical tube that comprises the shell is a portion in which there are no septa. This is called the body chamber. The camerae are connected to one another by a tube that runs through all the septa from the body chamber to the first camera at the tip of the cone; this inner tube is called the siphuncle. The line along which a particular septum meets the outer wall of the shell is called a suture.

All present-day cephalopods live in the oceans, and there is every reason to conclude that the fossil forms were marine creatures, too. During life, the aptly-named body chamber was occupied by the bulk of the soft parts of the cephalopod animal, and the other camerae apparently contained gas. (In present-day *Nautilus,* the gas is similar in composition to air, but without the oxygen.) Such a gas-filled shell would have served as a float, buoying the animal up in the water and, depending on how much gas was in the camerae, allowing the animal to stay at a particular water depth without the effort of swimming upwards or downwards. At great depths, of course, there is tremendous water pressure—so much pressure, in fact, that such a gas-filled shell would have been crushed. Thus, extinct cephalopods with external shells almost certainly lived in water no deeper than a few hundred meters, and most of them probably swam in water a good deal shallower than that.

Most present-day cephalopods are active swimmers. They take water into the mantle-cavity, and they expel it through a spout called the hyponoine which is located below the tentacles and mouth (Plate 4A). This causes the animal to move in the opposite direction; the hyponome, however, is very flexible, so that the animal can swim in almost any direction. We assume that extinct cephalopods swam the same way.

All cephalopods today are predators. There is no reason to suppose that extinct ones were any different. In fact, there are a few specimens known in which gut contents are preserved; these confirm that at least some extinct cephalopods ate other organisms. (Alas! No such specimens are known from the rocks of the Cincinnati region.)

All of the cephalopods known from the rocks of the area around Cincinnati commonly are lumped together as "nautiloids." In this sense, the assemblage of animals so denoted is a "waste basket" in that it includes animals from a number of different taxa that do not seem to be closely related biologically. (It is rather like lumping together horses, cattle, pigs, deer, rhinoceroses, tapirs, and so on, into "hoofed mammals.") What is worse, there is a formal taxon of cephalopods called subclass Nautiloidea. Part of the problem is that the "nautiloids," in the general sense (which includes those that actually belong in the Nautiloidea), can look rather similar externally. However, when well-preserved specimens are carefully broken or cut open, meticulous study reveals that a number of strikingly different

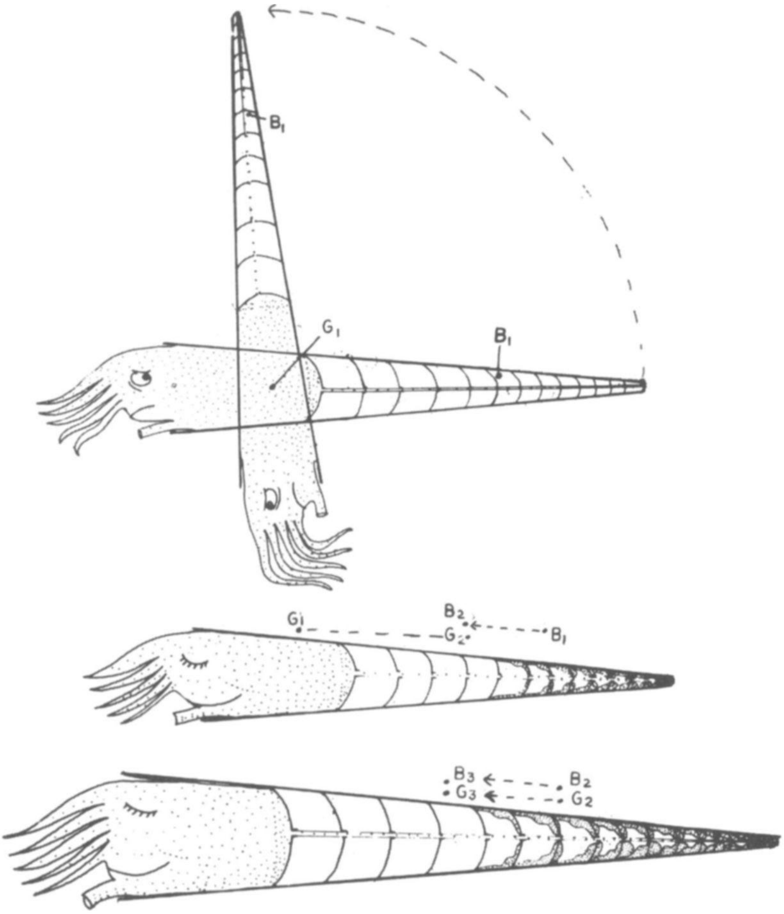


Figure 9.10. *How nautiloids attained happiness. In the top diagram, the center of gravity,* G, is *inferred to lie in the body chamber of the nautiloid, and the center of buoyancy,* 6, to *lie in the gas-filled phragmocone, forcing the animal into a vertical, head-down position. In this position it could not swim efficiently. In the middle diagram, the formation of calcareous cameral deposits in the apical part of the phragmocone should result in the center of gravity and center of buoyancy shifting toward the midpoint of the animal's length* (G_2 B_2), *permitting stability in a horizontal orientation. In the lower diagram, the nautiloid has grown, with additional cameral deposits formed closer to the head, so that the centers of gravity and buoyancy* (G_3,B_3) *maintain a stable horizontal orientation. See text for further discussion. From Flower (1957, figures 4-6) and reprinted by permission of the Geological Society of America.*

kinds of "nautiloids" are recognizable. This presents a double dilemma to the fossil collector. To cut a specimen open and study it carefully not only requires specialized equipment (which is expensive), but also training and experience. Moreover, one needs well-preserved material—and not many folk want to cut up that prized, "perfect" specimen. Sometimes taphonomy is kind, however, and a specimen is found that just happens to have been broken or been eroded in such a way that the inner secrets are revealed. Much of the time, however, it is tough to assign a given specimen to a higher taxon without damaging it.

Many of the internal details of the "nautiloids" seem to he related to hydrostatics, that is, to the position and orientation of the living animal in the water. Recall that the shell of most "nautiloids" in the rocks of the Cincinnati region is a long, straight cone. The bulk of the soft parts of the animal occupied the body chamber, whereas the part of the animal subdivided into camerae (technically called the phragmocone) seems mostly to have been filled with gas. Thus, the part of the shell toward the apex of the cone would have been lighter than the other end, which contained the weight of the body. The result would have been that the cone would have tended to be oriented in the water with its blunt end, and, hence, aperture, down—and, potentially, the animal's face in the mud of the sea floor.

Figure 9.11. *Cincinnatian orthoconic nautiloids.* A-C *from Davis and Mapes (1996), courtesy of the Ohio Department of Natural Resources Division of Geological Survey.* A, B. *Treptoceras duseri (Hall and Whitfield), Cincinnatian, scale bars = 1 cm.* A. *OSU 47422, internal mold of part of phragmocone and living chamber.*

B. *OSU 47417, part of external shell, with dark longitudinal lines which are remains of what, in life, were color bands.* C. *Cameroceras inaequabile (Miller), internal mold of portion of siphuncle, OSU 47420, Cincinnatian, scale bar = 1 cm.* D. *Endoceras sp., MUGM 29579, internal mold of part of phragmocone and siphuncle, Liberty Formation, Butler Co., Ohio, scale in mm.* E. *Gorbyoceras duncanae Flower, CMC IP 31393, external shell with fine longitudinal lines, Whitewater Formation, x 1.4.*

Apparently, from the point of view of organic evolution, this was not a beneficial situation. At least in a number of evolutionary lineages, changes in the shell occurred that solved this problem in one way or another, to a greater or less extent.

Before proceeding further on this tack, we need to talk a bit about organic evolution, per se—lest we go astray into thinking that, because the living cephalopod did not "like" its face in the mud, it deliberately evolved its shell morphology and structure to avoid that condition.

As far as is known, the volition of organisms has no effect on the organic evolution of a lineage. Thus, no creature can will the organic evolution of its descendents to go into any particular direction, no matter how beneficial (or enjoyable?) that direction might prove to be. Rather, it a particular direction means that more creatures will survive to pass their genes on to future generations, then the organic evolution of a lineage will tend in that direction. This mechanism is called organic evolution by natural selection, or natural selection, for short. Some paleontologists and other biologists speak of evolutionary "strategics" whereby a lineage "solves" some particular "problem." These are figures of speech. They are, in tact, generalization of what changes actually are seen in the fossil record of the particular lineage. they definitely do not imply that organisms perceived a problem and willfully evolved to solve it.

Let us return to the type-Cincinnatian. One way to bring the shell of an orthoconic cephalopod into a horizontal orientation would be to add weight to the phragmocone (figure 9.10). This was done in various ways in various lineages; there are two main categories in the "nautiloids":

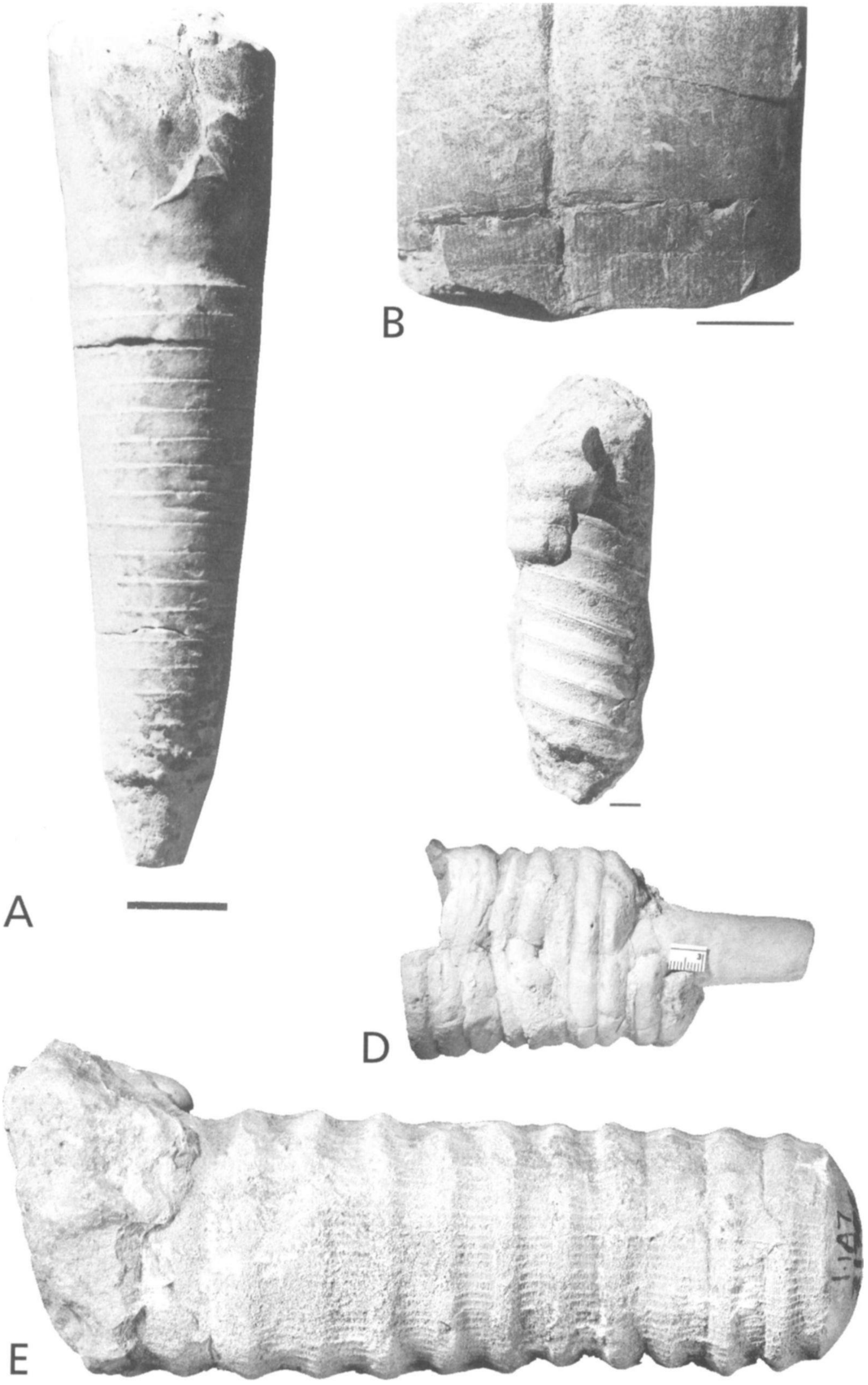
1. deposition of calcium carbonate within the camerae (result: cameral deposits);
2. deposition of calcium carbonate within the siphuncle (result: siphuncular deposits).

Whether these deposits are present, and, if so. where in the shell they occur and what form they take are very important in determining the proper taxonomic position of a given fossil. Siphuncular deposits occur in an especially great variety of configurations. In the subclass Endoceratoidea, for example, the siphuncular deposits comprise a Series of cones stacked each inside the next, with the larger end toward the aperture of the shell; these are called endocones.

Another way to "solve" the orientation "problem" would be to bring the center of buoyancy (resulting from the gas in the camerae) above the center of gravity (resulting especially from the mass of the animal in the body chamber). The most obvious way to do this would be to coil the shell so that the body chamber hangs beneath the gas-filled phragmocone; the present-day *Nautilus* is the product of such an evolutionary lineage.

Cephalopods of the Type — Cincinnatian

Nautiloid cephalopods are common fossils throughout the type-Cincinnatian. they generally occur as internal molds of partial phragmocones. Because the original aragonitic shell material was not preserved, the qual-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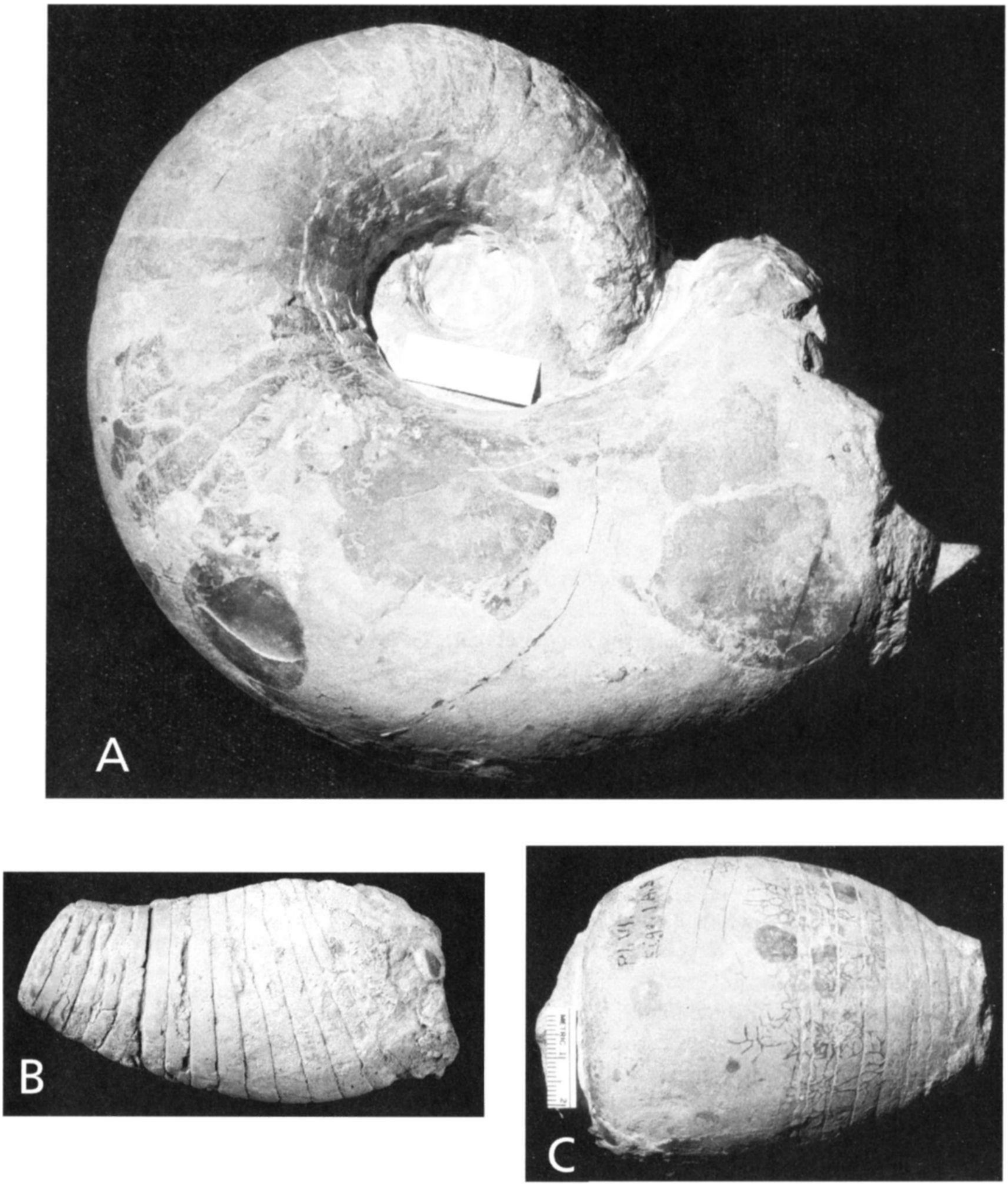


ity of nautiloid preservation is often poor, making identification difficult. However, exceptional preservation of nautiloids in a 1.5-meter-thick shale or claystone within the Waynesville formation formed the basis for a detailed study of type-Cincinnatian nautiloids by Robert C. Frey (1988,1989) that provided unique insight into the paleoecology of Cincinnatian nautiloids. This shale, informally called the ***"Treptoceras duseri*** shale" for the species of the most abundant nautiloids, occurs in Warren and Clinton counties of Ohio. Frey reported a total of twelve species of nautiloids, in eight genera, from this unit, of which three species of ***Treptoceras*** accounted for 76 percent of the 302 specimens found. Specimens of other species are much less abundant; included here are the cyrtoconic forms (having curved shells) *Manitoulinoceras tenuiseptum* and *M. williamsae* (8 percent), *Oncoceras delicatum* (4 percent), *Zittelloceras russelli,* and Z. *williamsae* (<1 percent), longiconic forms (having long, tapering, straight shells) tentatively assigned to genus *Isorthoceras* (6 percent), the endocerid *Cameroceras inaequabile* (6 percent, having a wide siphuncle infilled with conical deposits), the orthocerid *Gorbyoceras curvatum* (<1 percent, an orthoconic form), and the ascocerid *Schuchertoceras obscurum* (<1 percent, a form that lost part of the phragmocone during growth to maintain stability). The material of the outer wall of each shell was preserved only when encrusted by bryozoans, but the septa and siphuncular structures of the shell interiors were replaced by calcite. Body chambers and phragmocones were infilled with claystone, but, in some cases, the camerae remained empty or were infilled with calcite crystals. These preservational features led Frey to conclude that the nautiloid assemblage was buried in situ as complete, empty shells. Removal of encrusting bryozoans revealed the remarkable preservation of remnants of color patterns on the exterior of the shell. In contrast to shells of the present-day *Nautilus* that are known to float after death and drift with currents, the thinner shells and septal morphology of these Ordovician nautiloids suggest that dead animals sank to the bottom.

The assemblage probably is a good representation of the living nautiloid community, in which individuals of different species had distinctive, specialized modes of life. Longiconic forms probably were active swimmers close to the sea floor, whereas cyrtoconic forms may have lived closer to the substratum, perhaps crawling or swimming in short bursts. With no fish on the scene during the Cincinnatian, nautiloids were undoubtedly the top predators. The association in the so-called *Treptoceras duseri* shale of nautiloids with many complete trilobites, similar to other trilobite-nautiloid assemblages in the Ordovician of North America, suggests a biotic relationship between the two groups (Frey 1989). Individuals of present-day *Nautilus* each possess jaws that consist both of organic and mineralized components; on the other hand, the jaws of the squids of today's oceans consist exclusively of organic material, and, hence, would not be preserved ordinarily. Although jaw structures in the Ordovician nautiloids have not been found, it is possible that they possessed organic jaws by which they could have attacked prey such as trilobites. Interestingly, apparent wounds have been found in trilobites, for example, of genus *Isotelus,* from the "7. *duseri* shale" that could have resulted from attacks by nautiloid predators (Frey 1989; Babcock 2003). Other instances of injuries possibly caused by bites of nautiloids occur in brachiopods (Alexander 1986), gastropods (Felton, pers. comm.), and crinoids (Donovan and Schmidt 2001).

The association of specimens *of Treptoceras,* of the endocerid *Cameroceras,* and of *Oncoceras* is characteristic of Mavsvilllian-to-early-Richmondian shales in the Cincinnati region and elsewhere in eastern North America (Figure 9.11; Frey 1989,1995). A nautiloid fauna of much greater diversity is well known from Late Ordovician strata of the same age from a wide area of North America to the west and north, closer to the paleoequator, in an envi-

Figure 9.12. *Upper Cincinnatian (Richmondian) nautiloids.* A. *Charactoceras baeri (Meek and Worthen), MUGM 29591, Whitewater Formation Preble Co., Ohio, scale bar = 2 cm. Compare to present-day Nautilus, Plate 4.* B. *Beloitoceras amoenum (Miller), CMC IP 24415, internal mold of phragmocone of a cyrtoconic form, Whitewater Formation, Butler Co., Ohio,* x *1.* C. *Diestoceras eos (Hall and Whitfield), MUGM 382, internal mold of partial phragmocone and body chamber, Whitewater Formation, Preble Co., Ohio, scale in mm.*

ronment of predominantly limestone deposition (Frey 1989,1995). There are two incursions of this "tropical fauna" into the Cincinnati Arch region: the first during the Edenian, and the second, along with a host of other species of invertebrates, during middle-to-late Richmondian time (Frey 1989). The oldest Richmondian elements of this "tropical" nautiloid assemblage are seen in the Waynesville "*Treptoceras* ***duseri*** shale" in the form of specimens of *Sehuehertoceras ohscurum* and *Gorbyoceras curvatum* (Frey 1985,1995). Richmondian limestone-rich units, such as the Drakes, Saluda, and Whitewater Formations contain a diverse nautiloid fauna that represents the peak of this "Richmondian invasion." According to Flower (1946) and Frey (1995), this fauna totals sixty-five species in twenty-four genera, of which twenty species are common. Some characteristic forms are *Narthecoceras dunni* (Frey, 1981) and *Gharactoceras, Diestoceras,* and *Gorbyoceras,* shown in Figure 9.12.

Nautiloid Trace Fossils?

The late Rousseau H. Flower, one of the most prolific researchers on Paleozoic nautiloid cephalopods, was inspired by type-Cincinnatian cephalopods as the first doctoral student (Ph.D., 1939) of Kenneth E. Caster at the University of Cincinnati. In a 1955 paper, Flower drew attention to the tact that, despite the abundance of cephalopods in the Paleozoic fossil record, there were virtually no reports of trace fossils attributed to activities of nautiloid cephalopods. He went on to illustrate two type-Cincinnatian trace fossils that he concluded represented interactions of nektonic nautiloids with the sediments of the sea floor. Flower interpreted the common "turkey track," a trough-like impression now called *Trichophycus* (see chapter 14, Figure 14.1E) to result from a nautiloid ploughing into the bottom. In a rare case, a nautiloid rested at the end of one such trough. He showed a sketch of a bedding surface, two to three meters across, on which main troughs were oriented radially around a concentration of fossil debris, which suggested to him a feeding pattern. Flower illustrated another trace that consisted of a horseshoe-shaped pattern of shallow, curved grooves on the surface of a bed. These he interpreted to represent impressions of tentacles made as a nautiloid dug into the bottom for stability in high current flow. Subsequently, when Richard G. Osgood (1970) conducted his analysis of all known Cincinnatian trace fossils. Flowers nautiloid traces came under renewed scrutiny. Osgood concluded that those traces could not be attributed to nautiloid activity. The supposed nautiloid impressions were shown to be basal portions of burrow systems that extended upward into softer, usually eroded shales. In debunking the nautiloid interpretation, Osgood (1970) displayed notable good grace in naming the "tentacular impression" in Flower's honor: *Vascifodina floweri*. The potential for Cincinnatian nautiloid traces remains; in fact, Osgood (1970, plate 83, figure 3) illustrated one impression with raised edges that he considered a possible nautiloid touchdown.

The So-Called "Minor Molluscs

Although representatives of seven classes of the phylum Mollusca occur in the Ordovician rocks of the Cincinnati region or nearby, only three are common. These are the gastropods (snails), the pelecypods (clams), and the cephalopods (relatives of present-day *Nautilus,* squid, and octopus). Type— Cincinnatian representatives of each of these "major groups" are considered in some detail above. In addition to these better-known classes, specimens of four less well-known classes often referred to as the "minor molluscs" also occur in the Ordovician rocks of the Cincinnati area. These are the monoplacophorans, the rostroconchs, the polyplacophorans (chitons), and the scaphopods ("tusk shells").

Monoplacophorans

Monoplacophorans (there is no other "common name") are actually fairly diverse in the type-Cincinnatian, with twenty-three species in eight genera (Figure 9.2; Wahlman 1992; Holland 2005). Monoplacophorans are similar to the present-day gastropods called limpets in that each has a single, cap-shaped or planispirally coiled shell and a muscular foot for locomotion. Present-day forms like ***Neopilina*** graze on microbial mats through use of the radula. ***Cyrtolites*** is the most common type-Cincinnatian form (figures 9.2C, D) preserved either as a calcitic shell or as an internal mold, but commonly it is encrusted with bryozoans. The keeled, planispiral shell with a diamond-shaped aperture is distinctive.

Rostroconchs

Rostroconchs have a pseudobivalved shell that is sharply folded along the dorsal axis to give the appearance of being bivalved, although calcification is continuous across the axis (Pojeta 1987). Rostroconchs are restricted to rocks of the Paleozoic Era and are thought to represent an intermediate stage in the evolution from univalved to bivalved molluscs (Pojeta and Runnegar 1976). Only specimens of ***Technophorus*** occur in the type-Cincinnatian, with two species in the Edenian and Maysvillian, and a third species in the Richmondian (figures 9.7C, D). Rostroconchs probably lived infaunally as deposit or suspension feeders.

Polyplacophorans

Polyplacophorans, commonly called "chitons," are familiar to those who have explored the rocky intertidal zone of todays oceans. Chitons differ from all other molluscs in having a shell composed of eight separate plates (called valves) that overlap like shingles to provide a protective covering that permits flexibility. Present-day chitons creep over hard substrata and graze algae with the radula. The earliest fossil chitons are from the Upper Cambrian, but they occur more commonly in the Ordovician of North America (Hoare and Pojeta 2006). Although no chiton fossils have been reported as having been found in the type-Cincinnatian, disarticulated valves occur in older Upper Ordovician strata of the Krone Limestone of the High Bridge Group in central Kentucky.

Scaphopods

Scaphopods sometimes go by the common name "tusk shells." They are another group of molluscs of which specimens potentially could occur in the type-Cincinnatian, but, as yet, none have been documented in the scientific literature as having conic from the local rocks. Present-day scaphopods each have a small, curved conical shell open at both ends, and live partly buried in the sediment as deposit feeders. The oldest-known fossil scaphopod, ***Rhytiodentalium kentuckyensis,*** was described from the Lexington Limestone of Kentucky, the formation just below the base of the Cincinnatian (Pojeta and Runnegar 1979). Possible scaphopod specimens have been found in the type-Cincinnatian (Felton, pers. comm.).

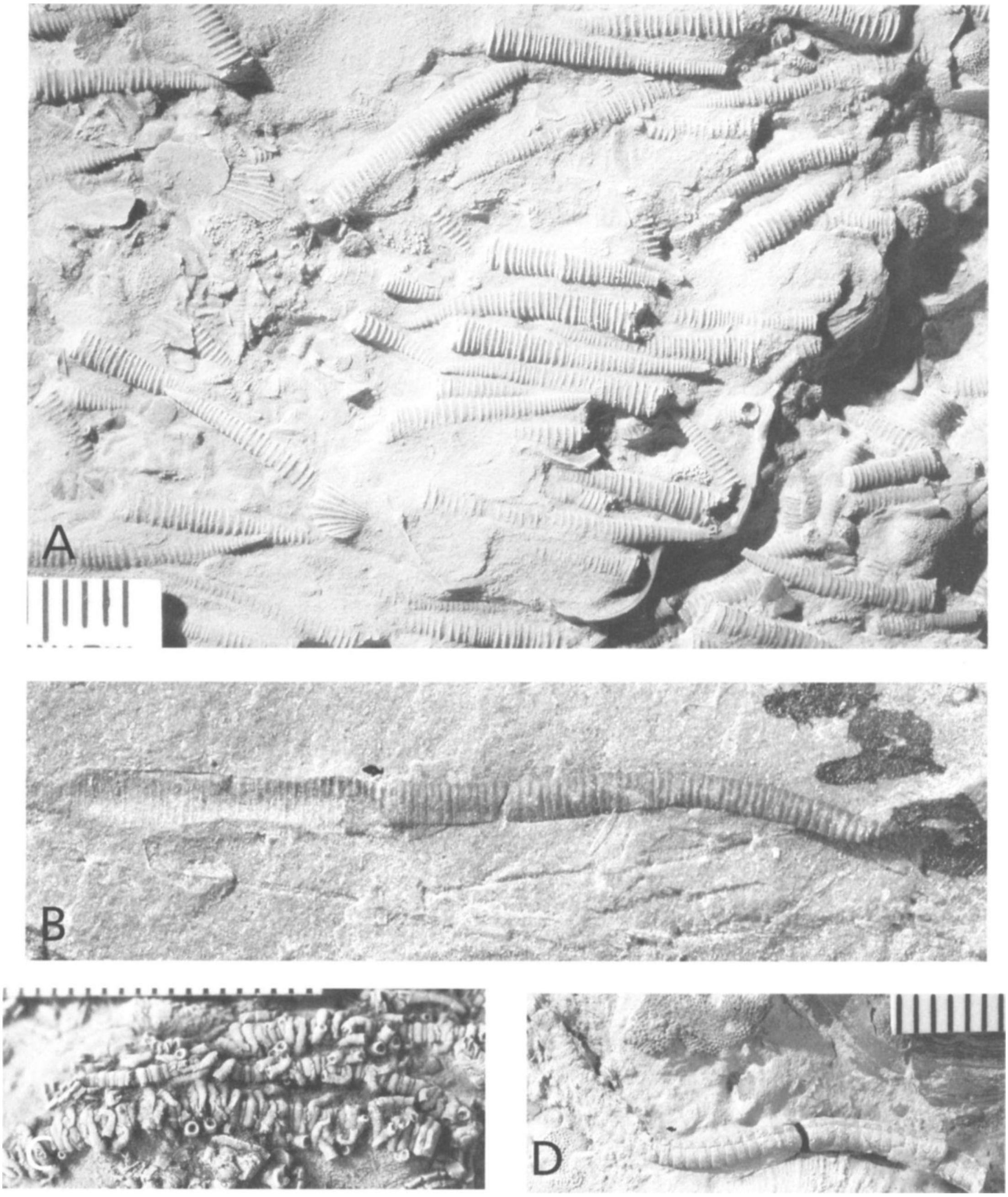


Figure 10.1. *Cincinnatian worms and worm-like fossils.* A. *Tentaculites richmondensis (Miller), CMC IP 17551, Waynesville Formation, Clinton Co., Ohio. Slab showing parallel alignment of shells. Scale in mm.* B. *Annelid worm, Protoscolex ornatus Ulrich, CMC IP 37990, Kope Formation, Covington, Kentucky. This is a rare case in the Cincinnatian of soft-body preservation,* x 7.5. C. *Tubes of Cornulites sp. attached to the column of the crinoid locrinus subcrassus, University of Cincinnati collections, Corryville Formation, Hamilton Co., Ohio. Scale in mm.* D. *The machaeridian Lepidocoleus sp. cf. L. jamesi (Hall and Whitfield), University of Cincinnati collections, Corryville Formation, Boone Co., Kentucky. Scale in mm.*

ANNELIDS AND WORM-LIKE FOSSILS

10

> . . . we *can easily imagine that the ocean beneath which the Cincinnati group was deposited, at times swarmed with innumerable worms, which have, so far as we at present know, left no traces of themselves excepting their jaws, tracks, and possibly a few rude impressions of their bodies.*
>
> **E. O. Ulrich 1878, 88**

Because worms are largely soft-bodied, their fossil record is rather limited. Nonetheless, numerous fossils occur in the Cincinnatian that can be attributed to the Phylum Annelida or related worms. Annelids, the segmented worms, include predominantly freshwater and terrestrial leeches and earthworms, and the predominantly marine polychaetes. In the modern oceans polychaetes are highly diverse and abundant and play many important ecological roles. Throughout the Cincinnatian common tooth-like microfossils called scolecodonts indicate that polychaetes were also components of the Ordovician marine ecosystem (Eriksson and Bergman 2003). Although they resemble conodonts, another category of tooth-like fossils, in size and form scolecodonts are distinct in having a jet black appearance in contrast to the amber color typical of conodonts (Plate 5). The definite polychaete affinity of scolecodonts is established by rare cases (not Cincinnatian) of scolecodonts found with the body fossil of a polychaete worm as assemblages of paired tooth-like elements forming a jaw apparatus. In modern polychaetes an entire apparatus consists of three pairs of different individual elements. Because scolecodonts usually occur as dissociated elements, their taxonomy has been complicated by assignment of separate names for each element. In recent work the recognition of likely associations of elements has begun to alleviate this problem.

The Cincinnatian was the source of the earliest report of scolecodonts as worm jaws (Grinnell 1877). In a recent study, scolecodonts collected from disaggregated shales or acid-insoluble residues from limestones were found to be common throughout the Cincinnatian section with a maximum abundance of 1545 elements per kilogram of rock (Eriksson and Bergman 2003). Eriksson and Bergman estimated that forty to fifty multielement species belonging to twelve families occur in the Cincinnatian. Although some scolecodonts resemble jaws of certain modern polychaete families, none of the Cincinnatian taxa represent living groups. Because modern jaw-bearing polychaetes are predatory, it is likely that Cincinnatian scolecodont-bearing forms were also predators, presumably on soft-bodied prey. Eriksson and Bergman recognized five stratigraphic associations of scolecodonts within the Cincinnatian; also, many Cincinnatian families and genera occur in the Upper Ordovician of the Baltic region of Europe, indicating an intercontinental distribution. Further refinement of scolecodont taxonomy will undoubtedly fulfill a great potential for the use of scolecodonts in biostratigraphic zonation and correlation.

In an extremely rare instance of soft-bodied preservation, Ulrich (1878) described actual body fossils of worms from a horizon in the Edenian. The specimens are very small, and have a distinctly segmented appearance (Figure 10.1 B; Robison 1987, figure 12.41F). Ulrich named this worm *Protoscolex* and described four species, all occurring in the Economy beds of the Edenian (now the Kope formation). Miller and Faber (1892b) described a fifth species also from the Edenian, from "near the low water mark" of the Ohio River, equivalent to the Fulton Member of the Kope Formation. A specimen in the collections of the Cincinnati Museum Center is labeled from the 400-foot elevation, which would place it in the Mavsvillian Corryville Formation. Although these fossils have not been restudied, their identification as worms has not been challenged. In the *Treatise on Invertebrate Paleontology. Protoscolex* is listed with worms for which the phylum is uncertain (Howell 1962). However. Robison (1987) illustrated a specimen from the Upper Ordovician of Kentucky as a fossil annelid.

Cornulites and Other Small, Conical Fossils

The conical encrusting fossil *Gornulites* is a common Cincinnatian macrofossil of uncertain zoological position but with possible worm affinities. *Cornulites* occurs throughout the Cincinnatian and several species have been described. In the *Treatise on Invertebrate Paleontology,* Fisher (1962) described *Cornulites* as small tubes of calcium carbonate, with a circular cross-section of 2 to 20 mm diameter and a length of 5 to 80 mm. Smaller *Gornulites* are smooth, but larger tubes have circumferential rings and longitudinal striations. Because the porous or vesicular internal wall structure differs from the microstructure of tube-forming annelids, Fisher did not assign *Gornulites* to a definite phylum. Although the nature of the animal remains uncertain, *Gornulites* is similar to modern polychaetes (like serpulids or spirorbids) that form encrusting tubes and live as filter feeders. In the Cincinnatian, *Gornulites* usually occurs as clusters of tubes encrusting a wide variety of shelly substrata such as brachiopods, bryozoans, molluscs, trilobites, and echinoderms (Figure KMC; see Figure 12.9B), but can also occur as solitary, unattached tubes (Morris and Rollins 1971; Morris and Felton 1993, 2003). The orientation of *Gornulites* with the aperture toward the margins of brachiopods and pelecypods suggests a possible commensal relationship by which the tube-dwelling filter feeder took advantage of the feeding currents of the host (Morris and Felton 1993, 2003). Moreover, cornulitids often encrusted crinoid columns and shells of the gastropod *Cyclonema* that frequently attached to the calyx of living crinoids (see Figure 12.9B). In this maimer, cornulitids gained a potentially advantageous feeding position above the sediment-water interlace (Morris and Felton 2003).

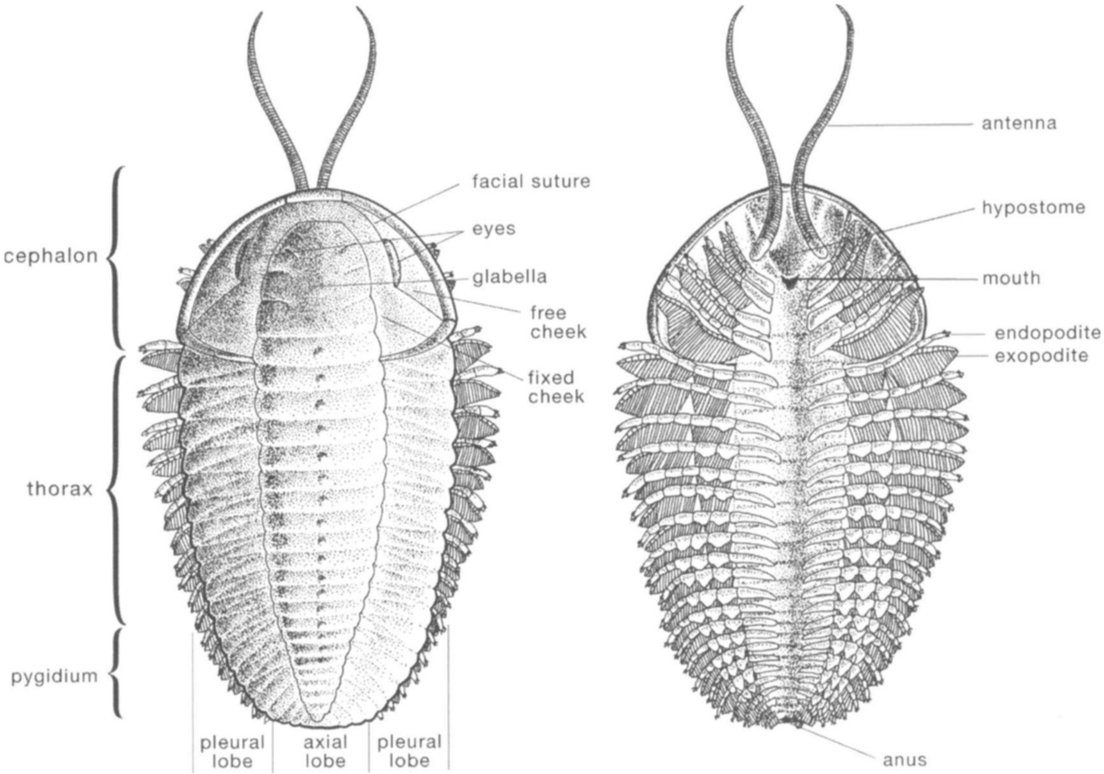
Tentaculitoids are small, calcareous conical fossils with circumferential rings. Tentaculitoids are similar in size and form to the probable annelid tubes called *Gornulites,* ranging from 1 to 40 mm in length (rarely up to 80 mm). Unlike most *Gornulites,* tentaculitoids are non-encrusting and have a think layered or lamellar shell structure and internal imperforated septa (Bergstrom 1996b). There is evidence of soft part anatomy from x-radiographs of a Devonian tentaculitoid from Germany that tentacles and a siphon were present (Blind and Stuermer 1977). This suggests a possible affiliation of tentaculitoids with cephalopods. In the *Treatise on Inverte-*

brate Paleontology, Fisher (1962) proposed that tentaculitoids and some other small conical shells be included in an extinct class Cricoconarida (meaning "small, ringed cones") belonging to the Mollusca. More recently, tentaculitoids have been treated as a class unto themselves, Tentaculitoidea, and not included with any known group (Bergstrom 1996b). Clusters of tentaculitoids are sometimes found on a bedding plane in parallel alignment probably caused by water movement (Figure 10.1A). Two species are known from the type-Cincinnatian, *Tentaculites sterlingensis* and T. *richmondensis,* both from the Richmondian.

Another group of small, calcareous, conical fossils that can be found in the Cincinnatian section are the hyolithids. Hyolithids are much smaller than either *Cornulites* or tentaculitids; those occurring in the Cincinnatian are about 2 to 3 mm long. Unlike *Cornulites* or tentaculitids, hyolithids have a smooth shell with a roughly triangular cross-section and an operculum or cap closing the aperture. In the *Treatise on Invertebrate Paleontology,* Fisher (1962) placed the hyolithids in the Calyptomatida, regarded as an extinct class of the Phylum Mollusca. Although there is uncertainty as to the correct taxonomic classification of hyolithids, most workers continue to favor affinity with the molluscs (Malinky et al. 2004). Some hyolithids may have been similar to the present-day planktonic pteropod molluscs, but others were probably benthonic and capable of movement along the sea floor (Fisher 1962). Well-preserved specimens retain the operculum and a pair of curved spines emerging from the aperture that could have been used in locomotion. Cincinnatian hyolithids are known from the Maysvillian and Richmondian and include two genera, H*yolithes* and *Coleolus* (see Dalve 1948).

Mysterious Machaeridians

Machaeridians are a very small and problematic group of fossils known from rocks of Ordovician through Permian age, and are represented in the Cincinnatian. These peculiar fossils are composed of a series of overlapping, calcareous segments that are each formed by a pair of plates (called sclerites). The paired plates form a heart-shaped tube in cross-section. Machaeridians occur either as articulated series of many segments, tapering at one end, or as disarticulated sclerites. It is possible that the series of sclerites is not a complete organism, but rather is a dissociated body part. In a detailed study of Cincinnatian specimens, John K. Pope (1975) argued that *Lepidocoleus* is a sheath of plates that covered spines that were attached to the theca of the carpoid echinoderm *Enoploura* (see chapter 12, Figure 12.17B). Pope's argument was based largely on the finding of abundant disarticulated carpoid plates and articulated series of machaeridian sclerites at two Cincinnatian localities. Machaeridians had been interpreted previously as belonging to the chitons, barnacles, annelids, trilobites, or echinoderms. In 2004 Hints et al. treated machaeridians as plates of an unknown, bilaterally symmetrical worm-like organism, but ignored Pope's carpoid echinoderm interpretation. *Lepidocoleus jamesi* (flail and Whitfield) occurs throughout the Cincinnatian (Dalve 1948). Machaeridians are usually regarded as rare fossils, but the occurrences reported by Pope show that they can be very abundant in some beds.


facial suture
eyes
cephalon
glabella
free cheek
fixed cheek
thorax
pygidium
pleural lobe
axial lobe
pleural lobe
antenna
hypostome
mouth
endopodite
exopodite
anus

ARTHROPODS: TRILOBITES AND OTHER LEGGED CREATURES

11

In terms of sheer abundance, species diversity, and exploitation of habitats, arthropods rank as the most successful of all living animals. More than 750,000 species (mostly insects) inhabit a cast range of environments on land, in the sea, and in fresh water. Living arthropods include the insects, crustaceans, horseshoe crabs, arachnids, centipedes, and millipedes. During the Ordovician, arthropods had not yet invaded the land, but trilobites were abundant and diverse in the sea, along with the eurypterids, ostracodes, and a few other minor groups.

Despite their bewildering variety of form, all arthropods share certain basic features. Like their close relatives, the annelid worms, arthropods have a segmented body. Unlike the annelids, the body and its appendages are encased in an exoskeleton composed of the protein chitin. The exoskeleton is much like a suit of armor in having rigid components articulated by flexible joints. (The name arthropod means "jointed legs.") Not only does the exoskeleton shield the internal organs from predation and some environmental hazards, but it also provides rigid points for muscle attachment. Consequently, arthropods are capable of rapid locomotion by walking, swimming, or flying. The nature of the exoskeleton has two important implications for the fossilization potential of arthropods. First, because the chitinous exoskeleton decomposes after death, main arthropods are poor candidates for fossil preservation. However, arthropods that have thicker exoskeletons or incorporation of calcium carbonate into their skeletons (such as some crustaceans and trilobites) will have enhanced potential for preservation. Second, all arthropods grow by periodically shedding the exoskeleton and forming a new skin that accommodates growth. Each individual arthropod can contribute numerous shed exoskeletons (molts) as potential fossils during its lifetime. Molting may thus explain in part the abundance of some arthropod fossils.

Figure 11.1. *The Ordovician trilobite Triarthrus. Left, dorsal view, right, ventral view. Drawings by Kevina Vulinec.*

Trilobites

Although trilobites achieved their maximum diversity during the Late Cambrian. They remained diverse and abundant during the Ordovician. Among the plethora of Cincinnatian fossils, trilobites are arguable the best known for their preservation and abundance. Trilobites are unique among the arthropods in having a characteristic lengthwise subdivision of the dorsal exoskeleton into three lobes, an axial lobe flanked by two pleural lobes (Figure 11.1). There is a distinct head shield or cephalon, a flexibly segmented thorax, and a tail shield or pygidium. The cephalon usually has a central, swollen region called the glabella. Although it resembles a nose or forehead, the glabella actually protected the trilobite's stomach. Transverse glabellar lobes and furrows indicate fused segmentation of the head region. A prominent pair of compound eyes usually flanks the glabella. A sinuous facial suture crosses the cephalon alongside the eyes, separating the lateral free cheeks from the fixed cheeks. The facial suture provided a line of breakage across the cephalon during molting. For this reason, isolated free checks are commonly found as well as the cranidium. a single unit comprising the glabella and fixed cheeks. A pair of genal spines is often developed at the posterior corners of the cephalon, as seen in ***Flexicalymene meeki, Isotelus maximus,*** and ***Cryptolithus tessellatus*** from the Cincinnatian.

The segments of the thorax were connected by a thin integument that allowed the trilobite to flex its body and in many cases to achieve complete enrollment like a modern pillbug (an isopod crustacean). After death, decay of the articulating integument often released individual thoracic segments that resemble brackets ({) when preserved. The pygidium is commonly preserved as a single unit because its segments were fused. As a consequence of molting and post-mortem decay, trilobite fragments are abundant, but complete, articulated specimens are uncommon. There is considerable debate about whether complete specimens represent trilobites buried intact, because some may have molted without the exoskeleton breaking apart. Usually, however, articulated specimens, particularly enrolled ones, represent trilobites buried alive or very soon after death.

On the ventral side of the cephalon, a plate called the labrum or hypostome was positioned beneath the mouth and connected to the anterior margin of the cephalon (Figures 11.1, 11.2, 11.4B). The labrum is often found as an isolated fossil, but it rarely will be found in place. Unlike that of a crab or lobster, the ventral exoskeleton of trilobites was a thin, chitinous membrane to which the appendages were attached. Trilobite appendages were also weakly constructed and thus were preserved only under exceptional conditions (Figure 11.4D). A pair of jointed antennae was attached to the ventral side of the cephalon, followed by a series of paired, jointed appendages underlying each segment of the cephalon, thorax and pygidium. Although appendages are known from very few species of trilobites, the appendages are similar in having two branches: the walking leg or endopodite and a branch called the exopodite extending from the basal segment of the endopodite (Figures 11.1, 11.2). The exopodite carried numerous filaments giving it a comb-like appearance.

Although at least sixteen genera of trilobites are known from the Cincinnatian, only a few are common. ***Flexicalymene*** and ***Isotelus*** are the most common and are distributed throughout the Cincinnatian Series. The widespread distribution of these two signature trilobites, in shales and limestones representing the full range of Cincinnatian depositional environments, clearly suggests that both had very generalized habitat preferences. In contrast, most other Cincinnatian trilobites have much more restricted stratigraphic distributions, suggesting more limited environmental tolerances.

Flexicalymene is one of the world's best-known trilobites, in large measure due to its abundance in Cincinnatian strata (Figure 11.3). Although a modern systematic review has not been done, as many as three species may

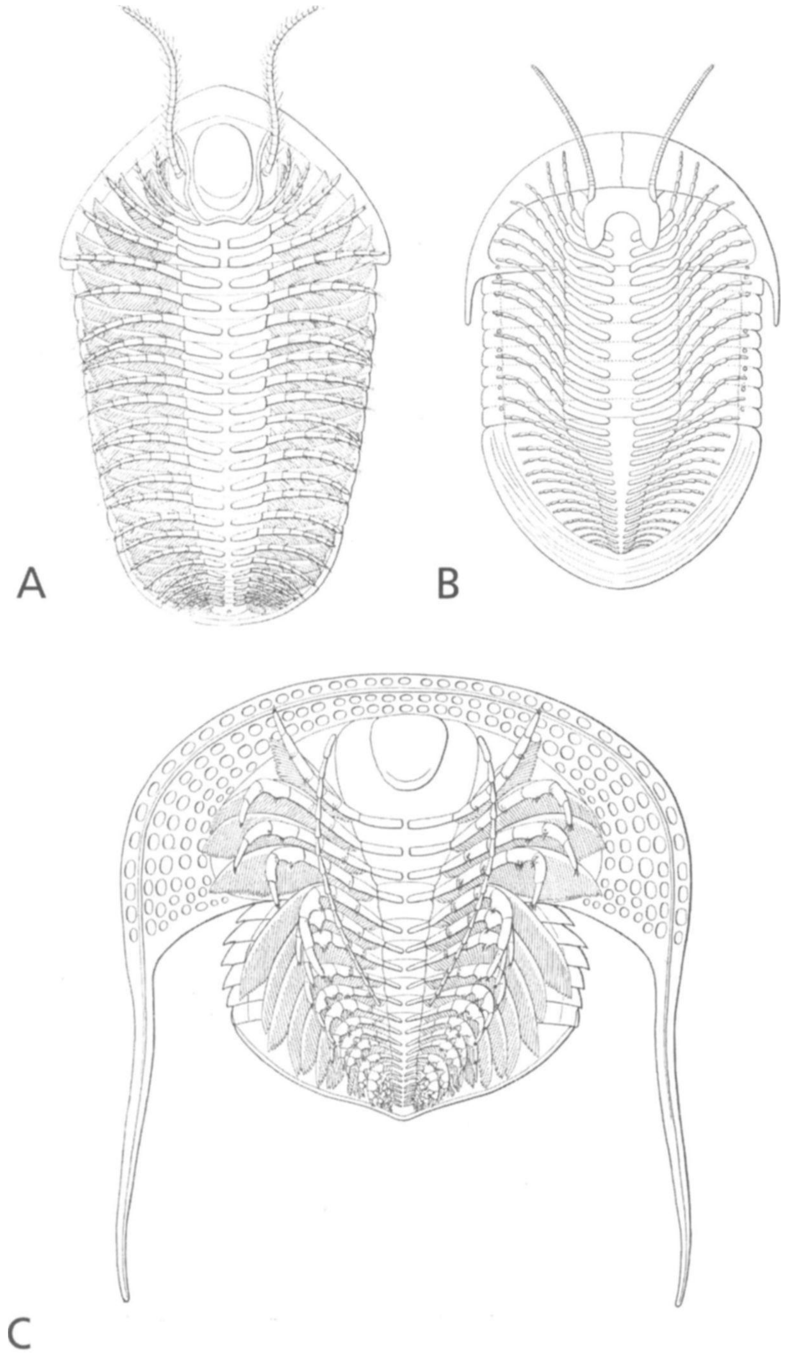
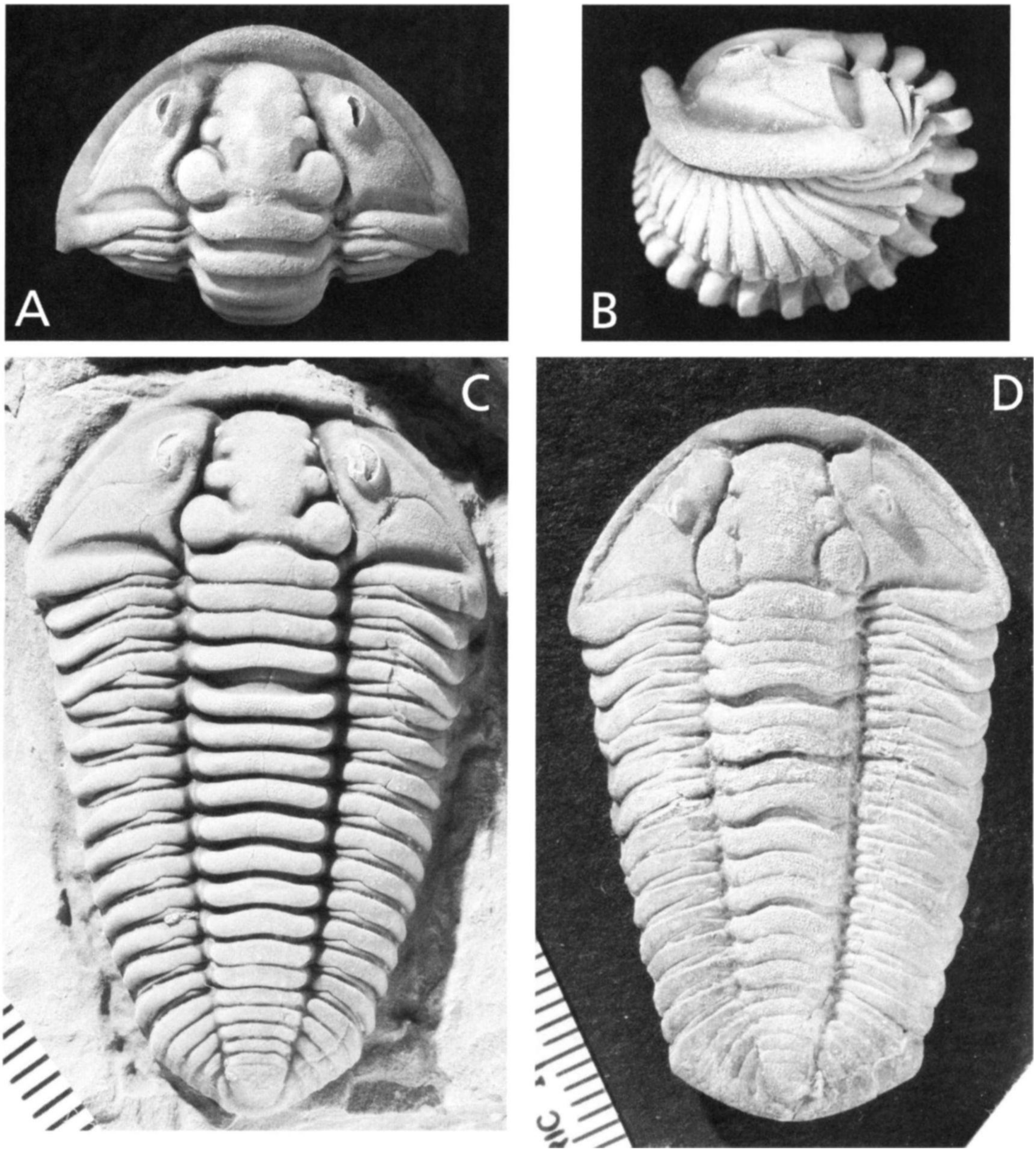


Figure 11.2. *Ventral views of three Ordovician trilobites, showing reconstructions of the appendages. Anterior at the top in each.* A. *Flexicalymene senaria (Conrad).* B. *Composite of Isotelus maximus and I. latus, (exopodites omitted because they are unknown).* C. *Cryptolithus tessellatus Green. From Raymond (1920, figures 9, 16, 20) and reprinted by permission of the Connecticut Academy of Arts and Sciences.*

be present: F. *meeki* (Foerste), by far the most abundant and widely distributed species, F. *granulosa* (Foerste), a small form restricted to the lower Cincinnatian Kope Formation, and F. *retrorsa* (Foerste), found only in the upper Cincinnatian Waynesville Formation. In the first volume of the *Geological Survey of Ohio* (1873), F. B. Meek included the Cincinnatian calymenid trilobites with *Calymene senaria,* originally described from New York by Conrad in 1841. Foerste (1910) proposed the name *Calymene meeki* for the



species so well described by Meek from the Cincinnatian rocks of Ohio, but provided only a five-line description and a single illustration of an enrolled specimen. In the same paper Foerste named C. *meeki-retrorsa,* a form of *Calymene meeki* from the Waynesville, which differs chiefly in the narrower posterior width of the cephalon, resulting in more obtuse genal angles. The anterior border of the cephalon is more strongly reflexed, bringing it closer to the anterior margin of the glabella. The British worker Shirley (1936) placed the Cincinnatian species in *Flexicalymene.* Ross (1967) provided a more complete description of F. *meeki* and also reviewed the status of Foerste's C. *meeki-retrorsa.* Ross considered F. *retrorsa* to be a valid species although it has little to distinguish it from *meeki* except the size, shape, and inclination of the anterior cranidial border. Ross was unable to verify the other differences asserted by Foerste. A morphometric analysis conducted by Danita Brandt (1980) in her unpublished master's thesis led her to conclude that only a single species, F. *meeki,* is valid, and that both F. *granulosa* and F. *retrorsa* should be synonymized with F. *meeki* as intraspecific variants. More recent work by Brenda Hunda (pers. comm.) supports the recognition of F. *meeki, F. retrorsa,* and F. *granulosa* as valid species.

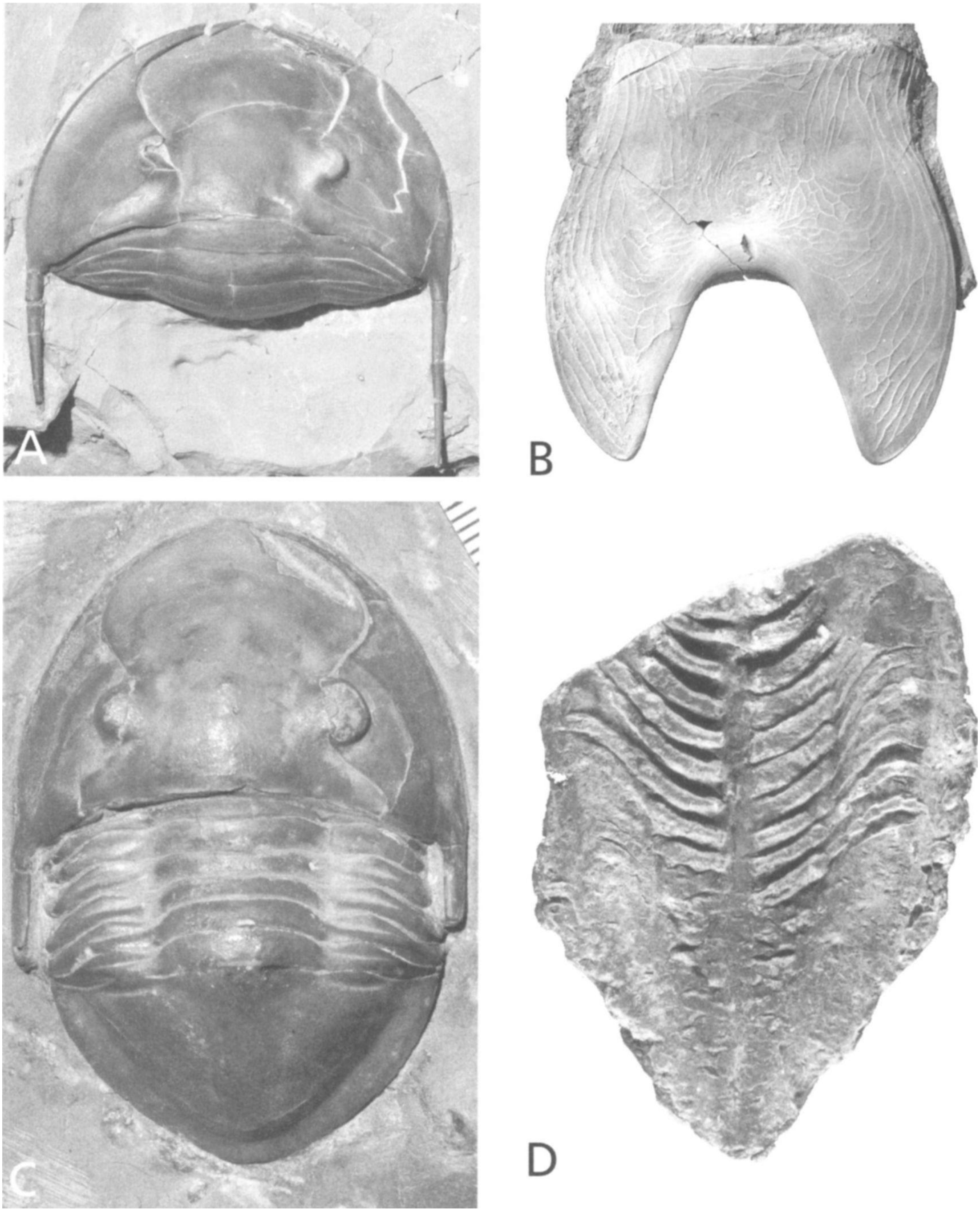
Flexicalymene is commonly found as isolated partial exoskeletons (cephala, cranidia, free cheeks, thoracic segments, pygidia) in Cincinnatian limestones; complete specimens are less common and are usually found in shales as either enrolled or extended individuals. On rare occasions, these trilobites can be found in great numbers in yellowish shales known as butter shales. One of the most prolific trilobite discoveries ever made in the Cincinnatian was in such a shale within the lower Richmondian Waynesville Formation during construction of an apartment complex at Boudinot Avenue and Westwood Northern Boulevard in northwest Cincinnati in the 1950s. Literally thousands of *Flexicalymene* were collected from two shalebeds 2.5 and 3 feet thick, and as the exposure weathered, trilobites became perched on pedestals of clay for easy picking (Caster, pers, comm.; Schweinfurth 1958). Taphonomic studies of occurrences of abundant, complete trilobites in Cincinnatian shales indicate that these are the result of mass mortalities of living trilobite populations smothered during storms or mass movements of fine-grained sediments (Brandt 1980, 1985; Schumacher and Shrake 1997; Hughes and Cooper 1999).

Life Habits of ***Flexicalymene***

Our understanding of the life habits of trilobites has been hampered by the fact that trilobites are extinct and have no close living relatives, although horseshoe crabs and some crustaceans are often regarded as possible models (Plate 3G). The form of the appendages is closely related to life habits in living arthropods, but in trilobites the appendages are so rarely preserved that little information can be gained from them. A recent review by Fortey and Owens (1999) demonstrated that other preserved morphological features of trilobites can be used to determine their feeding habits. Fortey and Owens regard the calymenid trilobites like *Flexicalymene* to have been predators or scavengers because the hypostome is rigidly attached to the underturned edge of the cephalon (doublure). The hypostome may have acted as a grinding or manipulating surface for small prey items held between the basal segments of the appendages.

Further evidence for the predatory behavior of *Flexicalymene* comes from characteristic burrows (trace fossils named *Rusophycus)* formed by this trilobite. *Rusophycus* trace fossils are well known in strata of late Precambrian through Devonian ages, and most are thought to have been produced by trilobites digging into the sediment using the paired appendages (Hantzschcl 1975). Although the digging activity could reflect different possible-behaviors including sheltering, resting, egg laying, or feeding, recent discoveries suggest that trilobites were actively hunting prey buried within the sedi-

Figure **11.3.** A, B. *Flexicalymene meeki (Foerste), University of Cincinnati collections, Maysvillian, Corryville Formation, Hamilton Co., Ohio, enrolled specimen, cephalic width 28 mm. C. Flexicalymene retrorsa (Foerste), CMC IP, Ferree Collection, Richmondian, Arnheim Formation, Highland Co., Ohio, x 1.4.* D. *Flexicalymene granulosa (Foerste), Mark Peter collection, Edenian, Kope Formation, Brown Co., Ohio,* x *2.5.*



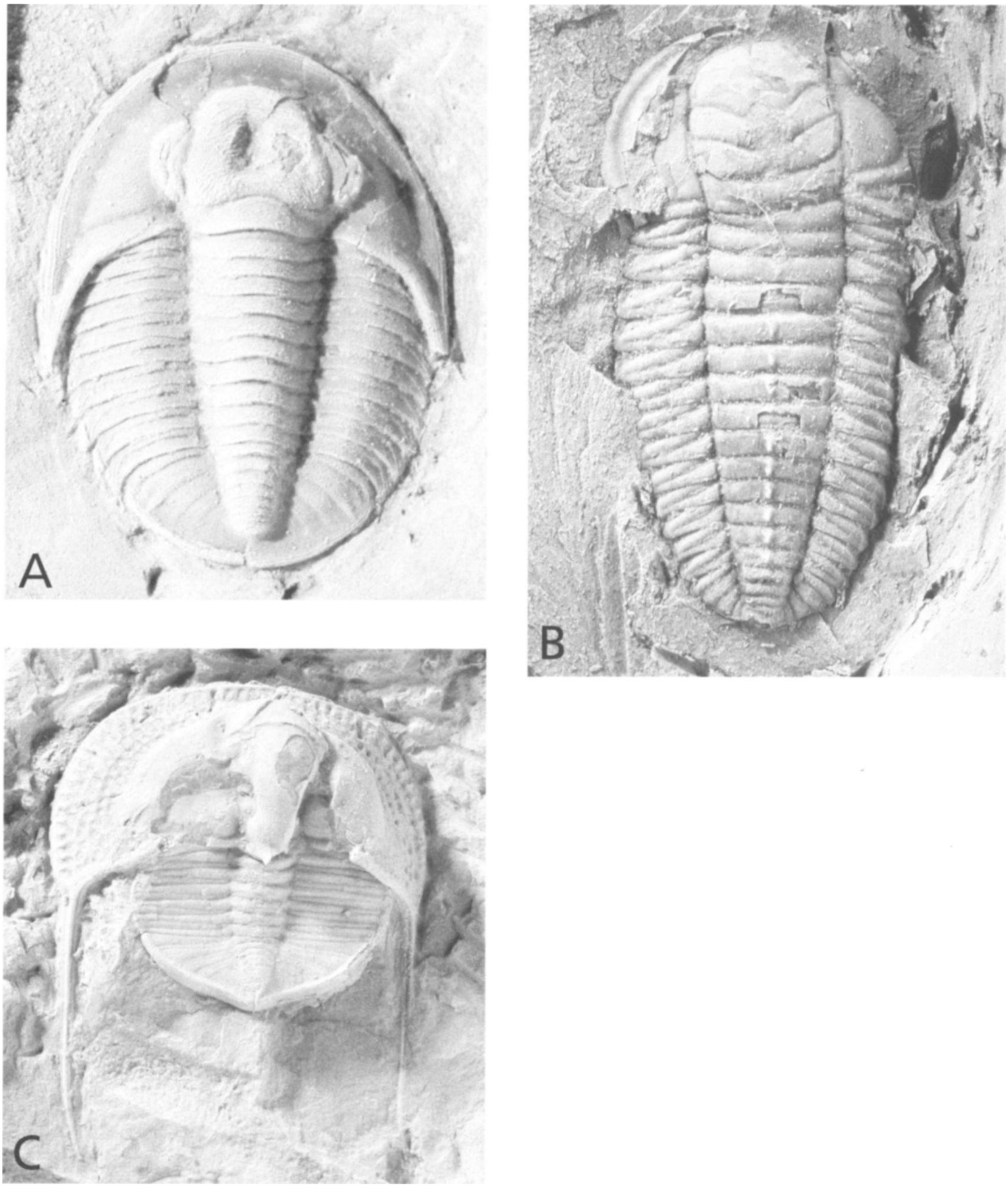
ment. Although by no means common, several remarkable cases of *Rusophycus* intersecting worm burrows are known from the Cambrian (Jensen 1990) and Cincinnatian (Brandt et al. 1995). In the Cincinnatian, *Flexicalymene* is unequivocally identified as the producer of one type of *Rusophycus* (R. *puclicum)* on the basis of a few exceedingly rare specimens that have the characteristic bilobate burrow preserved in place beneath the complete carapace of the trilobite (see Figure 14.2B; Osgood 1970). Although no specimens of *Rusophycus pudicum* from the Cincinnatian have been found intersecting worm burrows, the digging activity is consistent with predation on small, infaunal organisms (Fortey and Owens 1999).

Despite the excellent state of preservation found in Cincinnatian *Flexicalymene,* remnants of the appendages have never been found. Sturmer and Bergstrom (1973) carried out x-radiographic studies that revealed preserved appendages in some trilobites, but similar studies by Brandt (1980) and by Hughes and Cooper (1999) detected no evidence of appendages in *Flexicalymene.* The study by Hughes and Cooper revealed pyritized material concentrated within the body cavity of *Flexicalymene* that may have originated as decaying soft parts. An approximate idea of the nature of the appendages in Cincinnatian *Flexicalymene* species can be gained from the restoration of the closely related *F. senaria* (figure 11.2A; Raymond 1920).

Isotelus is the other highly characteristic and widely distributed trilobite of the Cincinnatian (Plate 7; figure 11.4). Fragments of this large trilobite are found in every Cincinnatian formation, in both limestones and shales. Complete specimens are quite rare, but in certain shale horizons, particularly in the Waynesville Formation, numerous complete specimens have been found (Schumacher and Shrake 1997). Specimens of *Isotelus* from the Cincinnatian arc among the largest-known trilobites. A specimen of *Isotelus* on exhibit at the Smithsonian Institution collected in 1919 during construction of the Huffman Dam near Dayton measures 37 cm long (14.5 in) by 26 cm wide (10.25 in). The complete specimen at Cincinnati Museum Center measures 37.5 cm in length (Plate 7). On the basis of partial specimens, *Isotelus* probably reached lengths of 80-90 cm (Babcock, pers. comm.). Recently, a specimen of *Isotelus* was found in Upper Ordovician strata in northern Manitoba that holds the current world record as the largest trilobite, at a length of over 70 cm (Rudkin et al. 2003).

Currently, two species of *Isotelus* are recognized in the Cincinnatian: *I. maximus* and *I. gigas. I. maximus* has well-developed genal spines. *I. gigas* has genal spines that are either shorter than those of *I. maximus* or lacking. Without a modern, critical analysis of the range of variation within these species, it is not clear how to separate *I. maximus* from *I. gigas* on the basis of genal spine length. Cincinnatian *Isotelus* having a very broad, flattened carapace were given the name *I. brachycephalus* by Foerste (1919), but this species was regarded as a variant of *I. maximus* by Babcock (1996), and hence a junior synonym of *I. maximus.* (If two different names have been given to the same species by different workers, one name can be subordinated as a junior anonym if it was described after the original name and if it is determined to be equivalent to the originally described taxon.) Because *I. maximus* and his *I. brachycephalus* occur together in the Riehmondian strata of the Cincinnatian, Foerste suggested the possibility that the broader *I. Brachycephalus* might represent females and the narrower *I. maximus* the males of a single species. This remains an intriguing possibility that has never been fully explored.

Figure 11.4. *Isotelus maximus Locke.* A. *Enrolled specimen, CMC IP 2250, Riehmondian, Arnheim Formation, Highland Co., Ohio, x 1.3.* B. *Large hypostome, CMC IP 33067, Maysvillian, Clermont Co., Ohio, x 7.* C. *CMC IP 51, Robert Nestor collection, Maysvillian, Corryville Formation, Clermont Co., Ohio, x 1.8.* D. *Appendages on ventral side of a complete specimen, USNM 33458, Riehmondian, Oxford, Butler Co., Ohio, x 0.75. This exceptional specimen was originally illustrated by Mickleborough (1883). Photo courtesy of Loren Babcock.*



Life Habits of *Isotelus*

Isotelus was one of the largest-known animals in the Cincinnatian sea, rivaled only by the less common euryptcrid *Megulograptus* and endocerid cephalopods. By virtue of its large size alone, *Isotelus* might be suspected to have been a predator, but additional evidence also points clearly toward this interpretation of its ecological role. Like ***Flexicalymene,*** *Isotelus* has a hypostome rigidly attached to the cephalic doublure (Figures 11.2B, 11.4B); in addition the anterior cephalic margin is strengthened (Fortey and Owens 1999). Fortey and Owens mentioned several other unique features of the ***Isotelus*** hypostome that suggest its function as a rigid platform like an anvil for the manipulation of bulky food: its forked shape, and development of anterior wings provide a larger surface area, and the fine raised ridges on the inner surfaces of the fork could make it easier to hold the prey rigidly using the appendages. This hypostome is the most heavily calcified part of the *Isotelus* exoskeleton and is often found as an isolated component (Figure 11.4B).

In the Cincinnatian, large ***Rusophycus*** burrows have been attributed to ***Isotelus*** on the basis of their size (R. ***carleyi,*** see Osgood 1970). Specimens often show not only furrows created by the appendages, but also impressions of the cephalic and pygidial margins and pleurae. A remarkable specimen shows a horizontal worm burrow apparently truncated in the approximate location of trilobites mouth (see Figure 14.2A; Brandt et al. 1995)—a trace fossil recording the very act of predation. The trilobite evidently dug and drew itself down into a semi-cohesive mud substratum so as to impress the margins of its carapace like a cookie cutter. The trace shows impressions of the basal segments (coxae) of the appendages that probably seized the prey along the ventral midline and worked it toward the mouth. A single exceptional specimen preserving the appendages of *Isotelus* was found in the Cincinnatian near Oxford, Ohio, and was first reported by Mickleborough (1883) (Figure 11.41D). Only the walking legs are poorly preserved, but the large size of the coxae is evident.

Other Trilobites

Cryptolithus, the lace-collared trilobite, is another common Cincinnatian trilobite in the Edenian and Mavsvillian formations; a single species, C. *tessellatus,* is present (Figure 11.5C). Its common name refers to the broad, perforated cephalon that bears genal spines. The thorax and pygidium form a small, short unit that is rarely found attached to the cephalon. Exceptionally well-preserved specimens from the Ordovician of New York revealed the appendages of *Cryptolithus.* Reconstruction of the appendages shows that each walking leg was accompanied by a branch (exopodite) that carried long, comb-like filaments (Figure 11.2C). The exopodites probably waved in unison to stir up the sediment and create a respiratory and feeding current. Trace fossils attributable to *Cryptolithus (Rusophycus cryptolithi)* suggest that this trilobite excavated a pit that created a filter-feeding chamber beneath the broad cephalon (Osgood 1970; Fortey and Owens 1999). Different workers agree that *Cryptolithus* used the appendages to extract food particles from the sediment stirred up in digging the pit, but there are varying interpretations of the function of the perforations of the cephalic fringe. The tunnel-like perforations could have acted as a sieve to separate fine particles from a feeding current passing from the exterior of the cephalon to the interior (Cisne 1970; Scilacher 1970). According to Fortey and Owens (1999), it is more reasonable to suppose that a feeding current created by the exopodites (gills) stirred *up* food particles beneath the trilobite, then exited through the perforations from the interior to the exterior. Campbell (1975),

Figure 11.**5**. A. *Decoroproetus parviusculus (Hall), CMC IP 46429, Edenian (figured in Davis [1992, plate 2, figure 23] as Proetus parviusculus), x 7.7.* B. *Triarthrus eatoni (Hall), Steve Brown collection, J. Rush collector, Edenian, Kope Formation, Hamilton Co., Ohio, x 4.6.* C. *Cryptolithus tessellatus Green, University of Cincinnati collections, Edenian, Kope Formation, Hamilton Co., Ohio,* x *3.7.*

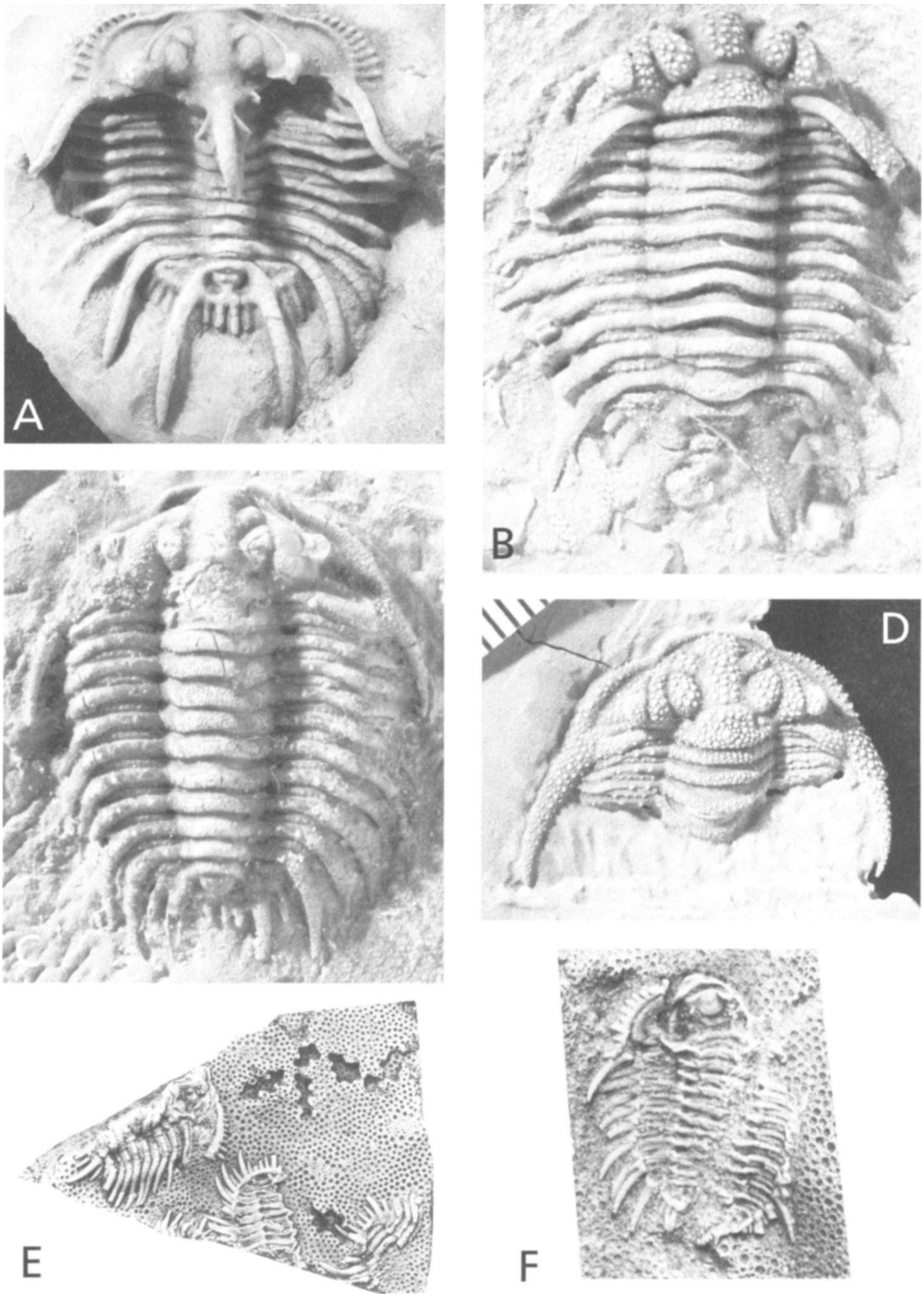


Figure 11.6. A. *Acidaspis cincinnatiensis Meek, Steve Brown collection, J. Rush collector,* x *2.6.* B, D. *Odontopleurid, gen. and sp. Undetermined.* B. *MUGM 29056, Richmondian, Oxford, Butler Co., Ohio,* x *4.0. D, Steve Brown collection, J. Rush collector,* x *2.6.* C. *Primaspis crosotus (Locke), University of Cincinnati collections, Kope Formation, Hamilton Co., Ohio,* x *6.* E. *Primaspis crosotus (Locke) on bryozoan Peronopora sp., MUGM 4001-A,* x *2.8, from Shrake (1989, plate 3C). Note Catellocaula vallata bioclaustrations in upper right part of bryozoan.* F. *Primaspis crosotus (Locke) on bryozoan, MUGM 4010, ventral side of trilobite showing hypostome in place,* x *5.2, from Shrake (1989, plate 4B).*

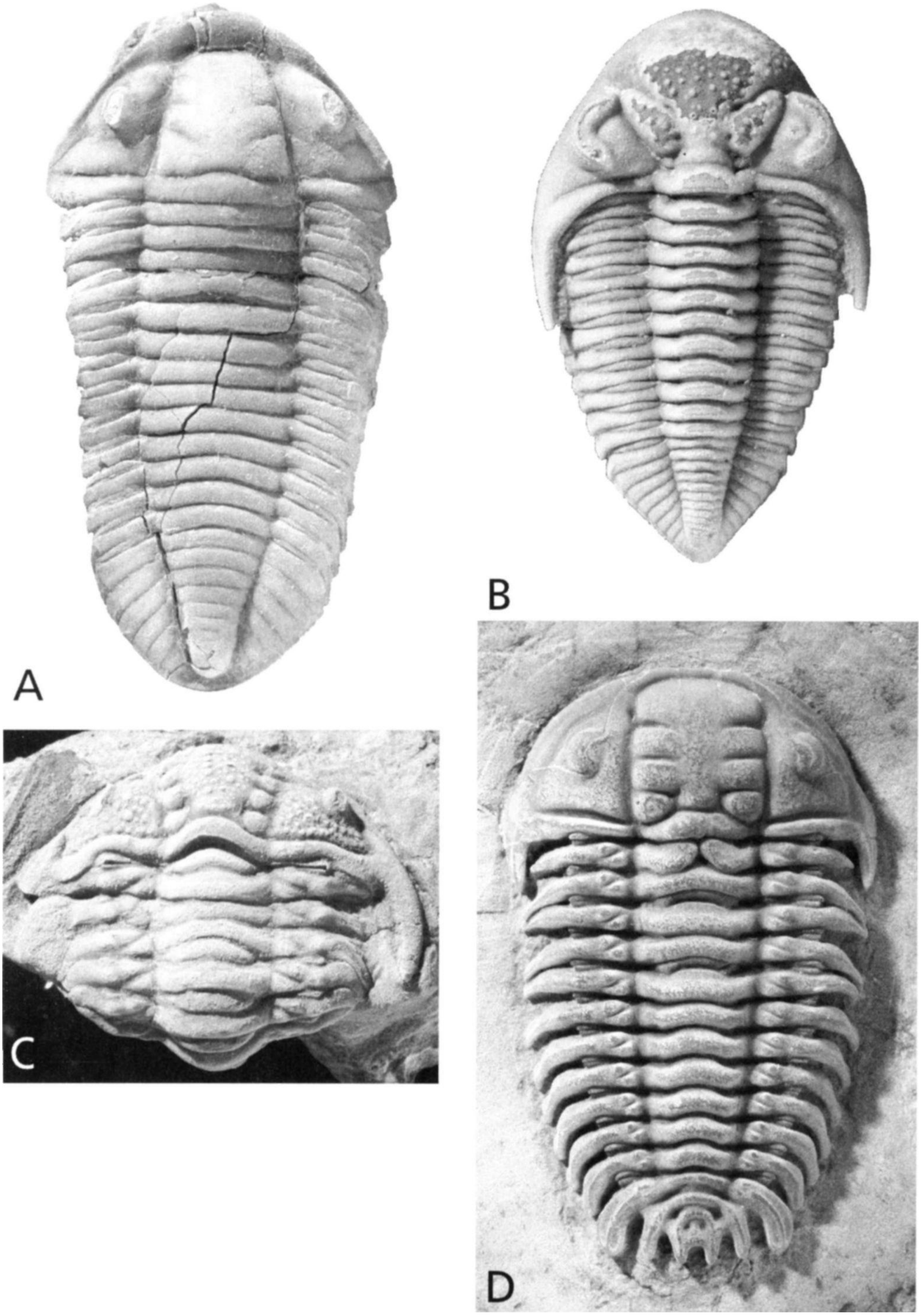


Figure 11.7. *Cincinnatian phacopid trilobites.* A. *Platycoryphe christyi (Hall), Mark Peter collection, Riehmondian, Waynesville Formation, Montgomery Co., Ohio,* x *2.6.* B. *Tricopelta breviceps (Hall), MUGM 29057, Riehmondian, Waynesville Formation, Franklin Co., Indiana,* x *5.5.* C. *Ceraurus milleranus Miller and Gurley, CMC IP 5199, enrolled, no unit or locality (figured in Davis [1992, plate 3, figure 28]),* x *2.5.* D. *Ceraurinus icarus (Billings), Steve Brown collection, J. Rush collector, Riehmondian,* x *2.*

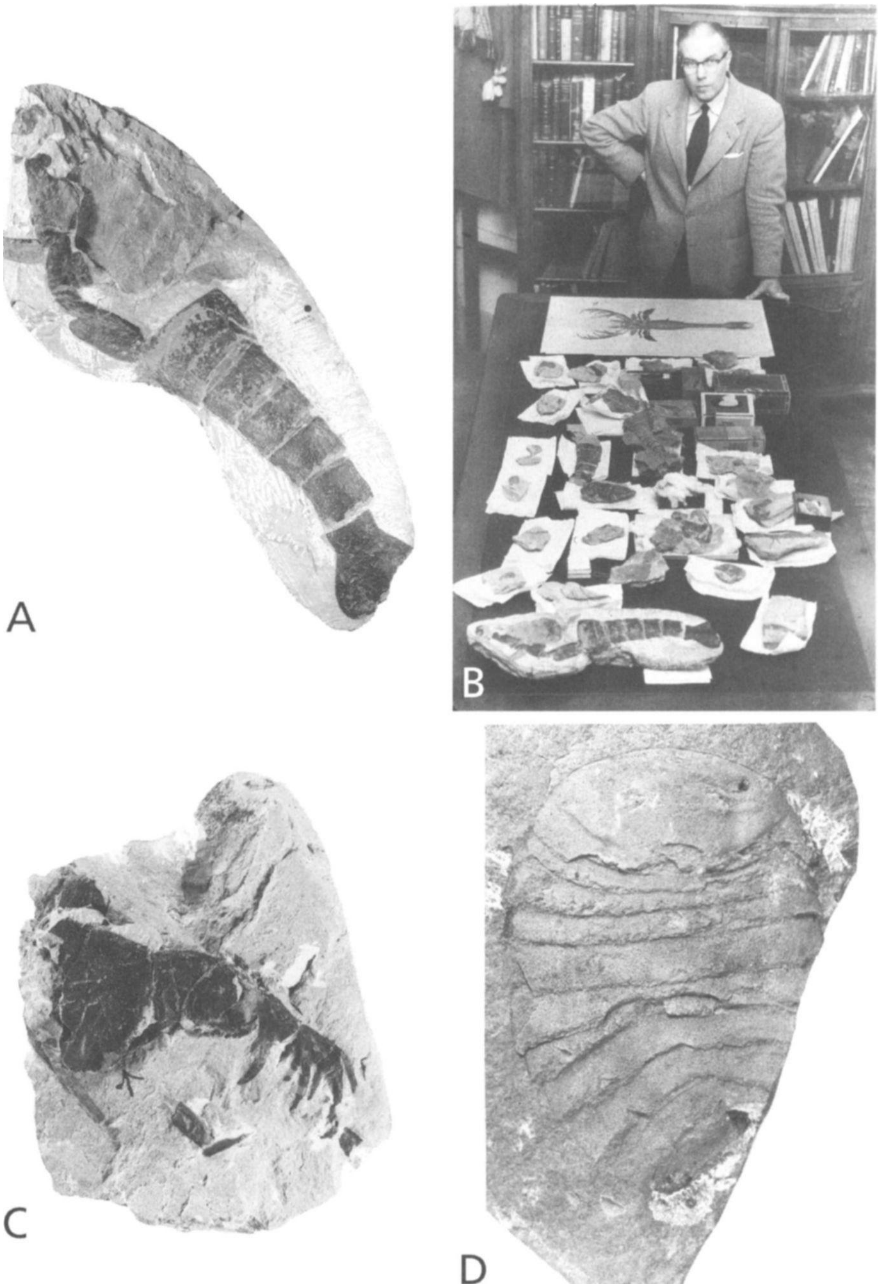


Figure 11.8. A, C *from Caster and Kjellesvig-Waering (1964, plate 45, figure 1, plate 46, figure 4) and reprinted by permission of the Paleontological Research Institution.* A. *Eurypterid Megalograptus ohioensis Caster and Kjellesvig-Waering, Richmondian, Elkhorn Formation, Adams Co., Ohio; ventral side of post-abdomen and last (sixth) pair of legs (darker segments), dorsal imprint of prosoma (grey segments turned to right near top), holotype, CMC IP 24119A, x 0.14.* B. *Professor Kenneth E. Caster with type specimens of Megalograptus ohioensis.* C. *First walking leg, paratype, CMC IP 24117A, x 0.9.* D. *Aglaspid Neostrabops martini Caster and Macke, holotype, CMC IP 25569, Maysvillian, Corryville Formation, Clermont Co., Ohio, x 1.4. From Caster and Macke (1952, plate 109, figure 2), and reprinted by permission of the Society for Sedimentary Geology.*

GALLERY

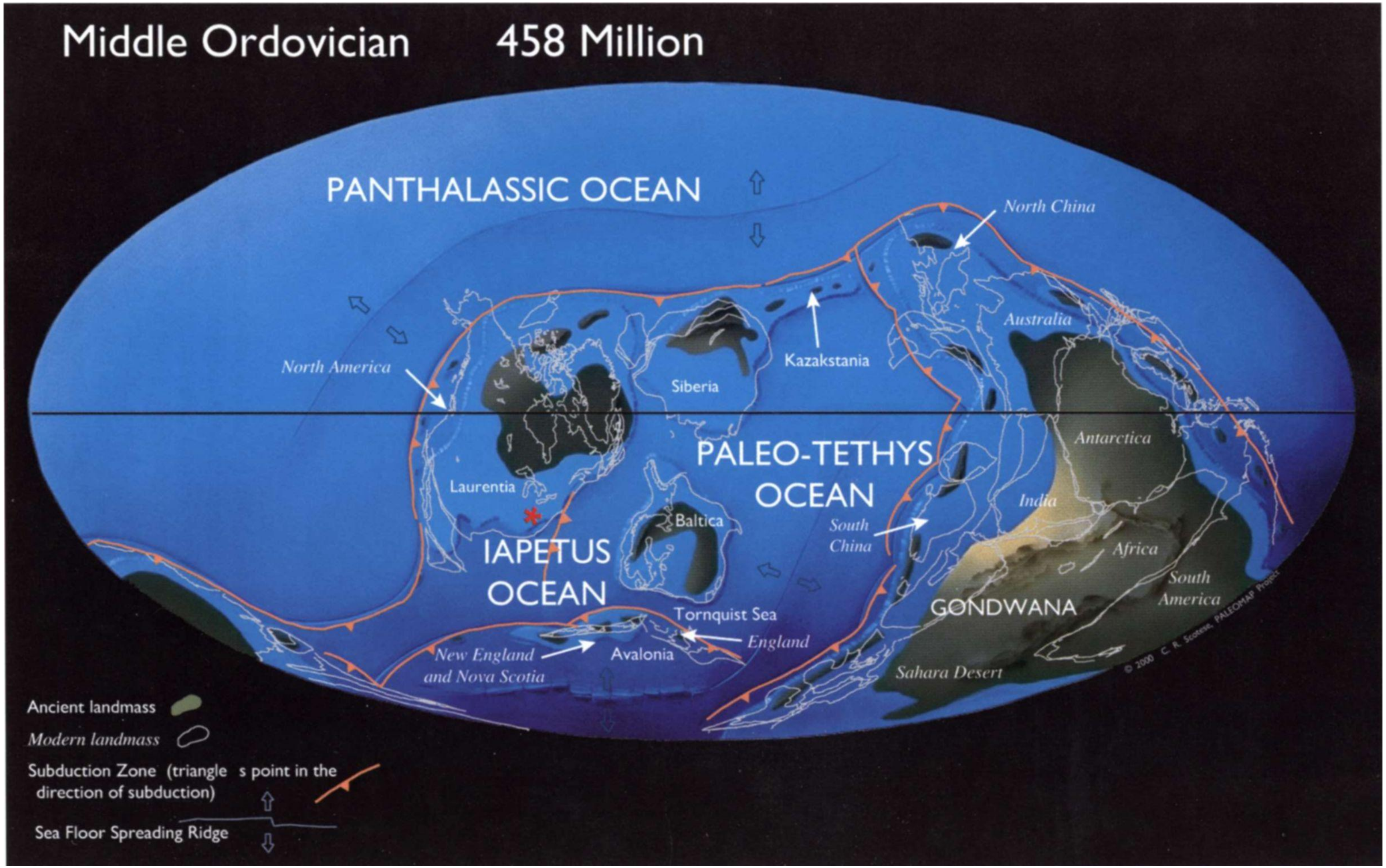


Plate 1. Ordovician continents and oceans. The reconstruction shown is for the Middle Ordovician, about 458 million years ago, about 5.5 million years older than the beginning of the Cincinnatian. Compare to Plate 2. The position of Cincinnati (*) on the paleo-continent Laurentia was south of the equator. *Map courtesy of* C. *R. Scotese, PALEOMAP Project (www.scotese.com).*

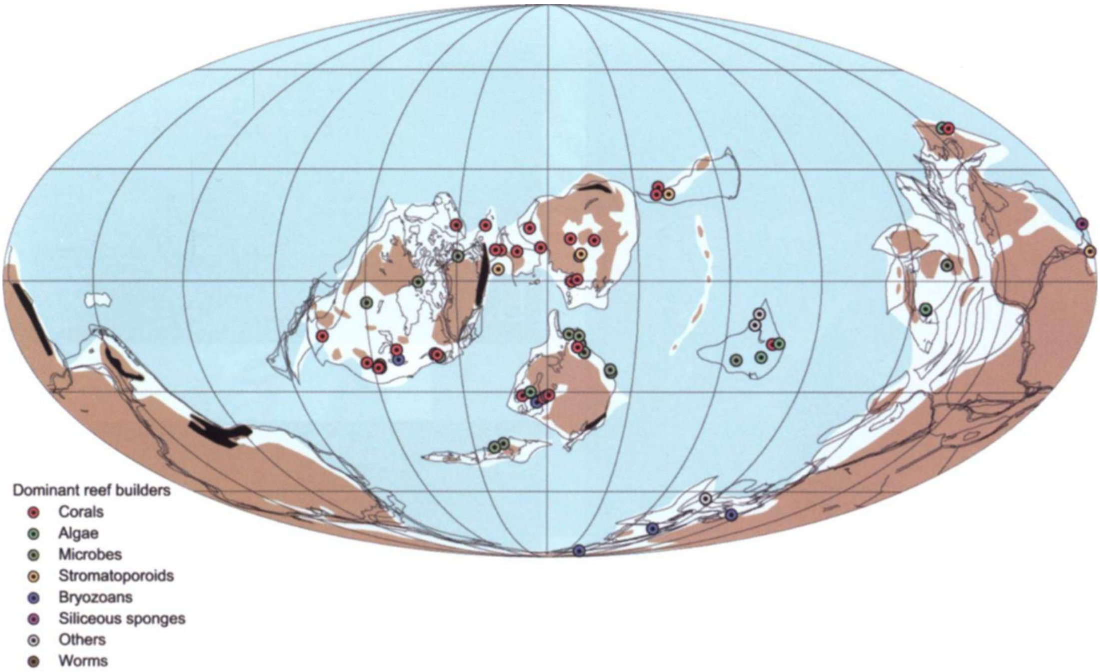


Plate 2. Late Ordovician continents and oceans. This reconstruction is for the youngest two stages of the Ordovician, the Ashgillian and Hirnantian. This timeslice includes the Cincinnatian interval. Dots indicate sites where reefs and related deposits are known for these stages, and colors indicate the dominant groups contributing to these deposits. Tan = land areas, light blue = epicontinental seas, and darker blue = deep oceans. *Map from Kiessling et al. (2003), and courtesy of Wolfgang Kiessling.*

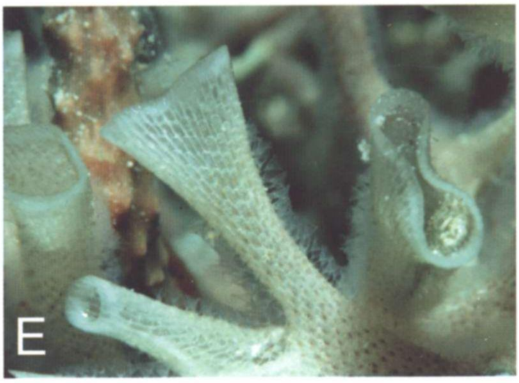
Plate 3. Living invertebrates related to type-Cincinnatian fossil groups. *All photos by D. L. Meyer except as noted.* **A.** Sponge, *Pericharax* sp., Lizard Island, Great Barrier Reef, Australia. Green fluorescent dye was released at base of sponge, taken into sponge's filtration system, and ejected as stream from osculum at top, as a demonstration of the sponge's filter-feeding capability. **B.** Coralline sponge, *Acanthochaetetes wellsi* Hartman and Goreau, submarine cave at 18 m depth, Palau Islands. Diameter 8 cm. Sponge tissue is a thin veneer over a calcareous skeleton. Coralline sponges are similar to Ordovician stromatoporoids. **C.** Scleractinian coral, *Tubastrea coccinea* Lesson, showing tentacle-bearing polyps, Curacao, Netherlands Antilles. *Photo by William K. Sacco.* **D.** Bryozoan, *Heteropora pacifica* Borg, San Juan Islands, Washington, depth 24 m. Colony form very similar to some Ordovician bryozoans. **E.** Bryozoan, unidentified cheilostome, Lizard Island, Great Barrier Reef. Australia, depth about 18 m. Note extended tentacles along funnel-shaped section at center. Funnel-shaped section will act as a "chimney" to direct water away from the colony after it has been filtered by the tentacles. **F.** Brachiopod, *Thecidellina,* Curacao, Netherlands Antilles. These brachiopods are cemented by the pedicle valve to the undersides of coral colonies. Note 90 degree gape of valves and extended tentacles of the lophophore. Width about 4 mm. *Photo by William K. Sacco.* **G.** Horseshoe crab, Family Limulidae, Subfamily Tachypleinae, Mersing, Malaysia.


A


B


C


D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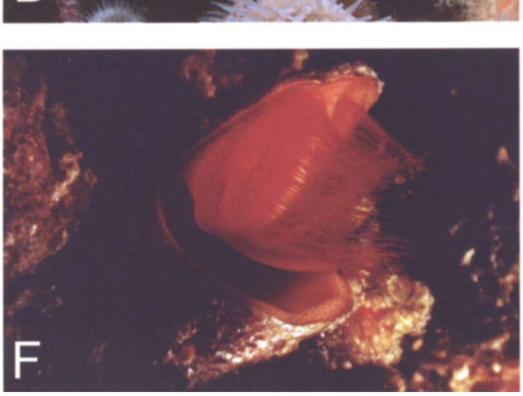
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Plate 4. *Nautilus,* the only living cephalopod with an external shell. *Photographs by Richard Arnold Davis.* **A., B.** *Nautilus macromphalus,* specimen trapped at Lifou and photographed in aquarium at Noumea, New Caledonia. **A.** Note the hyponome, the circular opening below the head. **B.** Note countershading pattern in which stripes are confined to upper side of shell. **C.** *Nautilus pompilius,* cross-section of shell, showing chambers and siphuncular tube.

Plate 5. A. Scolecodont, one element of an annelid worm jaw apparatus, *Nereigenys alata* Eller, CMC IP 1952, Fairview Formation, Dearborn Co., Indiana, x 70. B. Conodont, one element of an apparatus, *Phragmodus undatus* Branson and Mehl, CMC IP 50705, Kope Formation, Campbell Co., Kentucky, x 227.

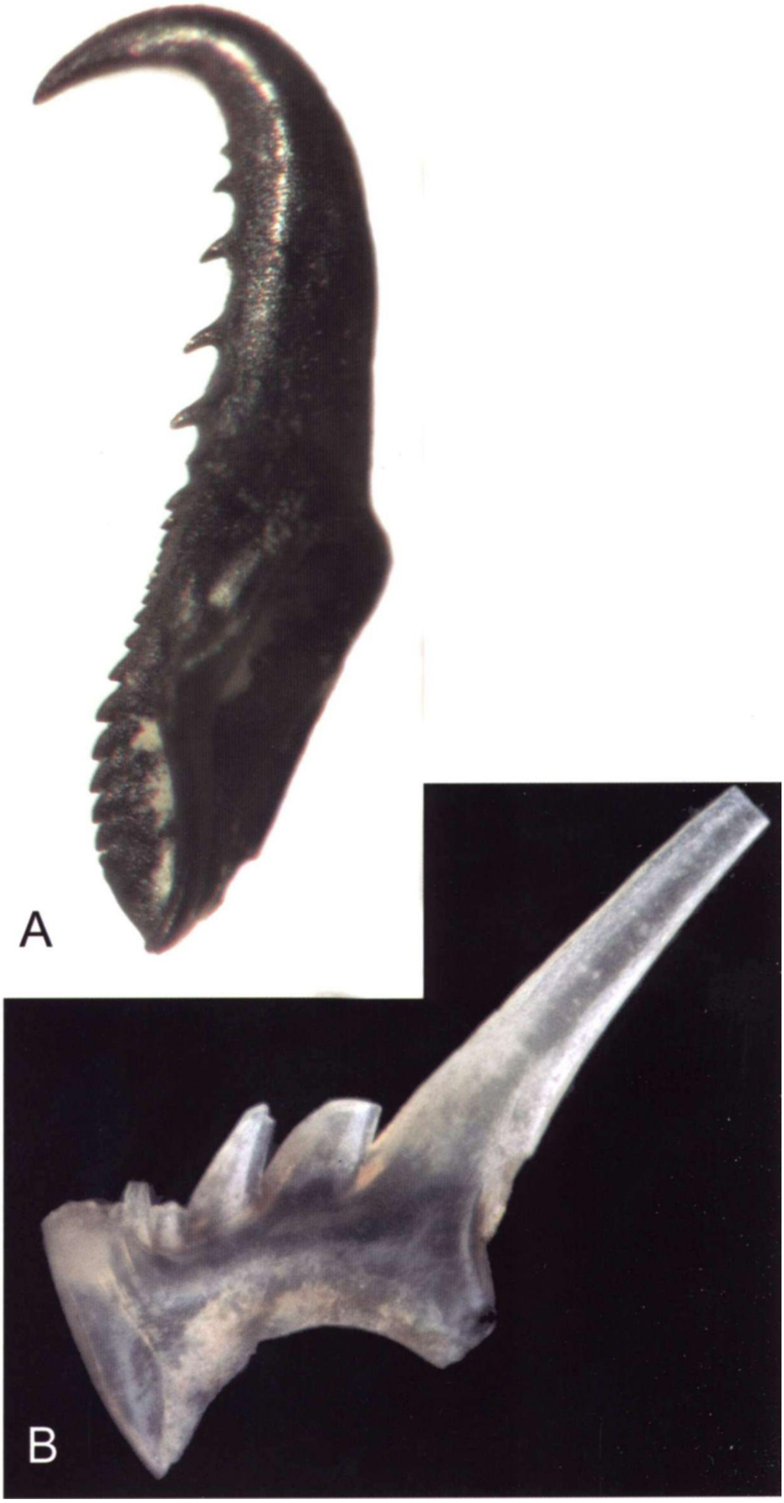


Plate **6.** *Allolichas halli* (Foerste), Dan Cooper collection, Richmondian, Waynesville Formation, Franklin Co., Indiana. This exceptionally rare, complete specimen shows a darker coloration around the margin of the carapace that may be a remnant of original coloration. This species was assigned to *Amphilichas* until 2002 when Holloway and Thomas placed it in *Allolichas*. Scale in mm.


3

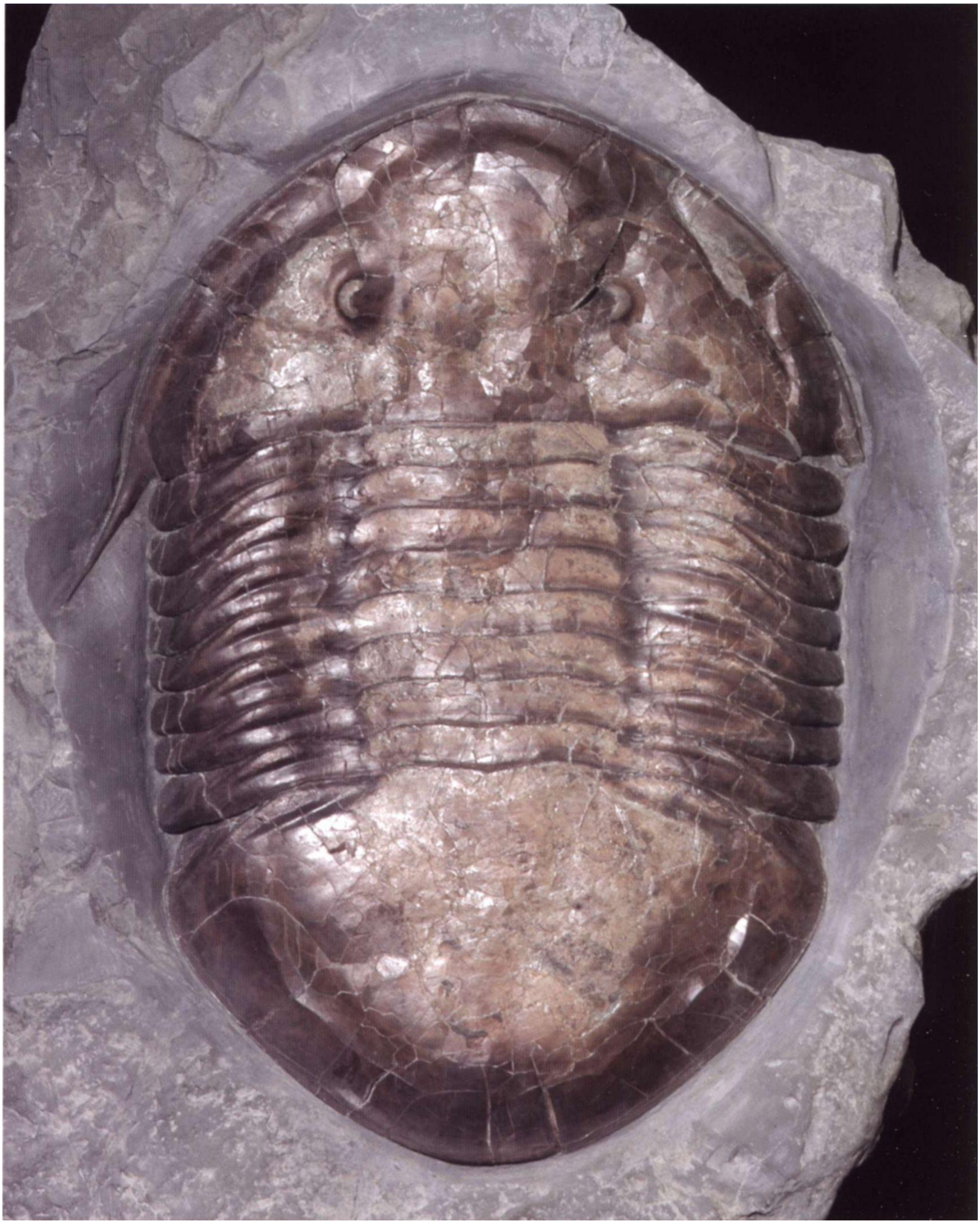


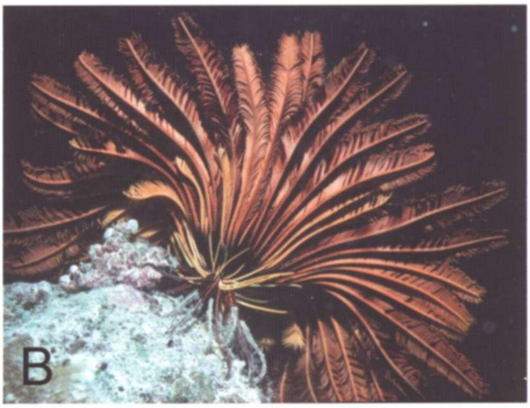
Plate **7.** *Isotelus maximus* Locke, CMC IP 50168, Richmondian, Adams Co., Ohio. This exceptional complete specimen is 37.5 cm in length and was collected and prepared by Thomas T. Johnson. *Isotelus* is the State Invertebrate Fossil of Ohio.

Plate **8.** A. *Flexicalymene retrorsa* on internal mold of nautiloid, CMC IP 50844, Arnheim Formation, Thomas Weaver Collection. Trilobite is located on phragmocone (chambered) section of the nautiloid mold, with head toward body chamber. Scale in mm. B. Parallel alignment of orthoconic nautiloids, CMC IP, Cincinnatian. Scale in mm. Note that not all specimens on the slab are aligned.


3
A


B


A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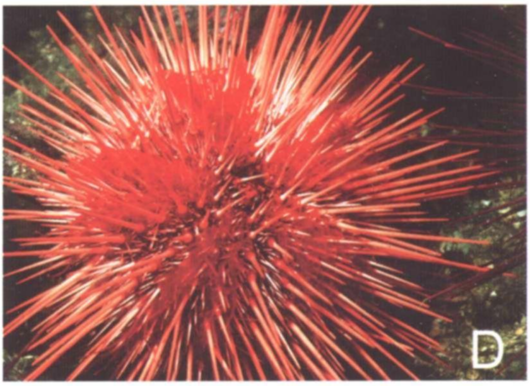
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Plate **9.** Living echinoderms. A. Stalked crinoids (sea lilies), *Neocrinus decorus* Thomson, northeastern Straits of Florida, height about 1 m, 420 m depth. B. Unstalked crinoid (feather star), *Pontiometra andersoni* (P. H. Carpenter), Palau Islands, 4 m depth, arm length about 12 cm. **C.** Ophiuroid (brittle star), *Ophiothrix* sp., Caribbean Panama, disk diameter 5-10 mm. **D.** Echinoid, *Strongylocentrotus franciscanus,* San Juan Islands, Washington, diameter about 15 cm. **E.** Asteroid (sea star), *Fromia nodosa* Clark, Seychelles, Indian Ocean, arm length about 40 mm. F. Holothuroid (sea cucumber), *Cucumaria miniata* (Brandt), San Juan Islands, Washington, height about 15 cm. *A. by Charles G. Messing, all others by D. L. Meyer.*

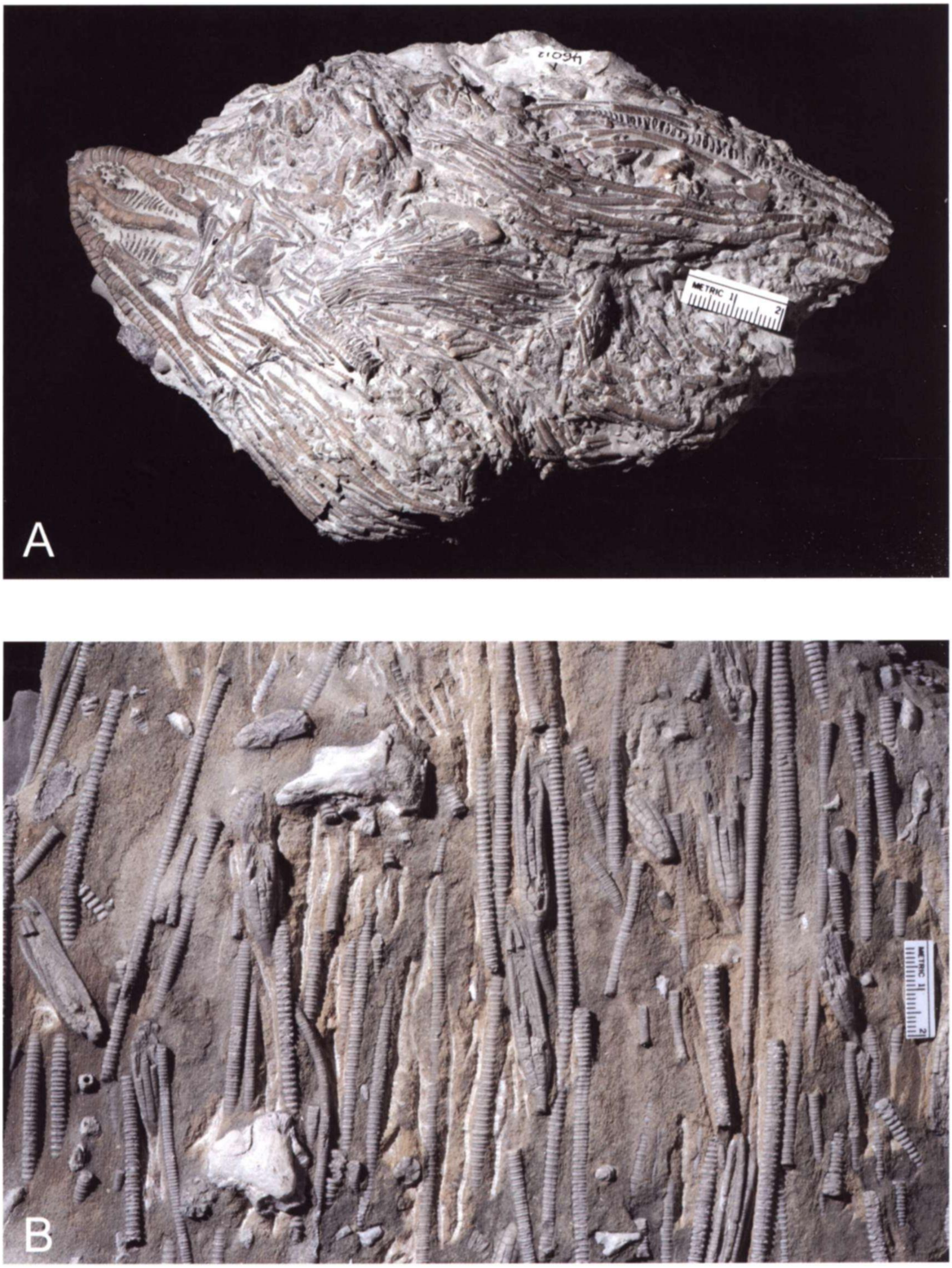


Plate 10. Cincinnatian disparid crinoids. **A.** *Iocrinus subcrassus* (Meek and Worthen), CMC IP 46012, Waynesville Formation, Franklin Co., Indiana; note large crown size and dense packing of crinoidal material. **B.** "Logjam" of *Ectenocrinus simplex* (Hall), CMC IP, Fairview Formation, Hamilton Co., Ohio; note parallel alignment of crinoids.

Plate 11. Cincinnatian cladid crinoids. A. *Cupulocrinus polydactylus* (Shumard), MUGM 28344, Oxford area, Butler Co., Ohio, six crowns, XI. B. *Plicodendrocrinus* casei(Meek), MUGM 28353, Liberty Formation, southwestern Ohio, two crowns, one overlaps the cup of the other, X1.3.

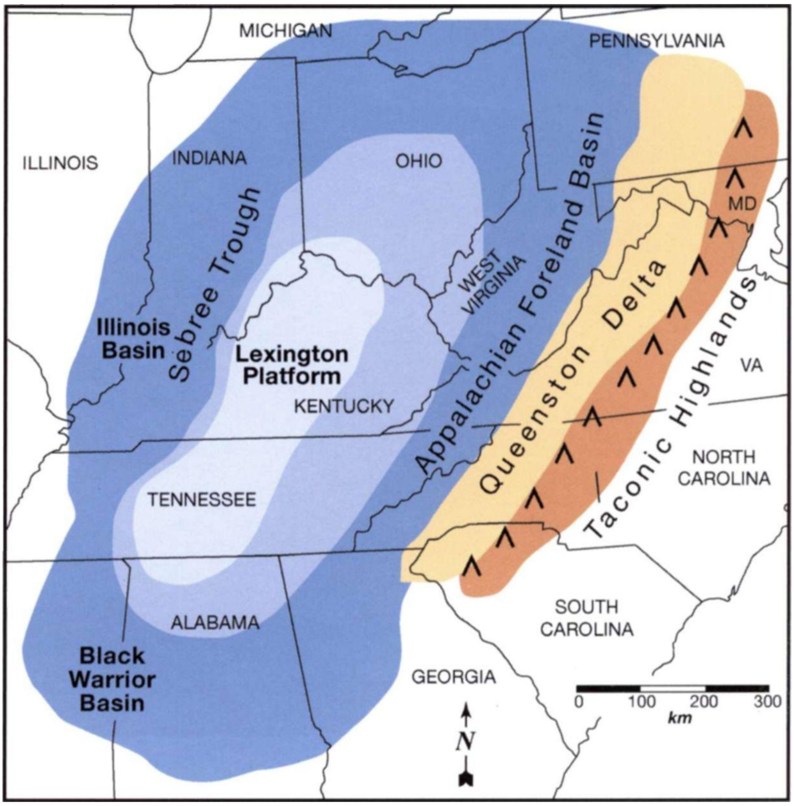


Plate 12. Late Ordovician paleogeography of the eastern United States. Light blue = shallowest water over Lexington Platform, medium blue = shallow subtidal depths, dark blue = deeper subtidal depths, buff = Queenston Delta, brown = Taconic highlands, the eventual location of the Appalachian Mountains. *Courtesy of Steven M. Holland.*

Plate 13. Dioramas of the Cincinnatian sea. A. Cincinnati Museum of Natural History, by Paul Marchand, about 1959, under direction of Kenneth E. Caster. B. Museum of Comparative Zoology, Harvard University.


A


B

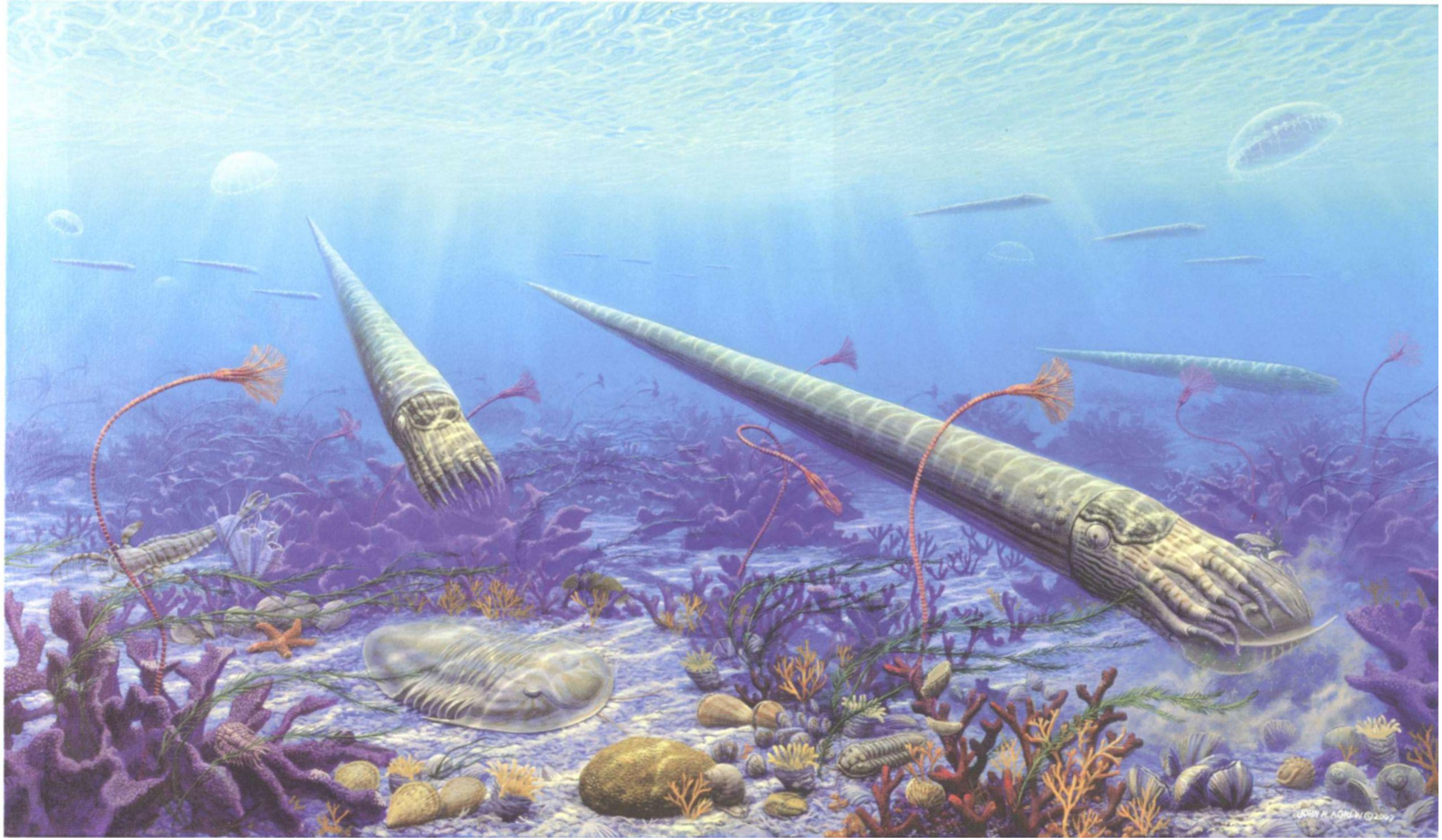


Plate 14. The Cincinnatian, by John Agnew, 2007.

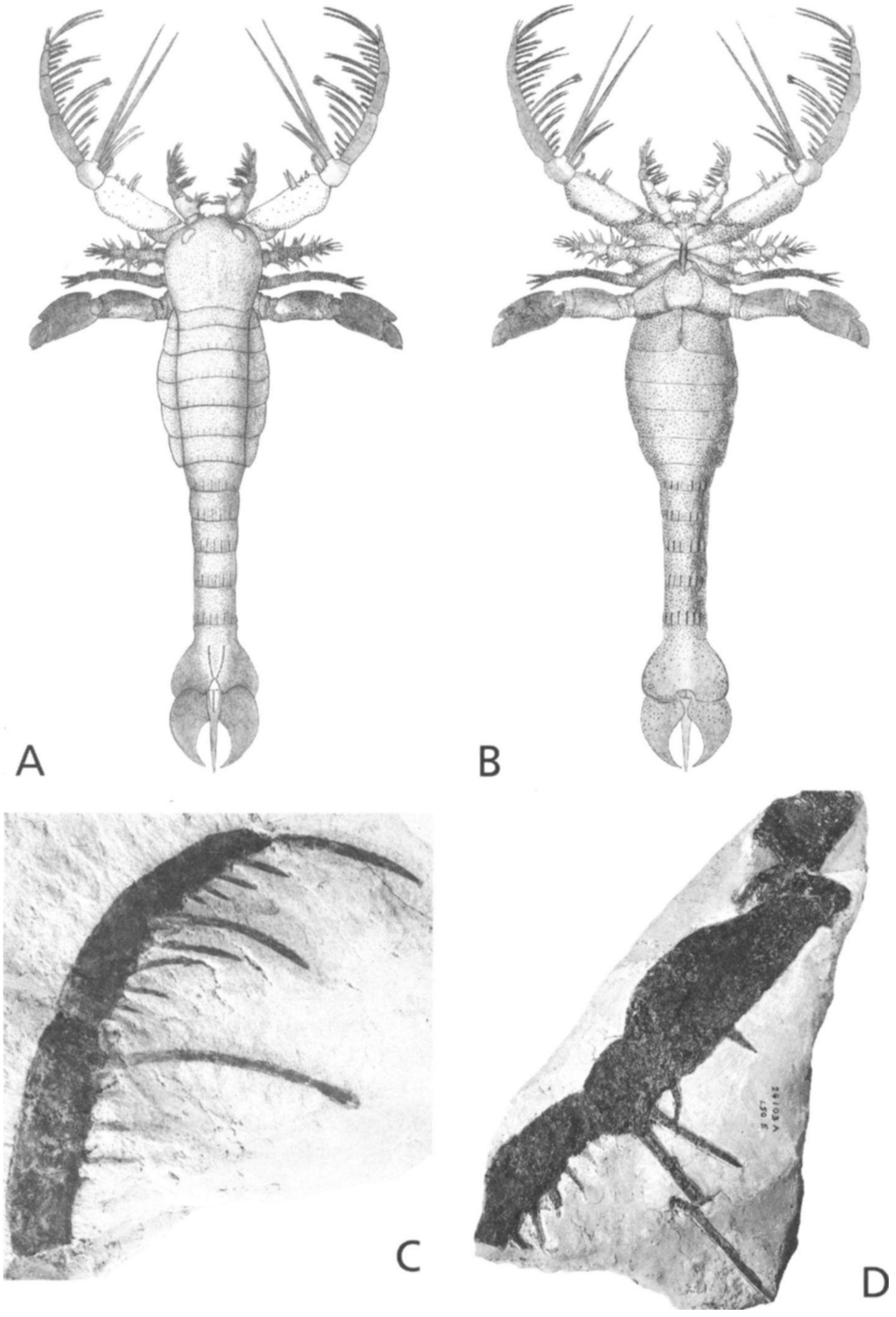


Figure 11.**9**. *Eurypterid Megalograptus ohioensis Caster and Kjellesvig-Waering.* C, D. *From Caster and Kjellesvig-Waering (1964, plate 49, figure 2, plate 48, figure 1).* A. *Reconstruction of dorsal surface of adult female (from Caster and Kjellesvig-Waering [1964, plate 43]),* x *0.14.* B. *Reconstruction of ventral surface of adult female (from Caster and Kjellesvig-Waering [1964, plate 44]),* x *0.14.* C. *Distal end of second walking leg, note bulbous expansion (sensory?) at end of longest spine, paratype, CMC IP 24115,* x *0.7.* D. *Third paired appendage, showing large coxa and part of first four joints, paratype, CMC IP 24103A.* x *0.4.* A-D *reprinted by permission of the Paleontological Research Institution.*

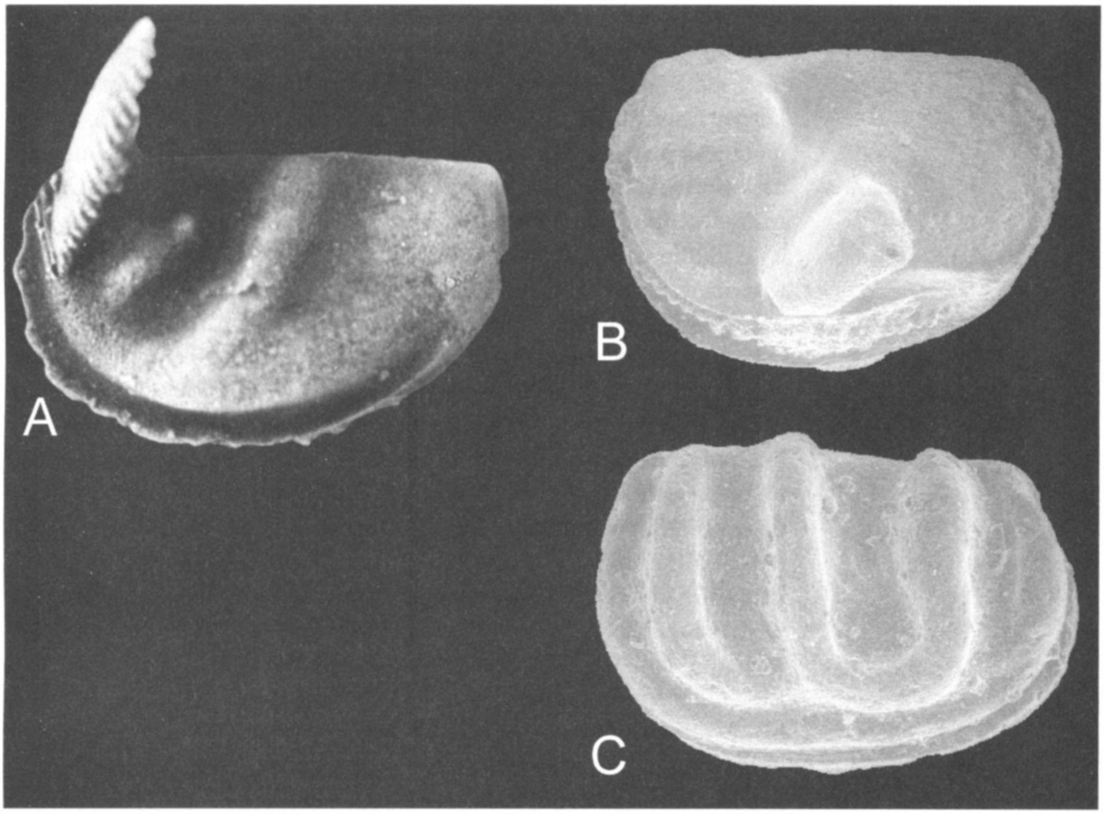
however, pointed out that very little flow could have passed through the minute pores and thus it is more likely that the pores had a sensory function to orient the animal into the current. It this is true, the pores may have been the sites of sensory hairs that were not preserved.

Triarthrus is restricted to the lowermost Kope formation but is significant for several reasons (figure 11.5B). *Triarthrus* is the last of the olenid trilobites that were prominent during the Cambrian. Pyritized specimens from the Upper Ordovician Utica Shale of New York are among the most well-preserved trilobites, from which detailed reconstructions of the appendages and internal soft anatomy have been made (Cisne 1970; Wliittington and Almond 1987). In the Cincinnatian, two species, *T. eatoni* and T. *spinosus,* are recognized (Babcock 1996a) but preserved appendages have not been found. The structure of the appendages in *Triarthrus* suggests that it was a particle feeder, sorting food particles with the thoracic appendages, which then passed them toward the mouth along the ventral axis (Fortey and Owens 1999). Enlarged, spine-bearing basal limb segments (gnathobases) beneath the cephalon acted like jaws to process the food and transfer it to the mouth. The restriction *of Triarthrus* to the dark shales of the lower Kope formation, and its dominance in some thin beds, both suggest that this trilobite was uniquely adapted to deeper water environments low in oxygen, as were other olenid trilobites (Fortey and Owens 1999).

Among Cincinnatian trilobites, two genera belonging to the Order Odontopleurida are unique in being festooned with spines and tubercles; these are *Acidaspis* and *Primaspis* (Figure 11.6). *Acidaspis* is distinguished by having a long spine originating on the occipital lobe of the cephalon and extending over the axial lobe of the thorax, as well as long genal spines and a fringe of short spines along the margin of the free checks (Figure 11.6A). A complete description of A. *cincinnatiensis* Meek is given by Whittington (1956). *Primaspis* lacks the occipital spine and has the cephalic spines lying in a curve (Figures 11.6C, E, F). Both genera have spines developed from the pleural lobes of the thorax and the pygidium. Ross (1979) provided excellent illustrations of these very small trilobites that are usually less than 1 cm in length and rarely found complete. *Acidaspis* occurs from the basal Kope Formation through the top of the Mavsvillian Ml. Auburn Formation, and reappears in the Richmondian Waynesville Formation. Whittington (1956) suggested that a single species, A. *cincinnatiensis,* is present. *Primaspis crosotus* (Locke) occurs in the Kope Formation where it was found in association with a cluster of *Flexicalymene* (Hughes and Cooper 1999).

The extreme spinosity of odontopleurids has prompted much debate-about their mode of life. The fringe of vertical cephalic spines in *Acidaspis* enabled the cephalon to be rested against the substratum with the thorax and pygidium outstretched and elevated slightly, in a probable feeding position (Whittington 1956). In this position the hypostome and mouth were situated close to the substratum. Clarkson (1969) pointed out that whereas *Acidaspis* had a single, fixed life position, *Primaspis* could assume the same feeding position and also a resting attitude by tilting the cephalon backwards so that the entire body was supported against the substratum. Odon-

Figure 11.10. *Cincinnatian ostracodes.* A. *Ceratopsis chambersi (Miller), CMC IP 40171, Kope Formation, Cincinnati, Ohio. From Warshauer (1972, plate 5),* x *30.* B. *Ctenobolbina alata Ulrich, CMC IP 33085, Kope Formation, Cincinnati, Ohio,* x *33.* C. *Quadrijugator regularis (Emmons), CMC IP 28245, Waynesville Formation, Butler Co., Ohio,* x *90.*



topleurids are considered to have been potential predators by Fortey and Owens (1999), but their prey must have been very small.

Plate 6 and Figure 11.7 illustrate exceptionally well-preserved specimens of some of the rarest of Cincinnatian trilobite species.

Eurypterids

One of the most intriguing fossils known from the Cincinnatian is the eurypterid ***Megalograptus*** (Figures 11.8, 11.9). Eurypterids are chelicerate arthropods, distinguished by having the first pair of appendages (chelicerae) equipped with small pincers. Modern chelicerates are the horseshoe crabs (Plate 3G), and arachnids (scorpions, spiders, mites, and ticks). The body of the eurypterid is unique, with a distinct head (prosoma) bearing compound eyes followed by an elongated, segmented section called the opisthosoma, divided into a wider preabdomen and a narrower, tail-like postabdomen (Figures 11.9A, B). Six pairs of appendages were attached to the underside of the head and served functions of feeding and locomotion. Because the exoskeleton was not calcified, preservation of the chitinous remains of eurypterids was unlikely, and therefore they are usually very rare fossils.

Eurypterids first appeared in the Early Ordovician and attained their maximum diversity in the Silurian, but *Megalograptus* is significant for being one of the oldest and most unusual. When fragments of the animal were first described in 1874 by S. A. Miller, they were thought to be parts of a graptolite, hence the name. Later workers corrected the error on the basis of additional, albeit fragmentary discoveries. A truly phenomenal discovery made in 1938 of exceptionally well-preserved and nearly complete specimens from a single bed in the uppermost Cincinnatian Elkhorn Formation of the Richmond Group in Adams County, Ohio, led to a better understanding of the animal (Figure 11.8B). This material, which included male and female specimens, became the basis for a new species, *M. ohioensis,* described by Kenneth F. Caster and Frik Kjellesvig-Waering in 1964. One additional eurypterid species, *Eocarcinosoma batrachophthalmus,* was described from this bed on the basis of an isolated prosoma.

Megalograptus ohioensis was one of the largest creatures in the Cincinnatian sea floor community, reaching a length of over 50 cm. The first pair of appendages, the chelicerae, is small and located beneath the head. The next three pairs of appendages bear well-developed spines (Figure 11.9). The third appendages are most striking for their length and long spines directed toward the midline (Figures 11.9C, D). Exactly how the eurypterid used these spiny appendages is uncertain. Caster and Kjellesvig-Waering considered *Megalograptus* to have been a predator, and thus the appendages likely had some function in grasping prey. The basket-like structure of the long spines of the third appendages suggests that the animal might have raked them through the sediment in order to extract prey in a sieving fashion. Only a few other eurypterids have similar long spiny appendages. Tubular castings filled with fragments of eurypterid integument associated with the eurypterid material could represent feces of the animal, indicating cannibalistic behavior like that found in living eurypterid relatives among the scorpions and spiders. The fourth pair of appendages lacks spines, and the fifth pair has expanded, flattened segments giving them a paddle-like appearance (Figures 11.9A, B). These were most likely employed in swimming.

One of the most peculiar features of *Megalograptus* is the development at the end of the postabdomen of a pair of expanded, hook-like cereal blades flanking a spine-like telson (Figures 11.9A, B). Caster and Kjellesvig-Waering thought that the cereal blades could move laterally in a scissor-like motion, possibly serving to grasp either in defense or copulation. The paired, incurved posterior spines of earwigs are similar, but nothing like this structure appears in any other eurypterid.

In addition to the Adams County occurrence *of Megalograptus ohioensis* in the Elkhorn beds. Caster and Kjellesvig-Waering described two other species from the Cincinnatian. M. *shideleri* is known from fragments occurring in the Saluda Formation of the Richmond Croup and *M. williamsae* from the Waynesville Formation of the Richmond Group. Fragments of M. *shideleri* suggest that it may have reached two meters in length. The type species, M. *welchi,* was originally described from the Liberty Formation, thereby indicating that the genus ranges through virtually the entire upper Cincinnatian. *Megalograptus* was not restricted to the Cincinnati Arch region, as *M. alveolatus* is known from the Upper Ordovician of Virginia.

In the Liberty occurrence, described by Foerste (1912), *Megalograptus* was found in a pocket together with crinoids. In the Elkhorn, *Megalograptus* was associated with a diverse marine fauna including trilobites, brachiopods, bryozoans, and molluscs. Despite the common notion that eurypterids lived in somewhat restricted or atypical marine environments, the Cincinnatian occurrences argue strongly for association with the normal marine biota. Their chitinous integument may account largely for their rarity in the Cincinnatian. The extraordinary quality and quantity of eurypterid preservation at the Adams County site may have resulted from smothering of the marine fauna by volcanic ashfall, because the 15 cm-thick shale within which the fossils were concentrated was found to contain bentonitic clays (Caster and Kjellesvig-Waering 1964).

Neostrabops

In 1952 Caster and Macke described what they termed a maverick merostome, *Neostnibops martini,* from a single specimen found in the Maysvillian Corryville formation in Clermont County, Ohio (figure 11.8D). This fossil could be taken to be a trilobite, but lacks the characteristic lengthwise division into three distinct lobes. It also resembles the aforementioned eurypterids in having numerous narrow segments, although it lacks any demarcation of pre-and postabdomen. *Neostrabops* does resemble other arthropods known as aglaspids from the Cambrian. Aglaspids are regarded as early offshoots of the evolutionary lineage of modern horseshoe crabs, the well-known *Limulus.*

Ostracodes

Crustaceans are one of the most abundant and diverse groups of living arthropods, yet they are represented in the Cincinnatian by only one group, the ostracodes (major living crustaceans such as shrimps, lobsters, and crabs evolved much later than the Ordovician, and thus are not found in the Cincinnatian). Ostracodes are generally very small, less than 1 mm in length, but can exceed 1 cm in forms like the Ordovician *Eoleperditia.* They are distinguished by a calcitic, bivalved shell or carapace that can be smooth or have various surface features such as knobs, ridges, or spines (figure 11.10). When the hinged valves of the carapace open, the appendages can be extended for feeding and locomotion. Modern ostracodes have a wide range of feeding habits, but many live as benthic suspension feeders and deposit feeders. It is very difficult to determine the specific habits of Cincinnatian species, because the appendages and other internal anatomy are not preserved

Ostracodes are diverse and abundant throughout the Cincinnatian Series, although this is generally unappreciated because few collectors or researchers encounter these microfossils. Two major studies on Cincinnatian ostracodes provide a modern analysis of their diversity and classification, but there is no single comprehensive study that gives an overview of total Cincinnatian ostracode diversity. Warshauer and Berdan (1982) reported fifty-three species and thirty-nine genera of ostracodes belonging to two major orders, the Palaeocopida and the Podocopida, from the Middle Ordovician Lexington Limestone and the Upper Ordovician (basal Cincinnatian) Clays Kerry formation of Kentucky. Species in these groups are all very small, and were extracted from disaggregated shales or by acid dissolution of the Lexington Limestone in which the fossils are silicified. fourteen genera occur in the Clays Ferry formation, but distribution within the rest of the Cincinnatian was not studied. Berdan (1984) reported on ostracodes of the order Leperditicopida from the Middle and Upper Ordovician of Kentucky and vicinity. These ostracodes are noteworthy for their size (sometimes > 1 cm long) and high abundance in single beds of fine-grained limestone. The occurrence of leperditicopids is restricted to fine-grained limestone facies deposited in extremely shallow subtidal to intertidal environments particularly well known from the Middle Ordovician High Bridge Group of Kentucky (Cressman and Noger 1976). This unique facies is absent from the deeper water facies of the lower and middle Cincinnatian but recurs in the Richmondian Sunset Member of the Arnheim Formation, in which four species are found.

Figure 12.1. *One skeletal element of a modern crinoid, showing the porous microstructure (stereom) typical of all echinoderms. The arm of a crinoid is composed of a series of these elements, connected by muscles and ligaments. Comactinia sp., Caribbean. Scanning electron micrograph,* x 79.

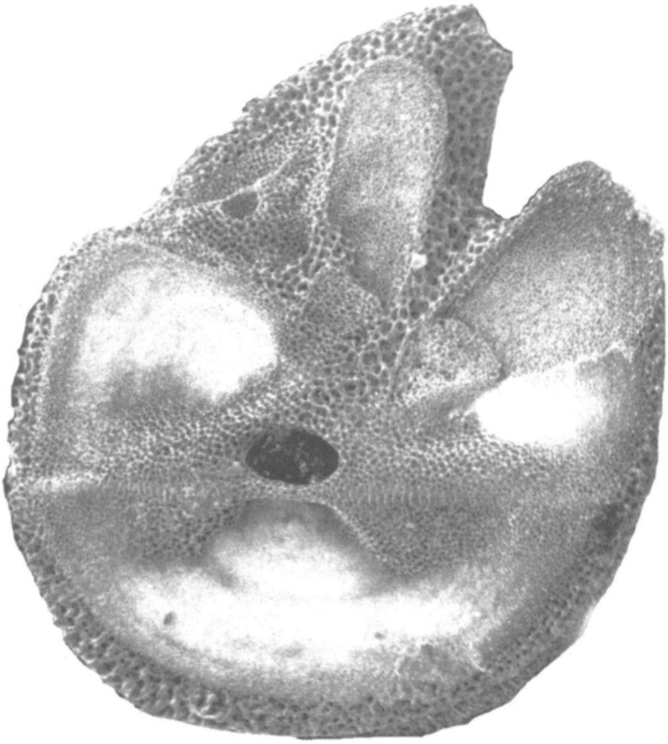


Figure 12.2. *Arm of modern crinoid (dark) with pinnules (light branches) bearing fine tube feet in feeding posture. Pinnule length about 1 cm. Aquarium photo, comasterid crinoid, Curacao, Netherlands Antilles*

ECHINODERMS: A WORLD UNTO THEMSELVES

12

I . . here salute the noble echinoderms as a noble group especially designed to puzzle the zoologist.

L. H. Hyman 1955, vi

Echinoderms are among the rarest and most sought-after fossils in the Cincinnatian rocks. Not only are they complex in form and structure, but they also possess a certain beauty and mystery that never fail to attract interest. Anyone who has visited the seashore is familiar with living echinoderms such as sea stars or starfish (asteroids), sea urchins, and sand dollars (both echinoids) (Plate 9), Other living echinoderms found in deeper marine waters are the sea lilies and feather stars (crinoids), brittle stars (ophiuroids), and sea cucumbers (holothuroids) (Plate 9). There are about 6650 living species of echinoderms, and over 3500 genera and 13,000 described fossil species.

The Ordovician Period marked a very significant time in the evolution of echinoderms, because many different major groups (usually regarded as classes) of echinoderms coexisted. Like other invertebrate phyla, the oldest fossil echinoderms are found in Early Cambrian rocks over 500 million years old, but it was not until Ordovician time that echinoderms began to leave a significant fossil record. Early in the Ordovician, echinoderms diversified along with many other marine invertebrates, and by Late Ordovician time a bewildering variety of echinoderms had appeared in shallow marine environments worldwide. Although the five classes of modern echinoderms (crinoids, asteroids, ophiuroids, echinoids, and holothuroids) existed then, many other classes were also present. In some strata of Late Ordovician | Mohawkian) age, as many as fourteen classes of echinoderms are found together (Sprinkle and Cuensburg 1997). Because some of these classes soon became extinct, echinoderm diversity had declined by Cincinnatian time, but still exceeded present levels, with seven classes found in the Cincinnati Arch region.

More than one observer has noted (tongue in cheek) that if ever any animal group could have originated as "alien beings" that landed on Earth from outer space, it would be the echinoderms—so bizarre are their body forms, particularly among the wide variety we see among Ordovician fossils. The features that identify all these strange fossils as echinoderms are not the traits we usually consider characteristic of echinoderms, the "spiny skin" that gives the group its name, and the five-fold (pentameral) symmetry of the body. The single most characteristic trait of echinoderms is the nature of their skeleton. All echinoderms have a mineralized skeleton composed of calcium carbonate as the mineral calcite. Unlike other invertebrates that have calcitic shells, the echinoderm skeleton is formed within the middle cell layer of the body (mesoderm), and has a thin outer layer *of* cells covering it (ectoderm), thus making it an internal skeleton. Because the outer cell layer is so thin, we often think of echinoderm skeletons such as sea urchin shells as external, but in other cases, such as the arms of many sea stars, the skeletal components, called ossicles, are clearly internal, beneath a leathery "skin." In addition, because it is truly mesodermal, the echinoderm skeleton has a unique microstructure not found in any other animal group. The calcite is formed around mesodermal cells into an intricate three-dimensional latticework called the stereom (Figure 12.1). Skelet al plates, spines, or ossicles thus have a highly porous structure in which over 50 percent of the volume can be taken up by pores. In life the nurturing cells occupy these pores, but after death, the cellular material decays, leaving the porous skeleton. Buried in sediment, these pores are usually infilled with secondary calcite, and the entire skeletal plate displays the typical rhombic cleavage of calcite. Often the microstructure is still visible in thin or polished sections. These features have enabled many fossil echinoderms to be correctly identified, even though their body form may be considerably different from any of the five familiar living groups.

Echinoderms are also peculiar in lacking structures like a distinct head, eyes, or internal systems such as a blood circulatory system or respiratory system. Instead, they are unique in having an internal system of branching vessels that contain not blood, but a watery fluid that circulates dissolved oxygen and dissolved wastes and pressurizes the vessels themselves. The vessels terminate in characteristic structures called tube feet, which serve important functions for all echinoderms (Figure 12.2). Dissolved oxygen is exchanged across the thin membrane of the tube feet and dissolved wastes are expelled. In groups like crinoids and ophiuroids, tubefeet are like minute bristles that capture food particles suspended in the water. Sea stars and sea urchins have tube feet with suction disks by which they cling to rocks, and which aid in pulling clamshells apart, in the case of sea stars, and in "walking" across the sea floor. Tube feet are practically never preserved in fossils, but traces of the canals are revealed in the skeleton, providing yet another indication of echinoderm affinity. Recently pyritized tube feet were discovered in a Cincinnatian ophiuroid, providing one of the few cases in the entire fossil record and rare evidence for preserved soft tissues among Cincinnatian fossils (Class 2006).

The five-fold or pentameral body plan seen in living echinoderms appears in many of the Cincinnatian fossil echinoderms (Figures 12.5, 12.10-12.16), but this is by no means a universal feature. The enigmatic "carpoids" lack any trace of pentameral form (Figure 12.17). The larvae of living echinoderms are actually bilaterally symmetrical, and pentamery appears only in adult stages. The five-part structure is virtually unique to echinoderms in the Animal Kingdom, and zoologists have debated its significance and origins. Sprinkle (1973) found that pentameral symmetry first appeared in the food-gathering system of Early and Middle Cambrian eocrinoids, and later developed in the calyx plates and respiratory structures. This suggests that pentameral symmetry provided an advantage for the sessile, filter-feeding habits of these early echinoderms. Initially, some eocrinoids actually have a three-fold radial arrangement of the food-gathering structures that later became five-fold by the branching of only two food grooves or ambulacra. Branching beyond the five-fold pattern may have been limited by the available space around the mouth, and thus the pentameral pattern may have been the most efficient solution. Once pentameral structure became genetically programmed in Echinoderms, it persisted even in groups that gave up the ancestral mode of life to become mobile sea stars or sea urchins.

Despite their many "alien" features, Echinoderms are significant as one of the invertebrate phyla most closely related to our own, the chordates. For a long time zoologists studying the embryonic development of echinoderms have recognized close similarities in the early development of echinoderms and chordates. Both groups have symmetrical cell division in the fertilized egg, indeterminate development (embryonic cells are not preprogrammed to form a specific adult tissue), and the internal body cavity, the coelom, forms in the same way in the embryo. Recent studies of molecular composition of animal phyla demonstrate that echinoderms are much more closely allied to hemichordates and chordates than to any other group (Raff 1996).

Complete fossil echinoderms are indeed rare fossils in Cincinnatian strata, but the abundance of their isolated skeletal components suggests that they were very common members of sea floor communities during the Ordovician. The reason for their rarity as complete fossils is found in the nature of the echinoderm skeleton, composed of myriad tiny plates or ossicles, all held together in life by fibers of connective tissue that penetrate pores of the stereomic skeleton. Upon death, these fibers rapidly decay; the skeletal components separate, and are usually dispersed by water movement (Figure 12.3A). Among the most common fossils found around Cincinnati are the disk-like or ring-like segments of the crinoid stem (columnals; Figures 12.3A, 12.5). These are often isolated like tiny LifeSavers or still connected in varying lengths like strings of beads. Entire limestone layers often consist of nothing but dissociated crinoid columnals, originally crinoidal sands, sometimes sorted by currents into zones of common size, and formed into rippled surfaces. Because echinoderms are so susceptible to breakup of the skeleton after death, the occurrence of complete, articulated skeletons usually requires rapid burial in sediment. Thus, complete crinoids are found within shales or on the upper surface of limestones covered by shales, or more rarely at the base of calcareous siltstones. The very nature of this complete preservation provides a valuable clue that the enclosing sediment was in fact deposited rapidly, probably timing storms, either as stirred up bottom sediments or underwater mudslides.

Echinoderms of the Cincinnatian

The seven classes of echinoderms found in Cincinnatian strata are the Crinoidea, Rhomhifera, Kdrioasteroidca, Asteroidea, Ophiuroidea, Cyclocystoidea, and Stylophora. of these, the crinoids are the most abundant in the field and the most diverse in number of species.

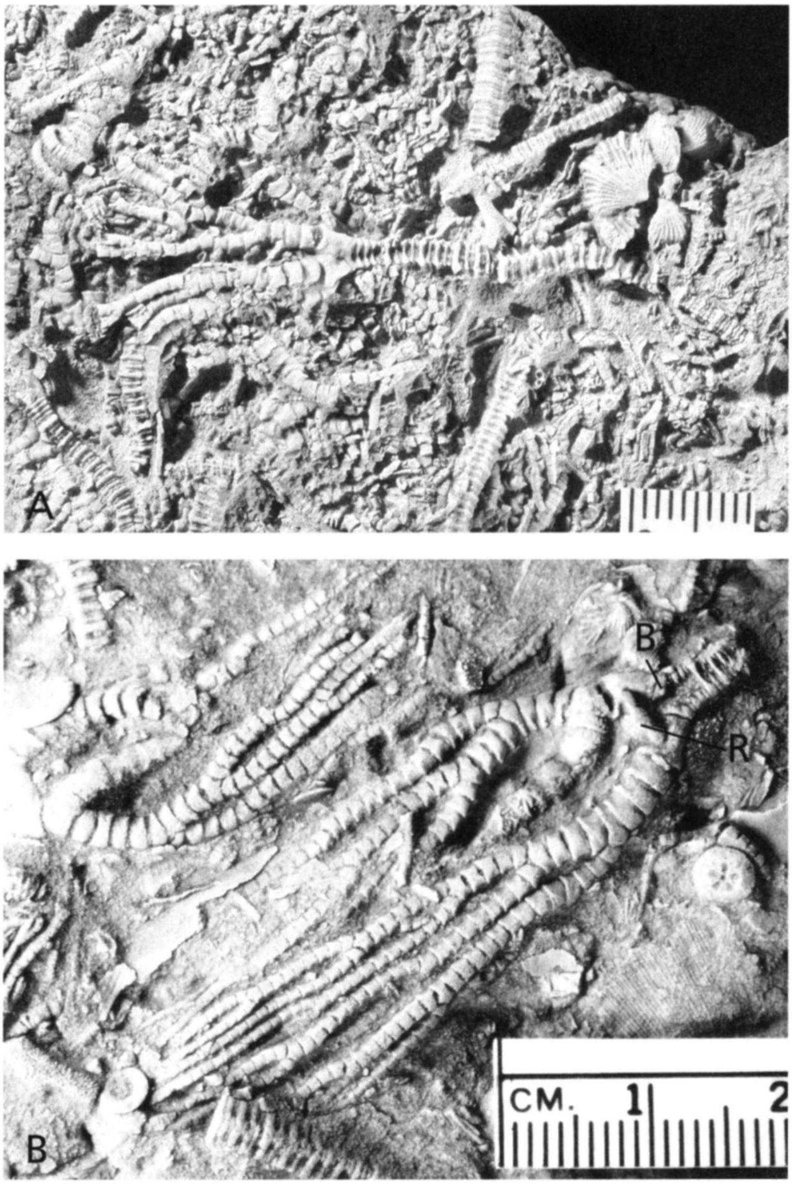
Crinoids

Stemmed crinoids (sea lilies) are attached to the sea floor by means of a holdfast or root, and elevated above the bottom by a stem composed of many co-

Figure 12.3. *Variable preservation of crinoids. Iocrinus subcrassus (Meek and Worthen).*

A. *Articulated individual with partially disarticulated sections of stalk, and matrix of disarticulated skeletal components. Upper Ordovician, Corryville Formation, Cincinnati, Ohio. University of Cincinnati collections.*

B. *Two articulated crowns, detached from stalk, oriented parallel but in opposite direction, preserved on base of bed. Upper Ordovician, Corryville Formation, Clermont Co., Ohio. CMC IP 44362. Scale in mm. B in upper right denotes basal plate; R denotes radial plate.*



There were also some *beautiful forms of Crinoidea, or stone-lilies . .*

Charles Lyell 1845, 50

lumnals (Figures 12.3-12.5). The body is enclosed within a plated calyx composed of the lower cup and a roof-like tegmen. The cup has a regular arrangement of plates: a circlet of five radials, and either one circlet (monocyclic) of basals or two circlets (dicyclic) of basals and infrabasals occurring above the stem (Figures 12.3B, 12.10A). The arms arise from the radials of the cup and usually branch and may support finer branches, the pinnules, giving the arm a feathery appearance (Figure 12.4). The arms and pinnules carry the food grooves (ambulacra) which convey tiny food particles to the mouth situated on the upper surface of the calyx. Living crinoids are passive suspension feeders, dependent on currents to supply food particles to the awaiting feeding apparatus. The animal constructs a filtration fan of the arms and pinnules

Figure 12.4. *Reconstruction of Glyptocrinus decadactylus in life position. Calyx is in a horizontal position, with the arms splayed into a filtration fan. By analogy with living crinoids, current flow was from left to right. Drawing by John Agnew.*

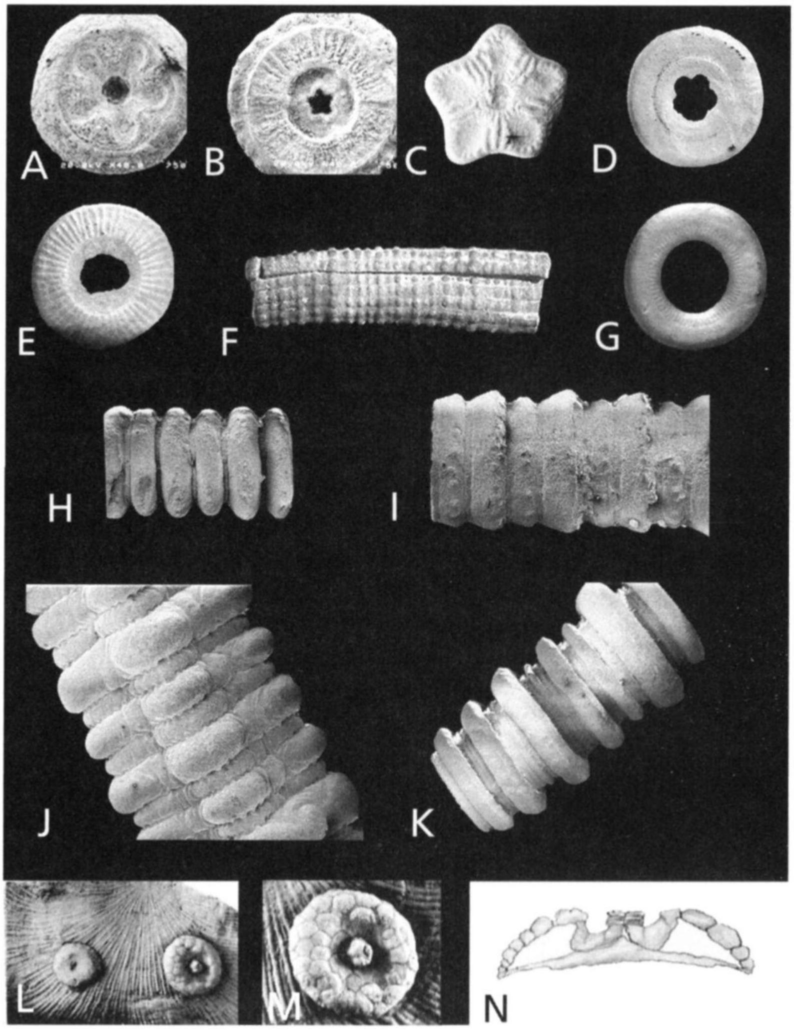


Figure 12.5. *Cincinnatian crinoid columnals and holdfasts.* A, H. *Cincinnaticrinus varibrachialus Warn and Strimple;* A. *Articular surface* x *9.6;* H. *Lateral view of mature section* x 5.9. B, I. *Ectenocrinus simplex (Hall).* B. *Articular surface* y.*9.6;* I. *Lateral view* 12.6. C,* J. *locrinus subcrassus (Meek and Worthen).* C. *Articular surface* x *5.2;* J. iafera/ *view* x 4.4. D, G, K. *Glyptocrinus decadactylus Hall;* D, G. *Articular surfaces of internodal, nodal respectively,* x 4.4; K. *Lateral view* x 6; note *three cycles ofinternodals.* E. *Merocrinus curtus Ulrich, articular surface* x *5.2.* F. *Anomalocrinus incurvus (Meek and Worthen), lateral view of compressed section with fracture separating meres,* x *1.* A-K, *from Meyer et al. (2002, figure 2) and reprinted by permission of The Paleontological Society. I,* M. *Lichenocrinus crateriformis Hall, FMNH8810.* L. *Two specimens attached to brachiopod,* x *1.6.* M. *Enlargement of larger specimen in I,* y.*3.7, Waynesville Formation, Warren Co., Ohio. From Faber (1929, plate 32, figures 5, 6) and reprinted by permission of the American Midland Naturalist.* N. *Lichenocrinus milleri Faber, CMC IP 10047, Elkhorn Formation, cross-section showing floor plate with central node, crater plates, and base of column,* y.*3.7, from Faber (1929, plate 33, figure 9).*

arrayed perpendicular to current flow, thus acting as a "flow-through" filter (Plates 9A, B). Tiny tube feet lining the pinnular food grooves snare food particles such as organic detritus and plankton and stuff them into the food groove for transport to the mouth. The close similarity of Ordovician crinoids to modern forms suggests that ancient crinoids used similar feeding postures and modes of capturing food, and we can imagine that they looked quite like stemmed crinoids that today exist only in the deep sea (Plate qA).

Crinoid columnals are among the most commonly encountered fossils in the Cincinnatian. They are found either as single columnals or articulated sections of the stem (figures 12.3, 12.5). Although superficially very similar in appearance, columnals can usually be identified to genus. Crinoid species are usually described from specimens of the calyx or crown that are less common.

Twenty-one genera of crinoids are known from the Cincinnati region. Some genera are monospecific (having only one species) and others have more than one species, bringing to twenty-eight the total number of species in the local area. Cincinnatian crinoids represent all three of the subclasses

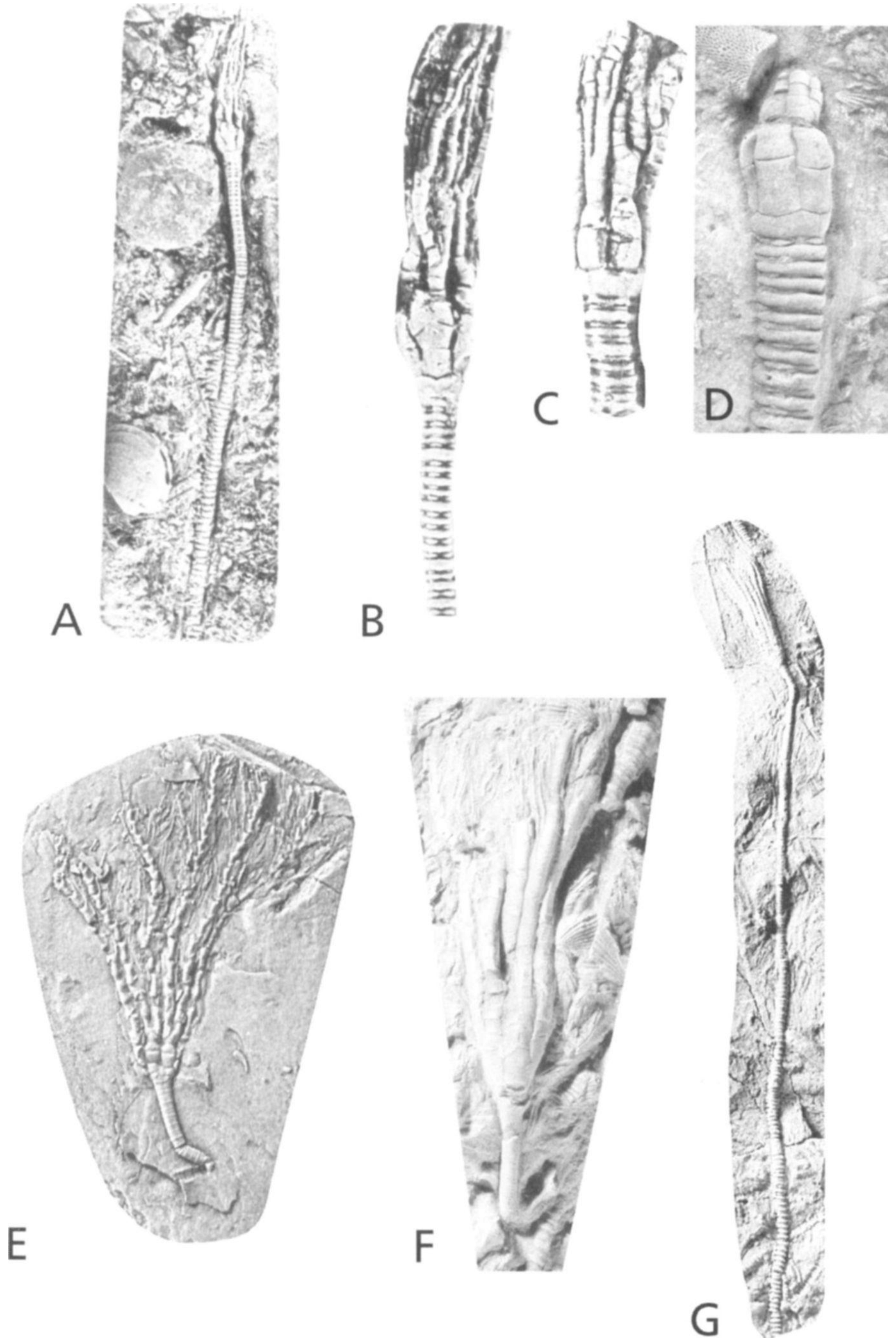


Figure 12.6. *Cincinnatian disparid crinoids.* A, B. *Cincinnaticrinus varibrachialus Warn andStrimple.* A, B. *Holotype, CMC IP 3871, Kope Formation, Cincinnati, Ohio,* x *1.0 and* x *3.1.* C. **C.** *pentagonus (Ulrich), YPM 24801, Fairview Formation, Cincinnati, Ohio,* x *1.3.* D. *Dystactocrinus constrictus (Hall), showing regeneration of arms, USNM 93223, Fairview Formation, Hamilton Co., Ohio,* x *2.0.* E. *Ectenocrinus geniculatus (Ulrich), CMC IP 36313, Kope Formation, Cincinnati, Ohio,* x 7.4. F, G. *E. simplex (Hall)* F. *CMC IP,* x 7.5. G. *CMC IP 42679,* x *0.3.* A-C, E, G *from Warn and Strimple (1977, plate 3, figures 1, 2, plate 6, figure 1, plate 13, figure 3, plate!4, figure 8) and reprinted by permission of the Paleontological Research Institution.*

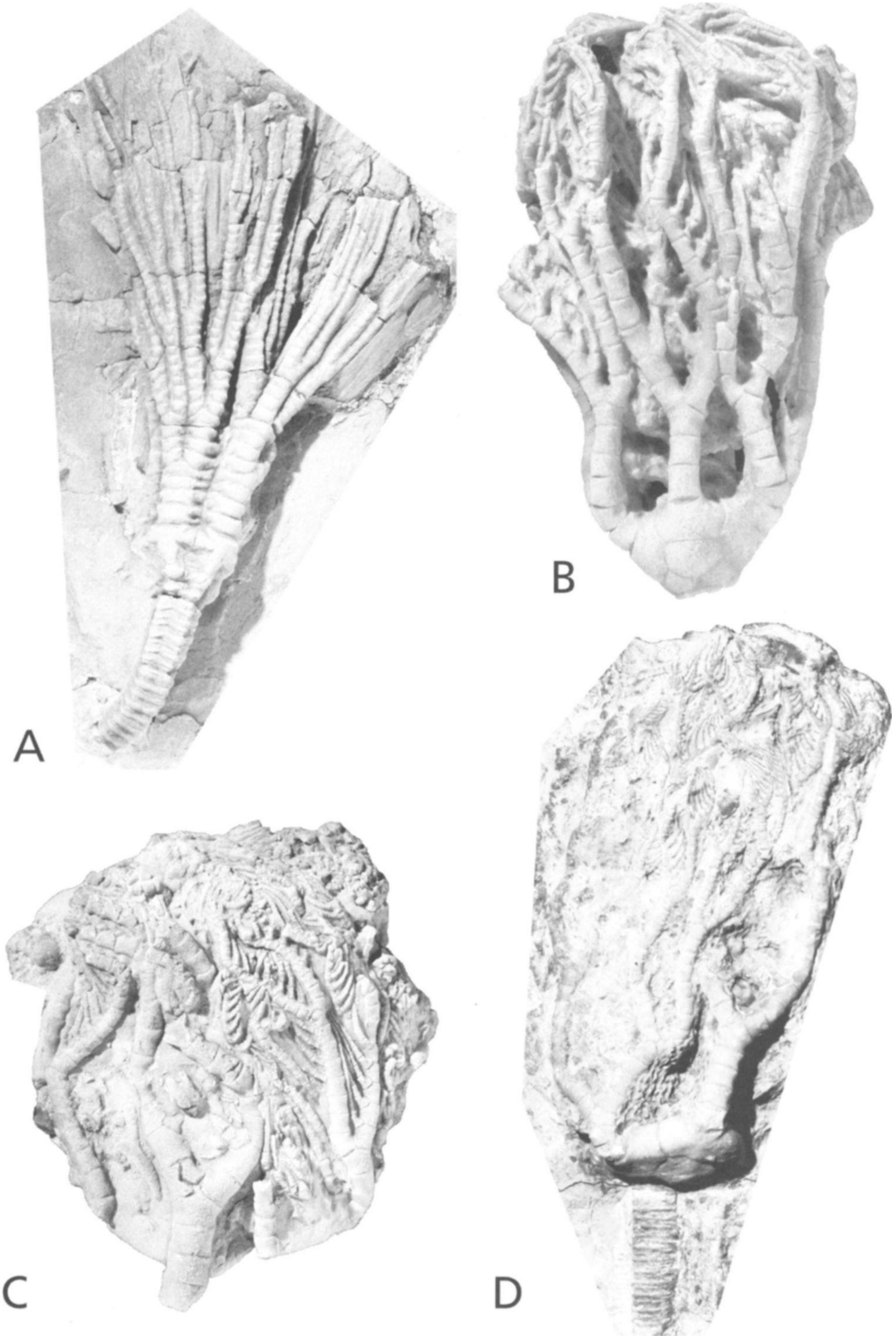


Figure 12.7. *Cincinnatian disparid crinoids.* A. *Iocrinus subcrassus (Meek and Worthen), MUGM 28048, horizon and locality unknown,* x *1.4.* B-D. *Anomalocrinus.* B. *A. sp, CMC IP 170, Bellevue-Corryville Formation, Cold Spring, Kentucky,* x *1.8.* C. *Arms of A. incurvus Meek and Worthen, CMC IP, uncatalogued, Cincinnati, OH,* x *1.4.* D. *A. sp, CMC IP 7341, Cincinnati, Ohio.*

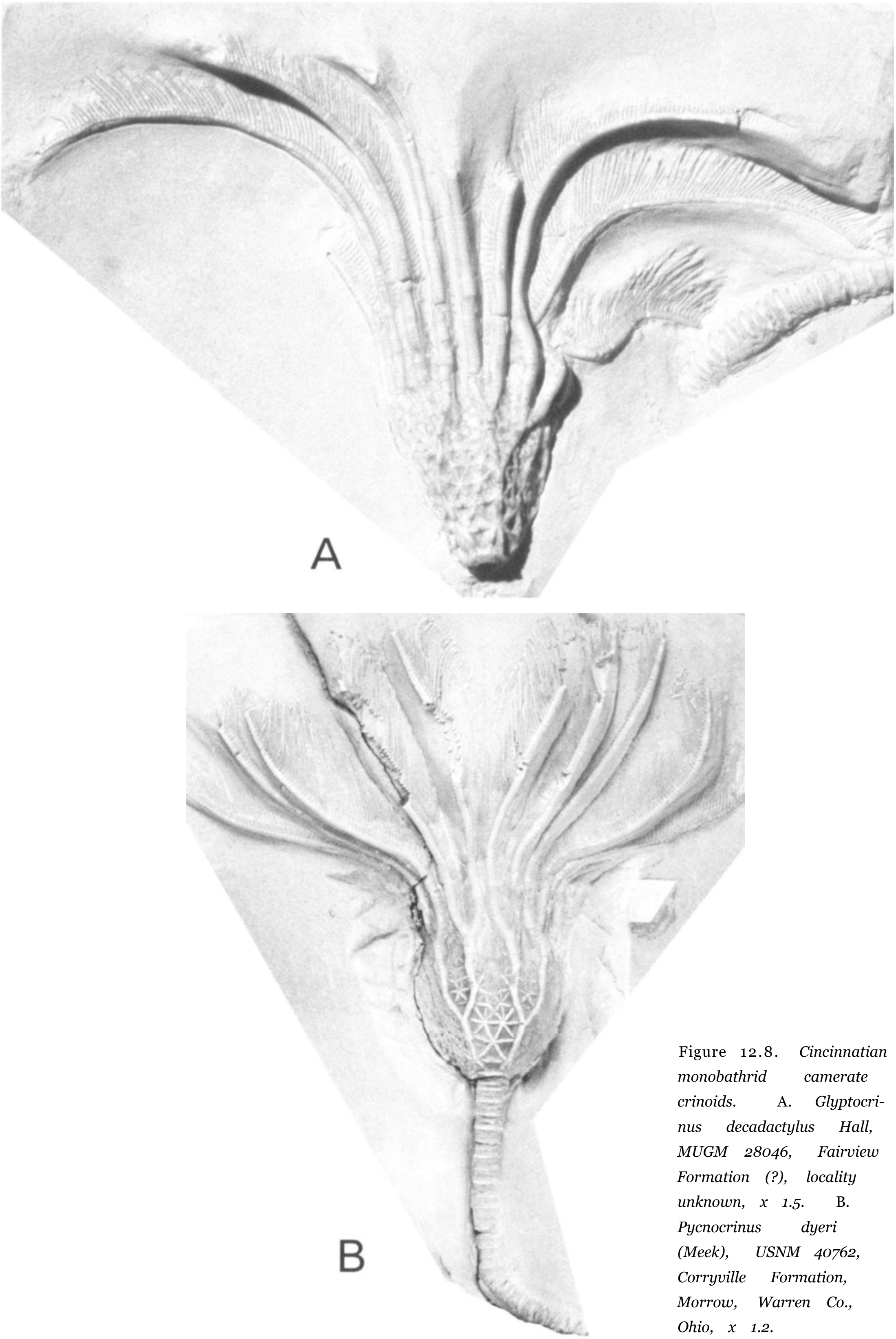


Figure 12.8. *Cincinnatian monobathrid camerate crinoids.* A. *Glyptocrinus decadactylus Hall, MUGM 28046, Fairview Formation (?), locality unknown, x 1.5.* B. *Pycnocrinus dyeri (Meek), USNM 40762, Corryville Formation, Morrow, Warren Co., Ohio, x 1.2.*

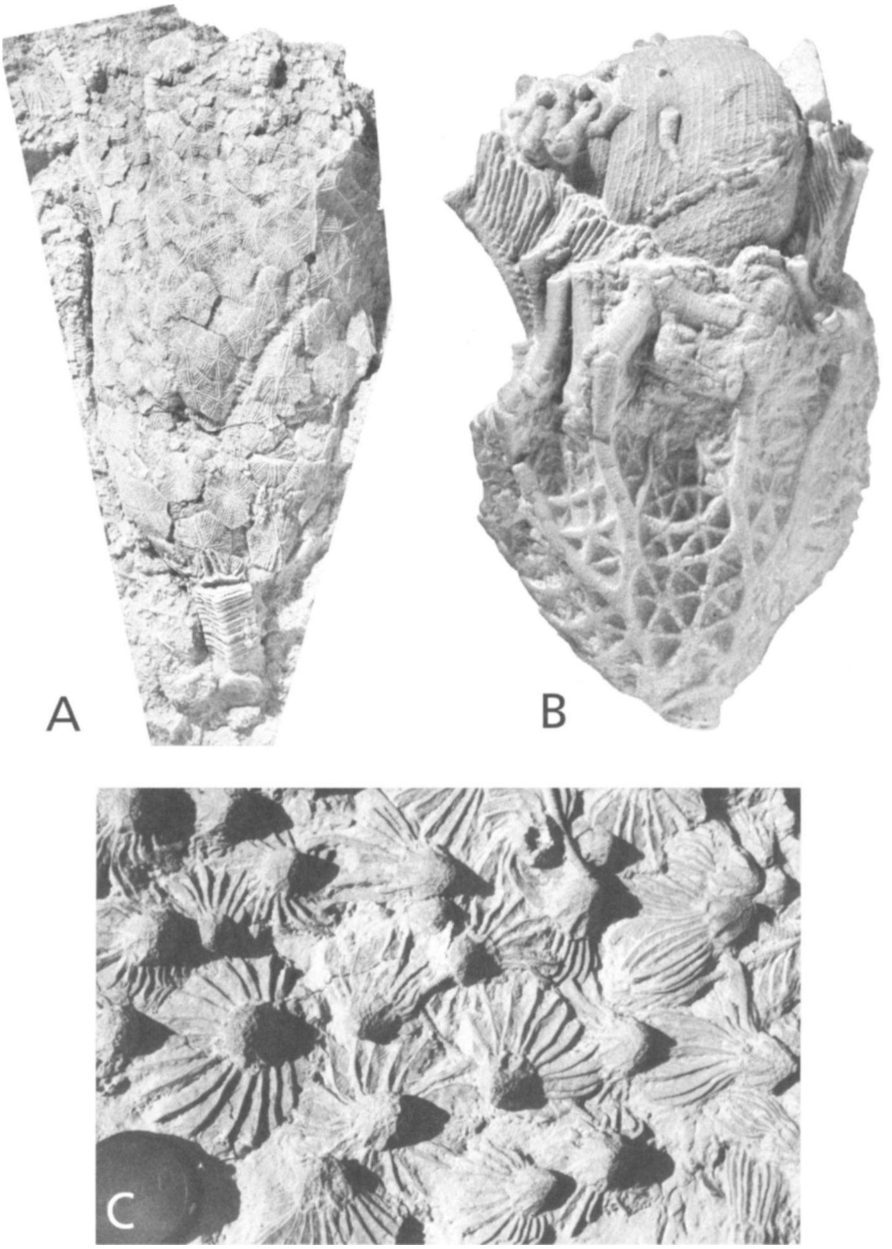
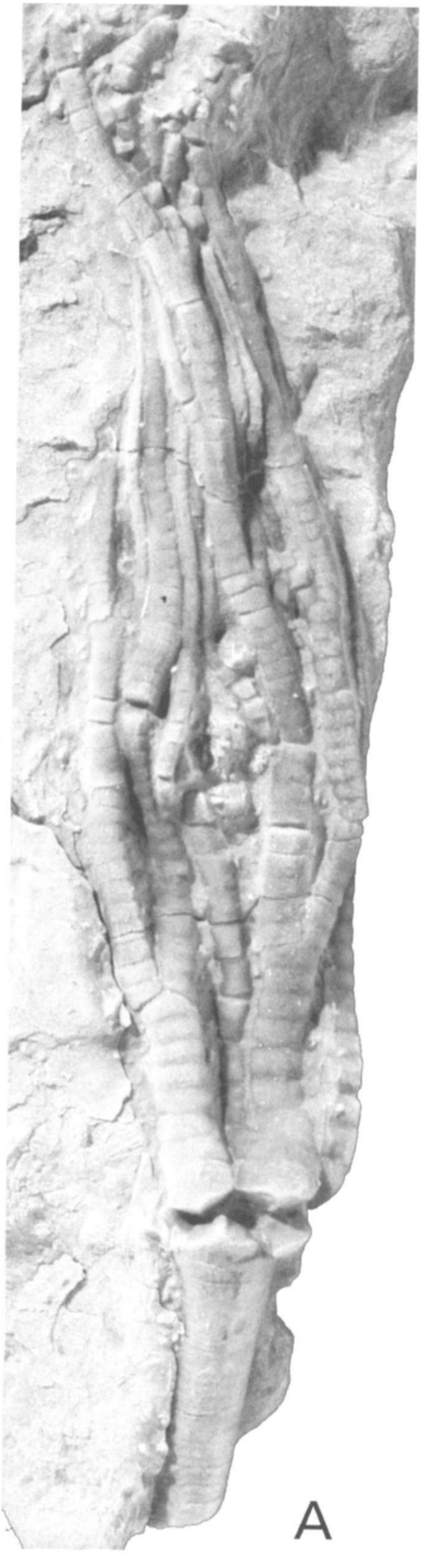


Figure 12.9. *Cincinnatian monobathrid camerate crinoids.* A. *Glyptocrinus fornshelli Miller, MUGM 28121, Liberty Formation, Butler Co., Ohio,* x *7.7.* B. *Pycnocrinus dyeri (Meek) with attached gastropod, Cyclonema sp., MUGM uncatalogued, Arnheim Formation, Dent, Hamilton Co., Ohio,* x *2.0.* C. *P. dyeri, Wayne State University Collection, Arnheim Formation, Dent, Hamilton Co., Ohio, lens cap 55 mm diameter. Note remarkable preservation of articulated crowns, some splayed oralside down.*

Figure 12.10. A. *Cladid crinoid, Merocrinus curtus Ulrich, No. 366, Bruce and Charlotte Gibson Collection, Kope Formation, Hamilton Co., Ohio,* x *4.2.* B. *Xenocrinus baeri (Meek), MUGM 28347, Liberty Formation, southwestern Ohio,* x *7.2.* C. *Diplobathrid camerate crinoid, Gaurocrinus nealli (Hall) USNM S9I, Waynesville Formation, east of Lebanon, Warren Co., Ohio,* x *1.3. This specimen was illustrated by Meek (1873, plate 2, figure 3a).*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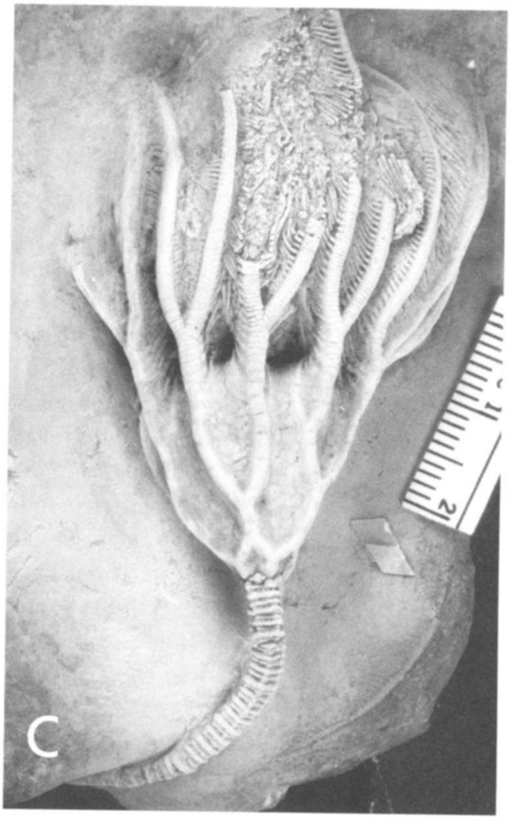
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Figure **12.11.** *Cincinnatian rhombiferans.* A, B. *Lepadocystis moorei (Meek), CMC IP 24680, Elkhorn Formation, Preble Co., Ohio,* x *4.3.* C. *Cheirocystis fultonensis Sumrall and Schumacher, holotype, CMC IP 50402, Kope Formation, Bracken Co., Kentucky,* x *3.5.* D. *Reconstruction of late Riehmondian sea floor of southeastern Indiana and southwestern Ohio, showing Lepadocystis moorei (A) attached to bryozoans (B), brachiopods, Zygospira modesta (C), and an edrioasteroid, Carneyella sp. (D).* A, B, D *from Kesling and Mintz (1961, plate 6, figures 8, 10, plate 7) and reprinted by permission of the Museum of Paleontology, University of Michigan.*

of crinoids, the disparids, the cladids, and tlic camcratcs. Disparids have a small, monocyclic cup- or howl-shaped calyx with branching arms that do not bear pinnules. An elongate, plated tube, the anal sac. is often present between the arms and has the anal opening at its end. The most common Cincinnatian crinoids, *Cincinnaticrinus, Ectenocrimts,* and *locrinus* are disparids (Figures 12.6,12.7; Plate 10). *Cincinnaticrinus* and probably *Ectenocri**mis*** had a unique, button-like holdfast composed of main tiny plates, often found attached to brachiopod shells and other hard substrata. Before it was recognized that this holdfast belongs to these types of crinoids, if was given the name *Lichenocrinus* with numerous species (Figures 12.5L-N; Faber 1929; Warn and Strimple 1977). Quite often in paleontology isolated parts of one organism are described as distinct species before sufficiently well preserved fossils are found that reveal the entire animal.

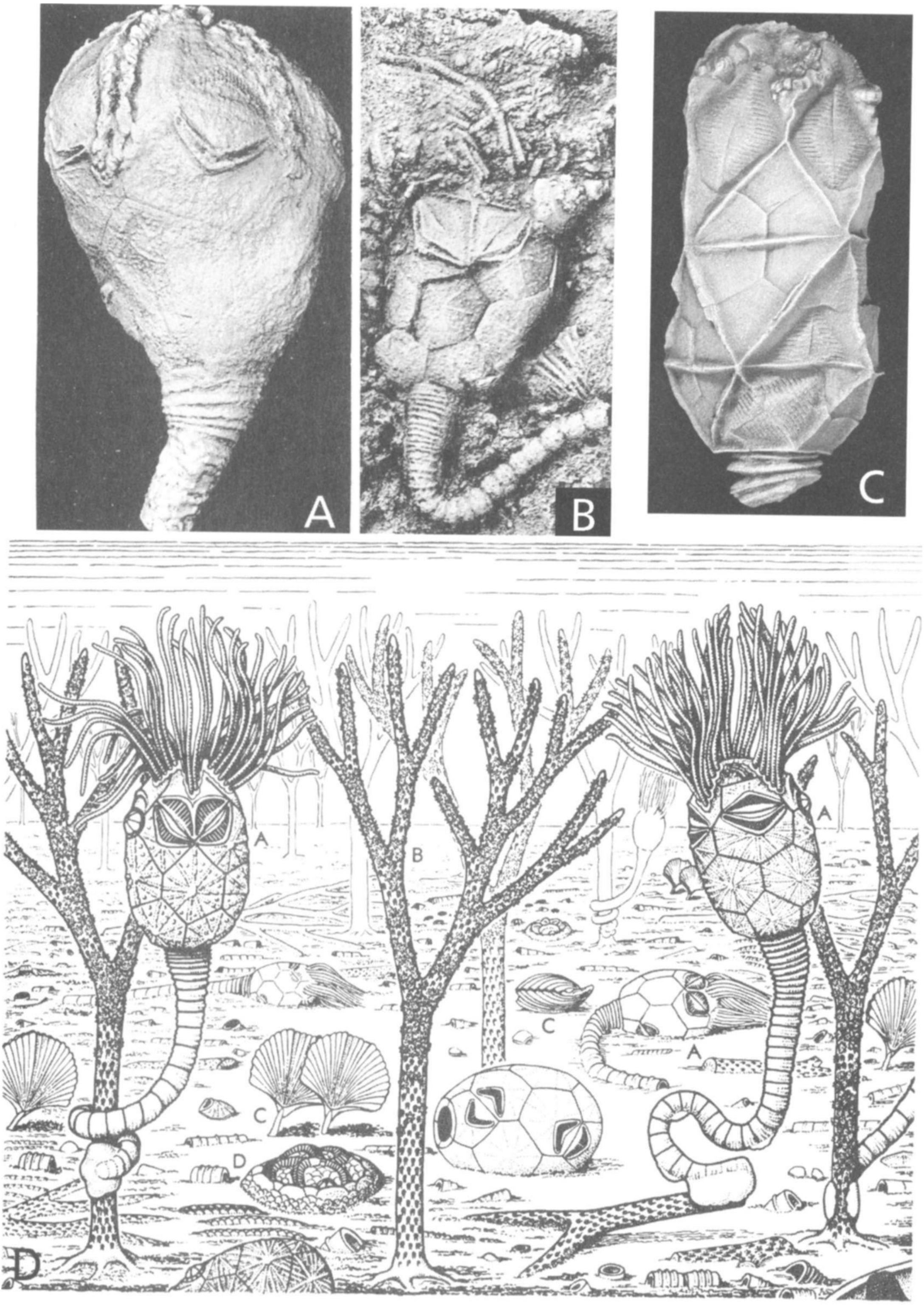
Cincinnaticrinus and *Ectenocrinus* are frequently found together in the Kope Formation, where their disarticulated colunmals can form entire limestone beds. Sometimes the articulated stalks are packed tightlv together like logjams where the collector should look closely for the small, delicate crowns (Plate 10B). These "logjams" were probahlv formed during ancient storms that disrupted the sea floor.

locrinus is another common disparid crinoid in the Cincinnatian, but is larger and more robust in structure than (*lincinnaticrinus* and *Ectenocrinus* (Figure 12.7A; Plate 10A). *locrinus* has a low, conical cup with dec]) indentations marking the junction of each basal plate with the two radials above. The colunmals are pentagonal or star-shaped (Figures 12.5C, J). Adult *locrinus* attached to bryozoans by coiling the stalk tightly around the branches. Slabs covered with *locrinus* crowns have been found in the upper Corryville Formation. In one ease, the crowns are concentrated at the base of the fine-grained limestone bed and are aligned parallel to a narrow gutter eroded into the sea floor (Figures 12.^B; Meyer el al. 19(81). Curved lengths of the *locrinus* stalks cover the upper surface of the bed in a random fashion. These preservational features suggest that the crowns were snapped off the stalks by a violent disturbance (possibly storm-related) and swept downslope, to he followed by their stalks that settled on top of them.

Anomalocrinus was the giant among the crinoids of the Cincinnatian (Figures 12.7B-D). Its stem reached a length of about one meter, with colunmals over a centimeter in diameter (Figure 12.5F). The crown was at least 10 cm high and had up to 500 branches. The stem was attached by means of a stump-like holdfast cemented directly to hard substrata. The holdfasts are found as worn, crater-like lumps encrusting limestone nodules, hardgrounds, bryozoans, or shells.

Cladids have a conical, dievclic cup. *Mcrocrinus* is restricted to the lowermost Kope Formation where its stems are easily recognized by their thin, wafer-like colunmals (Figures 12.5E, 12.10A). *Cupulocrinus*and *Plicodendrocrinus* are cladids found in the Riehmondian formations (Plate 11).

Camerate crinoids have a rigid conical calyx that includes main' fixed brachials, that is, arm plates above the radials that are incorporated into the calyx. There is a plated tcginen covering the mouth. The pinnule-bearing free arms have a feathery appearance. (*'dyptocrinus* and *Pycnocrinus,* 1110110-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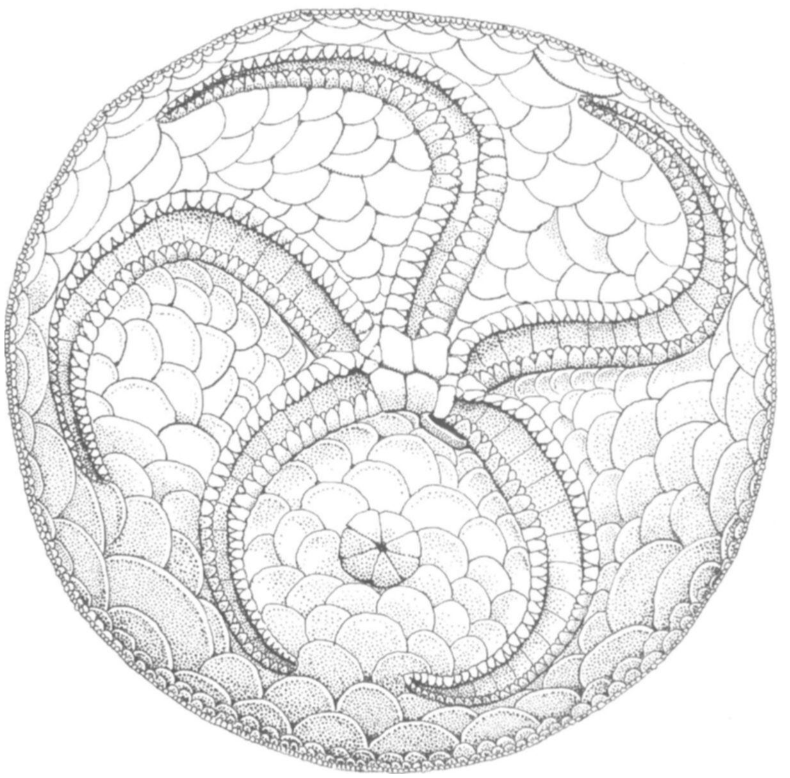

Figure 12.12. *Edrioasteroid Isorophus cincinnatiensis (Roemer), reconstructed as in life, with food grooves open for feeding. Drawing by John Agnew.*

Figure 12.13. *Cincinnatian edrioasteroids* A, B. *Isorophus cincinnatiensis (Roemer).* A. *Corryville Formation, Hamilton Co., Ohio, University of Cincinnati collection,* x *2.2.* B. *Large individual crowding against smaller individual, Corryville Formation, Boone Co., Kentucky, University of Cincinnati collection,* x *3.* C-E. *Carneyella pilea (Hall).* C. *CMC IP 34537,* x *3.2.* D, E. *Attached to crinoid column, CMC IP 26324,* x *2.1.* F. *Streptaster vorticellatus (Hall), CMC IP 24700, x3.2.* G. Cys*taster stellatus (Hall), CMC IP 40481,* x *6.2. Photos* C-G *from Bell (1976a, plate 16, figure 10, plate 17, figures 1, 3, plate 10, figure14, plate 13, figure 7) and reprinted by permission of the New York State Museum, Albany, N.Y., 12230.*

bathrid camerates (monocyclic calyx), are very similar and are the most common Cincinnatian camerates (Figure 12.8). Both have a distinct geodesic pattern of ridges on the calyx plates. *Glyptocrinus decadactylus* occurs in the lower Cincinnatian Kope and Fairview Formations and has two secundibraehs (calyx plates following the first branching of a rav) and twenty free arms. *Pycnocrinus* occurs in the Corryville, Arnheim, and Waynesville Formations and has several seeundibrachs and ten free arms that branch once near the base, producing a total of twenty arms. Both *Glyptocrinus* and *Pycnocrinus* coiled the stem around objects such as bryozoans for attachment (Figure 12.4). Occasionally, muds stirred up during storms smothered dense aggregations of these crinoids. A spectacular *Pycnocrinus* aggregation of this type was found in the Arnheim Formation at Dent, Hamilton County, around 1960 (Figure 12.9C), and recently a dense aggregation of hundreds of *Glyptocrinus,* preserved complete with arms, pinnules, and attached stalks was recovered from the Fairview Formation near Maysville, Kentucky (in preparation at the Cincinnati Museum Center). *Glyptocrinus fornshelli* is very distinct from G. *decadactylus* in having finer ridges on the calyx plates and unique thin, pentagonal columnals (Figure 12.9A).

Xenocrinus is another monobathrid camerate crinoid found in the Liberty Formation of the Richmondian Stage (Figure 12.10B). This crinoid is noteworthy for having four-sided columnals and also having the ability to coil around other objects (Donovan et al. 1995). Diplobathrid camerates have an additional circlet of plates, the infrabasals, at the base of the calyx and are quite rare in the Cincinnatian. *Gaurocrinus nealli* is shown in Figure 12.10C.

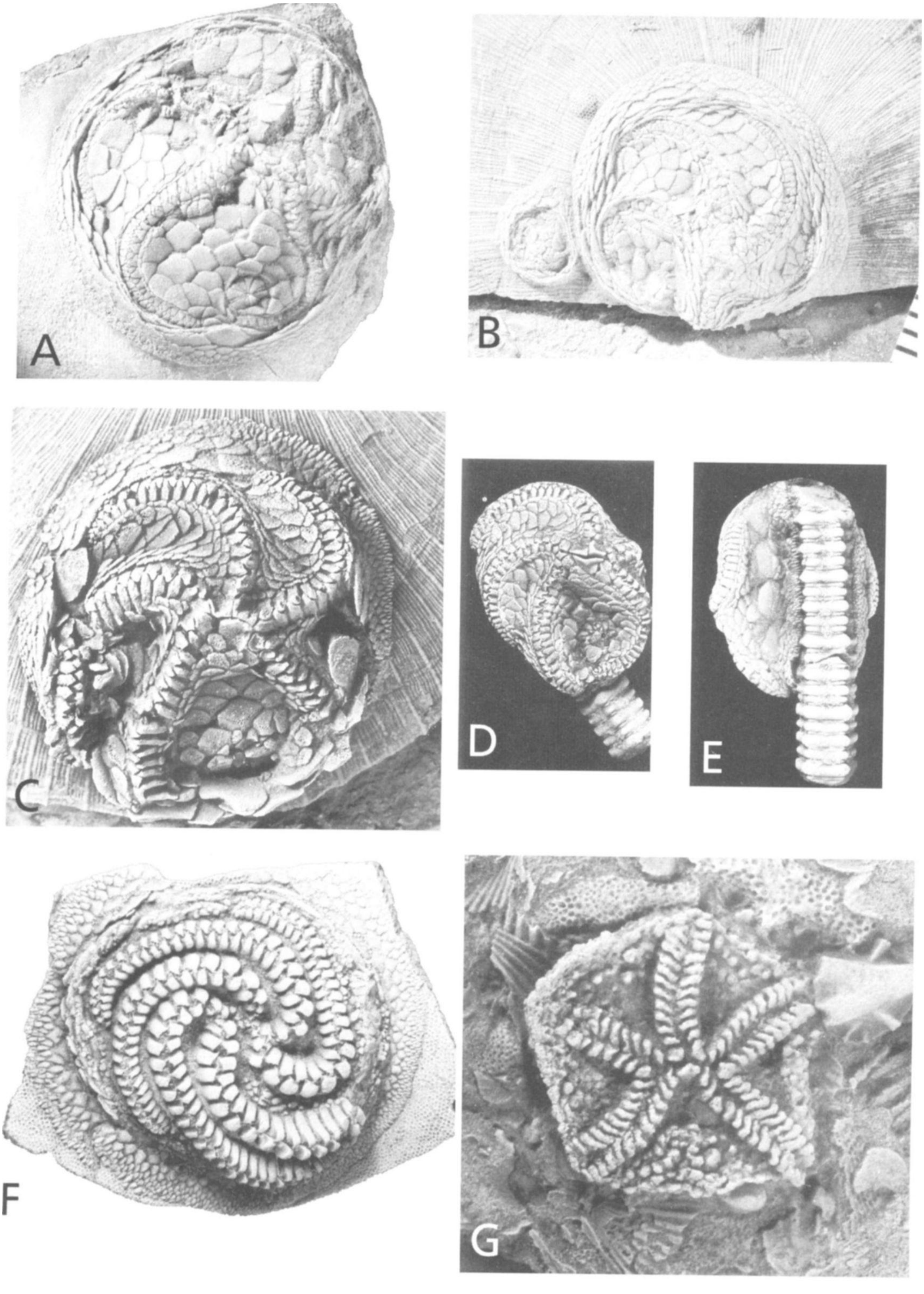
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Figure 12.14. *Cincinnatian asteroids.* A, B. *Promopalaeaster speciosus (Meek).* A. *Oral side.* B. *Aboral side, holotype, Maysvillian, Cincinnati, Ohio, MCI 108059,* x 2. *C,* D. *Promopalaeaster magnifies (Miller)* C. *Oral side.* D. *Aboral side, holotype, USNM 40883, Richmondian, Waynesville, Warren Co., Ohio,* x *0.8. Photos courtesy of Jon W. Branstrator.*

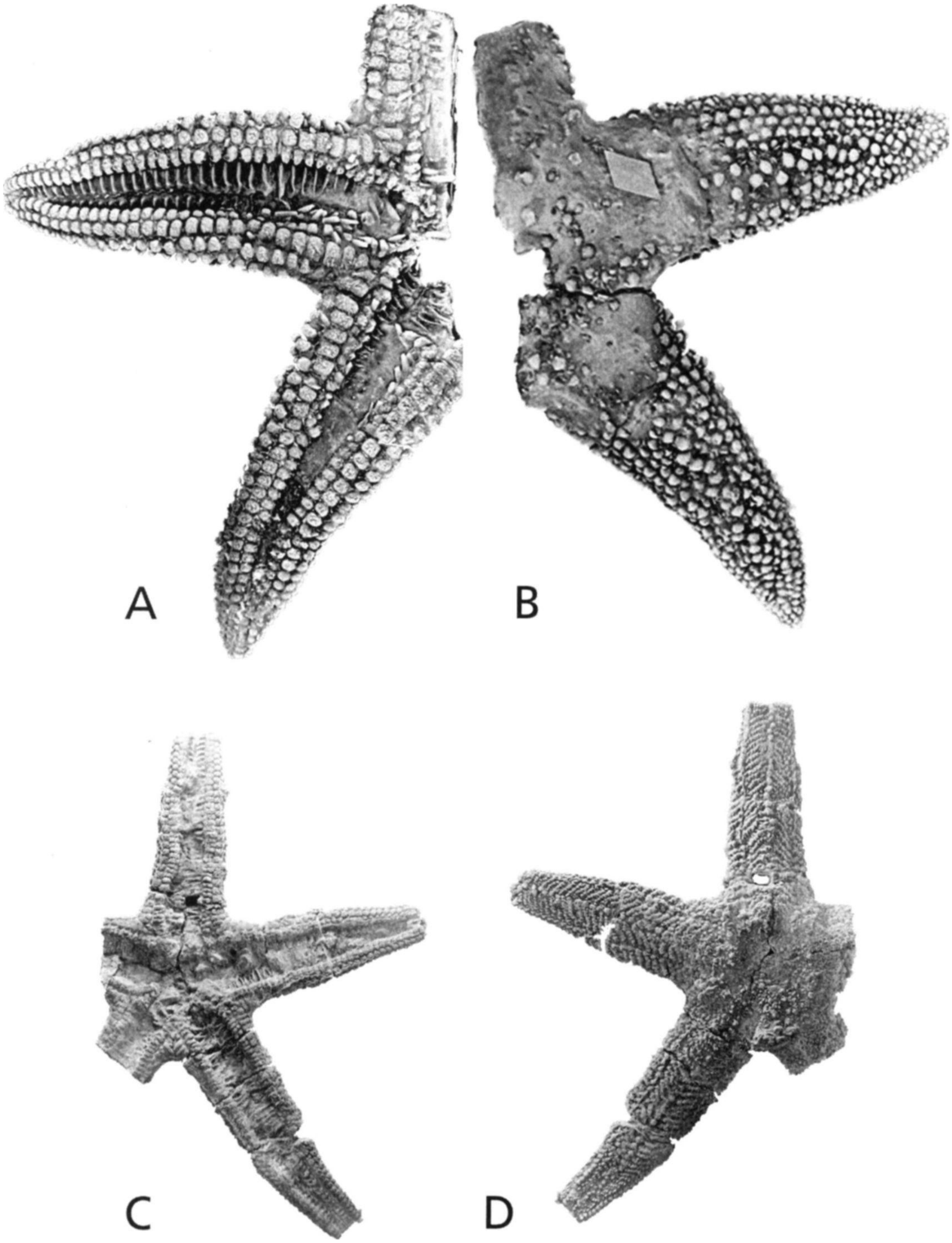
Associations of Crinoids with Other Species

Interesting information about the ecology of Cincinnatian crinoids can be gained by observing close associations between crinoids and other organisms. As mentioned above, some Cincinnatian crinoids used other organisms on the sea floor, usually bryozoans, for attachment. This habit allowed the crinoids to gain elevation above the sea floor that exposed them to unrestricted current flow, an advantage in passive suspension feeding and a means of avoiding competitors. Crinoids were thus members of some of the earliest-known "tiered" marine bottom communities, in which particular species, especially suspension feeders, occupy preferred levels or tiers above the substratum. Crinoids have been "upper story" occupants of tiered communities from Ordovician time up through the present (Ausich and Bottjer 1982).

Many Cincinnatian species in turn used crinoids as attachment sites. Crinoid stems are frequently encrusted with bryozoans, corals, cornulitid worm tubes, brachiopods, edrioasteroid echinoderms (Figures 12.13D, F), and even other crinoid holdfasts. Because these encrusters often encircle the stalk, it is likely some were attached during the life of the crinoid, providing the encrusters the advantage of a higher tiering level.

Pits, borings, and gall-like swellings in crinoid stems indicate that other organisms used the stems as dwelling sites or even parasitized the crinoid host. Stems of ***Cincinnaticrinus*** sometimes have gall-like swellings penetrated by a pit. Calcium phosphatic rings found either within the pit or on the surfaces of unpitted columnals (Warn 1974) were probably formed by the organism making the pits, although its identification is disputed. Warn (1974) concluded that the Ordovician deformities and rings were caused by myzostomid annelid worms that also form galls in living crinoids. Welch (1976) pointed out that no modern myzostomids form phosphatic linings within their pits. He recognized that the Ordovician structures resemble others found in younger Paleozoic crinoid stems and thus could be assigned to the genus ***Phosphannulus.*** Bischoff (1989) considered ***Phosphannulus*** to be a junior synonym of ***Byronia,*** which belongs to a group of phosphatic and/or organic tube-shaped fossils (byroniids) found in Cambrian through Permian strata. Although some workers interpret byroniids as tubes of tiny suspension feeding worms, Bischoff argued that they are sheaths of the polypoid larval stage of scyphozoan jellyfish. (We discussed the association between crinoids and gastropods [Figure 12.9] in chapter 9.)

Thanks to modern oceanography, marine biologists can examine many living deep sea animals such as stalked crinoids that were previously inaccessible except by dredging. One of the most surprising recent discoveries about living crinoids was occasional columns lacking crowns standing in the midst of deep sea crinoid "gardens" (Conan et al. 1981). A further surprise came when Japanese workers discovered that "headless" columns of Recent *Metacrinus* can live indefinitely in aquaria and even regenerate the crown if regeneration occurs above the basal circlet of plates (Amemiya and Oji 1992). This survival and regeneration is presumably enabled by direct absorption of dissolved nutrients. Foss of the crowns among wild populations of crinoids is most likely the result of predation.



Cincinnatian fossil crinoids provide some of the earliest evidence that predators inflicted similar damage on Ordovician crinoids and that regeneration was a survival mechanism. In a study of the impact of predation on Paleozoic crinoids, Baumiller and Calm (2004) illustrated a remarkable specimen of the disparid ***Dystactocrinus comtrictus*** (Hall) from the Cin-

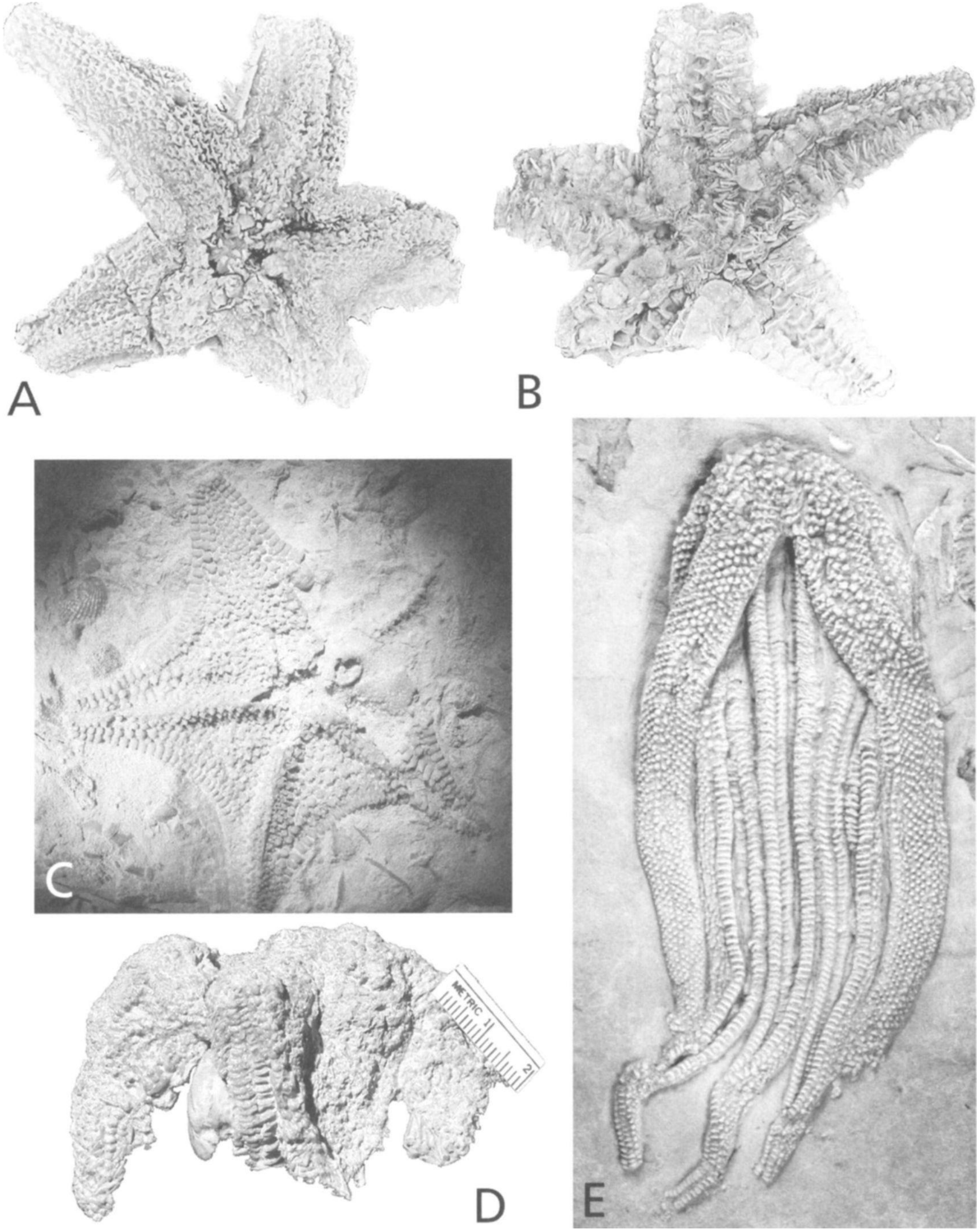


Figure 12.15. *Cincinnatian asteroids.* A, B. *Lanthanaster intermedius (Schuchert).* A. *Aboral side.* B. *Oral side, holotype, FMNH 9575, Maysvillian, Cincinnati, Ohio, x 3.* C. *Petraster speciosus (Miller and Dyer), holotype, MCZ 108063, Maysvillian, Preble Co., Ohio,* x 7. D. *Promopalaeaster dyeri (Meek), MUGM 29664, with arms wrapped around bivalve in presumed feeding posture, Waynesville Formation, Brookville, Franklin Co., Indiana.* E. *Salteraster grandis (Meek), USNM 40885, Richmondian, Waynesville, Warrern Co., Ohio,* x *3. Photos* A, B *courtesy of Jon W. Branstrator.*

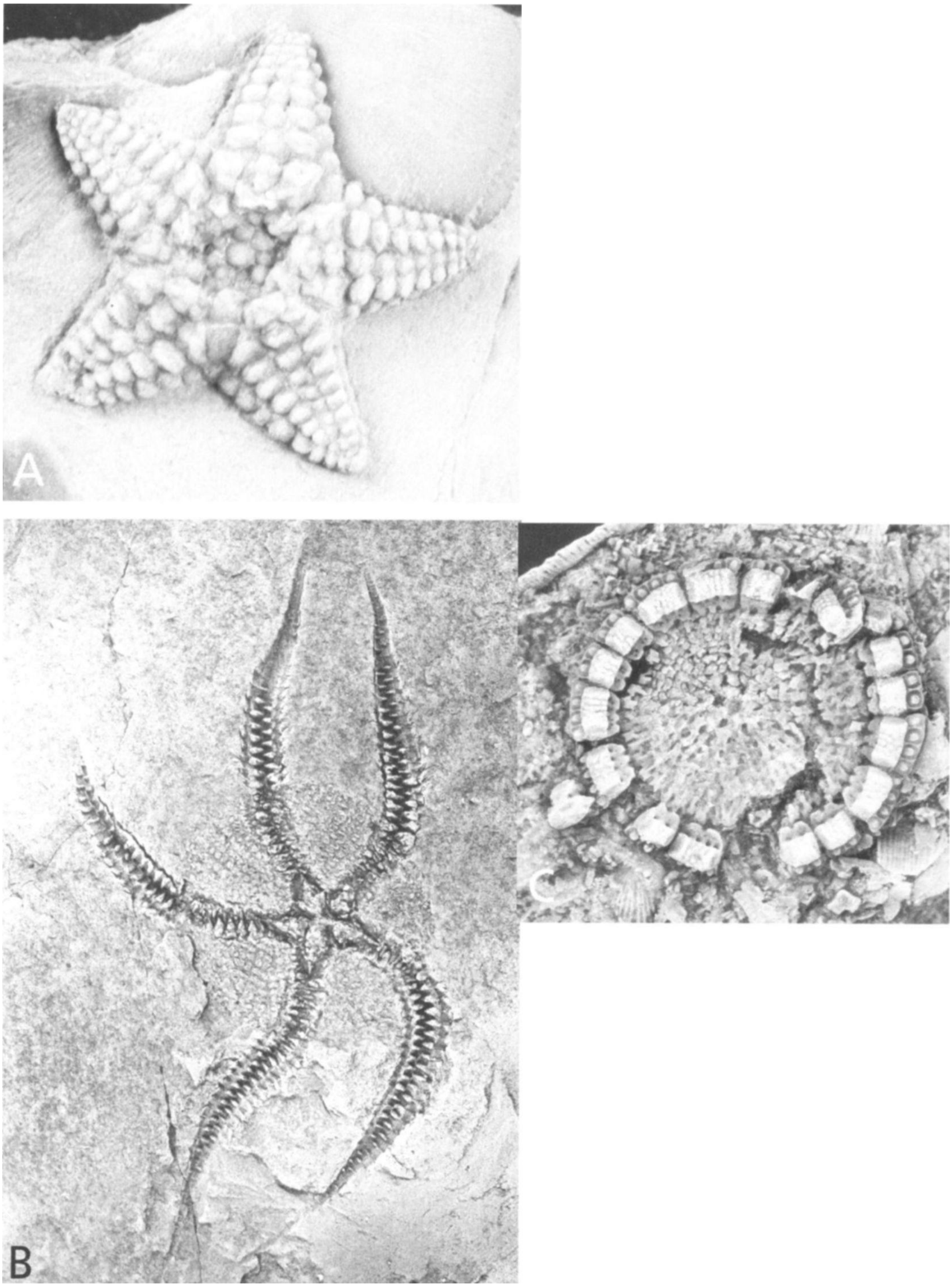


Figure 12.16. A. *Asteroid, Hudsonaster simplex (Miller and Dyer), USNM 40882, Richmondian, near Waynesville, Warren Co., Ohio,* x *3.1.* B. *Taeniaster spinosus (Billings), USNM, Middle or Upper Ordovician, southern Pennsylvania,* x *1.4.* C. *Cyclocystoid, Zygocycloides magnus (Miller and Dyer).* B, *from Boardman et al. (1987, figure 18.45B), courtesy of James Sprinkle, and reprinted by permission of Blackwell Publishing; C, courtesy of Colin Sumrall.*

Figure 12.17. *Cincinnatian stylophoran carpoids.* A. 1-6. *Enoploura* popei *Caster.* 1-3. *Holotype, CMC IP 25993, Corryville Formation, Clermont Co., Ohio.* 1. *Ventral view.* 2. *Dorsal view.* 3. *Lateral view, x 2.3.* 4-6. *Paratype, CMC IP 25257, Corryville Formation, Hamilton Co., Ohio.* 4. *Dorsal view.* 5. *Lateral view.* 6. *Ventral view, x 2.3.* 1-6 *from Caster (1952, plate 1).* B. *Reconstruction of E. popei, from Parsley (1991, text-figure 1). All reprinted by permission of the Paleontological Research Institution.*

cinnatian in which all of the arms are in the process of regeneration (Figure 12.6D). They concluded that the regeneration followed the loss of the arms to an attack by an unknown predator. Ausich and Baumiller (1993) reported regeneration of a column attached to the holdfast *Lichenocrinus* ***dubius*** (known to be the holdfast of ***Cincinnaticrinus*** or other disparids). Donovan and Schmidt (2001) illustrated pluricolumnals (sections of several columnals) of *Cincinnaticrinus* showing rounded overgrowths of one end. They suggested that the overgrowths formed after decapitation of the crowns by predation, leaving a "headless" column. In light of the new knowledge of predation damage in living crinoids, it is most likely that predators also caused loss of crowns and arms in Ordovician crinoids, although the identity of the culprits remains uncertain.

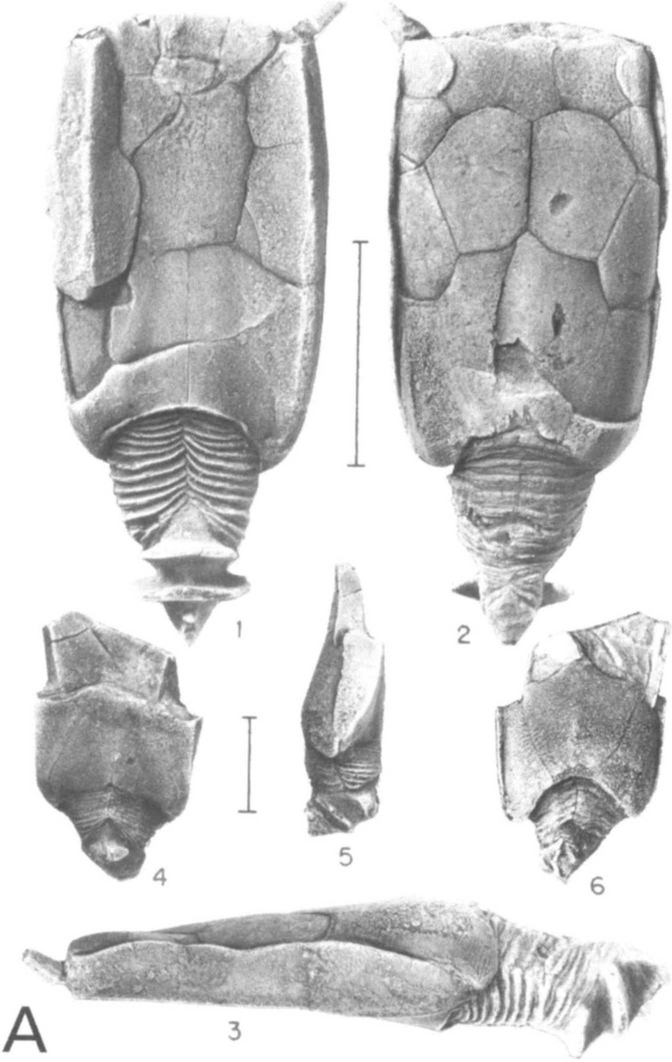
Rhombiferan "cystoids"

Rhombiferans are stalked echinoderms that appeared in the Early Ordovician and became extinct by the Late Devonian. The term "cystoid" (saclike) refers to the plated theca that has four to five circlets of large plates arranged in a pentameral pattern. Rhombiferans were originally a subgroup of the cystoids but have been elevated to a separate class. They lived as suspension feeders, but unlike crinoids, the feeding appendages of rhombiferans are thin plated brachioles arising from ambulacra that are either incorporated into the theca or less commonly stand erect (Figure 12.11C). Rhombiferans are named for a unique rhombic structure found on the thecal plates. A set of narrow slits in a rhombic outline crosses boundaries of adjacent plates; these slits led to interconnecting internal canals. The purpose of these distinctive canals was to provide water flow through the interior of the theca for respiratory purposes. The relatively short brachioles of rhombiferans may have carried fewer tube feet than those used for respiration in crinoids, or may have lacked them entirely. Therefore the heavily plated rhombiferans may have needed a different means to supply oxygenated water and to remove dissolved carbon dioxide from the thecal interior.

Two species of rhombiferans are found in the Cincinnatian. *Cheirocystis fultonensis* is restricted to the lowermost Kope Formation (Fulton Shale) (Sumrall and Schumacher 2002). This species has an elongate theca and a long, tapering, attached stalk (Figure 12.11C). *Lepadocystis moorei* (Meek) is found only in the Elkhorn Formation (Richmondian). This rhombiferan has a rounded theca and a shorter, tapering unattached stalk (Sumrall and Sprinkle 1999; Figures 12.11A, B, D). Some complete specimens are still attached by a holdfast cemented to various objects.

E-drioasteroids

Next to the crinoids, edrioasteroids are the most common echinoderm fossils in Cincinnatian strata. Edrioasteroids constitute a class of echinoderms that originated during the Cambrian and became extinct in the Permian. At first glance, an edrioasteroid resembles a sea star with a ring around it



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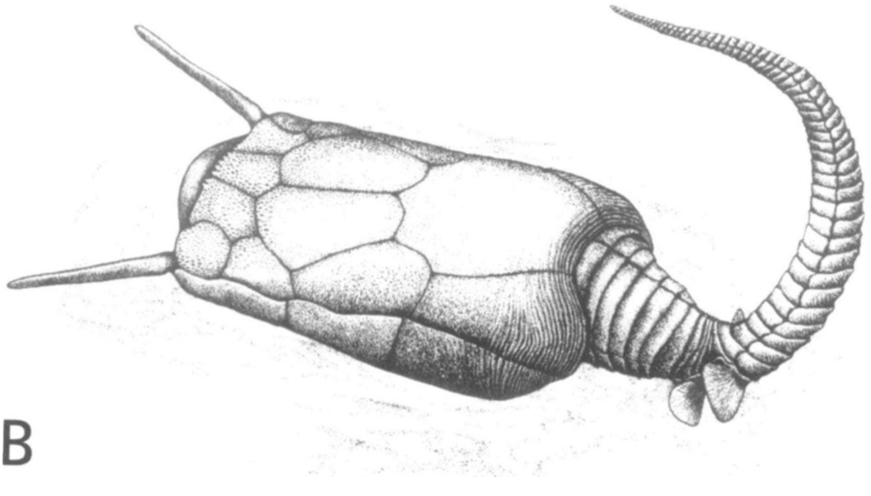

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(the name means "seated-star"). The sea star resemblance derives from the five usually curving food grooves or ambulacral tracts that converge on the central mouth (Figure 12.12). Thin, overlapping calcitic plates called interambulacrals take up the space between the ambulacra. A more rigid series of marginal plates forms the ring. Usually the ambulacral and interambulacral plates appear to have collapsed inside the marginal ring; thus it is assumed that the multiplated theca was flexible in life. Rarely, uncollapsed or "inflated" specimens are found that reveal how the animal probably appeared in life. Most Cincinnatian edrioasteroids had a low dome shape, but some were more cylindrical (Sumrall 1994). A total of six genera and eleven species are known from Cincinnatian strata (Figure 12.13).

Because edrioasteroids are extinct, their mode of life must be inferred by analogy to living echinoderms. Edrioasteroids are always found attached to a hard surface such as a brachiopod shell, bryozoan, or hardground. The lower surface was plated in some species, but in Cincinnatian species apparently only a soft tissue membrane served to adhere to the substratum, possibly in the way sea anemones attach by their pedal disk. Some species actually cemented to the substratum like a barnacle, but those adhering by a basal membrane may have been capable of limited movement. Because the mouth and ambulacral tracts are directed upwards in edrioasteroids, they apparently lived as passive filter feeders. The ambulacral grooves are lined with tiny, zipper-like coverplates capable of opening and closing (Figure 12.12). Opening the coverplates exposed the food groove lined with tube feet and/or cilia that served to collect suspended food particles and convey them to the mouth in a manner similar to that of living crinoids. Fecal waste was expelled through a valve-like anal opening on the thecal surface. Two other openings located near the mouth are assumed to be a gonopore (for release of gametes) and a hydropore. The hydropore allowed for water intake to the water vascular system and for control of the amount of thecal inflation. Cylindrical forms such as the Cincinnatian *Streptaster* were capable of telescoping the thecal plates during inflation so as to achieve an elevated feeding position and during deflation assuming a low-profile, protective position (Sumrall 1994).

Although edrioasteroids are usually considered to be rare fossils, they can occasionally be found by the hundreds or thousands in Cincinnatian strata when the appropriate preservational conditions are present (Meyer 1990). Thin limestones covered with strophomenid brachiopods (shell pavements) or hardgrounds (calcareous sediments lithified on the sea floor) are the ideal substrata for edrioasteroids (Wilson 1985). Despite the abundance of these types of beds in the Cincinnatian, edrioasteroid-bearing pavements are rare. Preservation of edrioasteroids in their life position on pavements required a rapid, catastrophic burial with fine mud. Without such a rapid smothering, the delicate, multiplated edrioasteroid theca disarticulated soon after death, leaving little or no trace.

The discovery of pavements bearing abundant edrioasteroids in the Cincinnatian led to pioneering studies of the life history of edrioasteroids and their population paleoecology. Because pavements contained specimens ranging in size from a few millimeters in diameter to the largest individuals over thirty millimeters in diameter, Bell (1976) was able to determine how several species changed in morphology during growth. This information was used by Meyer (1990) to study the population paleoecology of three different species found on a single pavement. Small individuals of the common species *Isorophus cincinnatiensis* (Figures 12.13A, B) clustered near the margins of articulated (likely living) shells of the host brachiopod *Rafinesquina.* The small edrioasteroids may have lived in a commensal relationship with the living brachiopod, taking advantage of the feeding currents generated by the brachiopod and protection along the overhanging margin of the host shell. Because a single large *Isorophus* occupies almost an entire brachiopod shell, it is likely that either mortality or relocation to avoid overcrowding depleted the juvenile clusters. In time, the edrioasteroids may have outlived the brachiopod host, because the larger individuals are found on disarticulated, abraded (hence dead) host shells. Pavements found at different stratigraphic horizons in the Cincinnatian have different edrioasteroid species populations (Sumrall et al. 2001).

Asteroids

Sea stars are exceptionally rare fossils in the Cincinnatian; often, specimens are hard to recognize because they are fragmentary or distorted. Nevertheless, six genera and ten species are valid from the Cincinnatian (Figures 12.14-12.16). Sea stars are the most recognizable echinoderms, having the stereotypical pentaradial symmetry. they differ from brittle stars (ophiuroids) in having arms that are not sharply differentiated from the central disk.

Cincinnatian sea stars, like modern forms (Plate 9E), had a wide range of body forms that can be related to a diversity of feeding habits. The best-known Cincinnatian sea star, *Promopalaeaster,* is found throughout the stratigraphic section. An extraordinary specimen of a *Promopalaeaster* wrapped around a bivalve mollusc provides a rare example of a sea star caught in an ancient act of predation (Figure 12.15D; Blake and Guensburg 1994). This case demonstrates that some sea stars of the Ordovician had the ability to prey on pelecypods by prying their valves apart just as do modern sea stars. The stomach is everted through the mouth and the prey is digested within its own shell. Branstrator (1975) concluded that *Mesopalaeaster* was also a stomach-everting sea star. *Hudsonaster* is a small sea star with large, blocky plates, at least superficially similar to certain present-day members of the Goniasteridae or Ophidiasteridae, which feed on passive, colonial organisms, small prey, and detritus (Figure 12.16A; Jangoux 1982). Another Cincinnatian asteroid, *Petraster speciosus* (Richmondian), has short, broad arms and a flattened profile (Figure 12.15C). It is very similar to modern sea stars that live by ingesting sediment and digesting organic materials (Blake and Guensburg 1988). In contrast, *Salteraster* had very long, narrow arms, with small ossicles (Figure 12.15E). Specimens are often preserved in a contorted manner suggesting great flexibility and ability to handle small or large prey. Both *Salteraster* and *Lanthanaster* (Figures 12.15A, B) are thought to have burrowed into fine sediment in search of prey, and both may have produced the rare star-shaped burrows in the Cincinnatian called *Asteriacites* (see Figure 14.3D; Branstrator 1975).

Ophiuroids

The ophiuroids (brittle stars or serpent stars) are distinguished from the asteroids by having the five arms sharply differentiated from the central disk (Plate 9C). The arms are quite flexible because they are composed of a series of vertebra-like ossicles connected by muscles and ligaments. Ophiuroids can move quite rapidly on the sea floor by lashing the arms and some can flex the arms vertically as well. The arms are equipped with tube feet that are used to gather organic particles either directly from the sediment or as suspended particles. Ophiuroids are usually considered to be deposit feeders, but some are also capable of suspension feeding and even predation. ***Taeniaster spinosus*** (Billings) occurs in the Cincinnatian (Ilotchkiss 1970; Figure 12.16B), and like asteroids, it is very rare. Modern ophiuroids can live in very dense aggregations on the sea floor. Rarely slabs have been found in the Cincinnatian bearing dense assemblages ***of*** *Taeniaster,* suggesting that aggregation behavior was achieved in this very early member of the group. In the only other known Cincinnatian ophiuroid, *Protasterina flexuosa,* pyritized tube feet have been reported in a specimen from the Kope Formation (Glass 2006).

Cyclocystoids

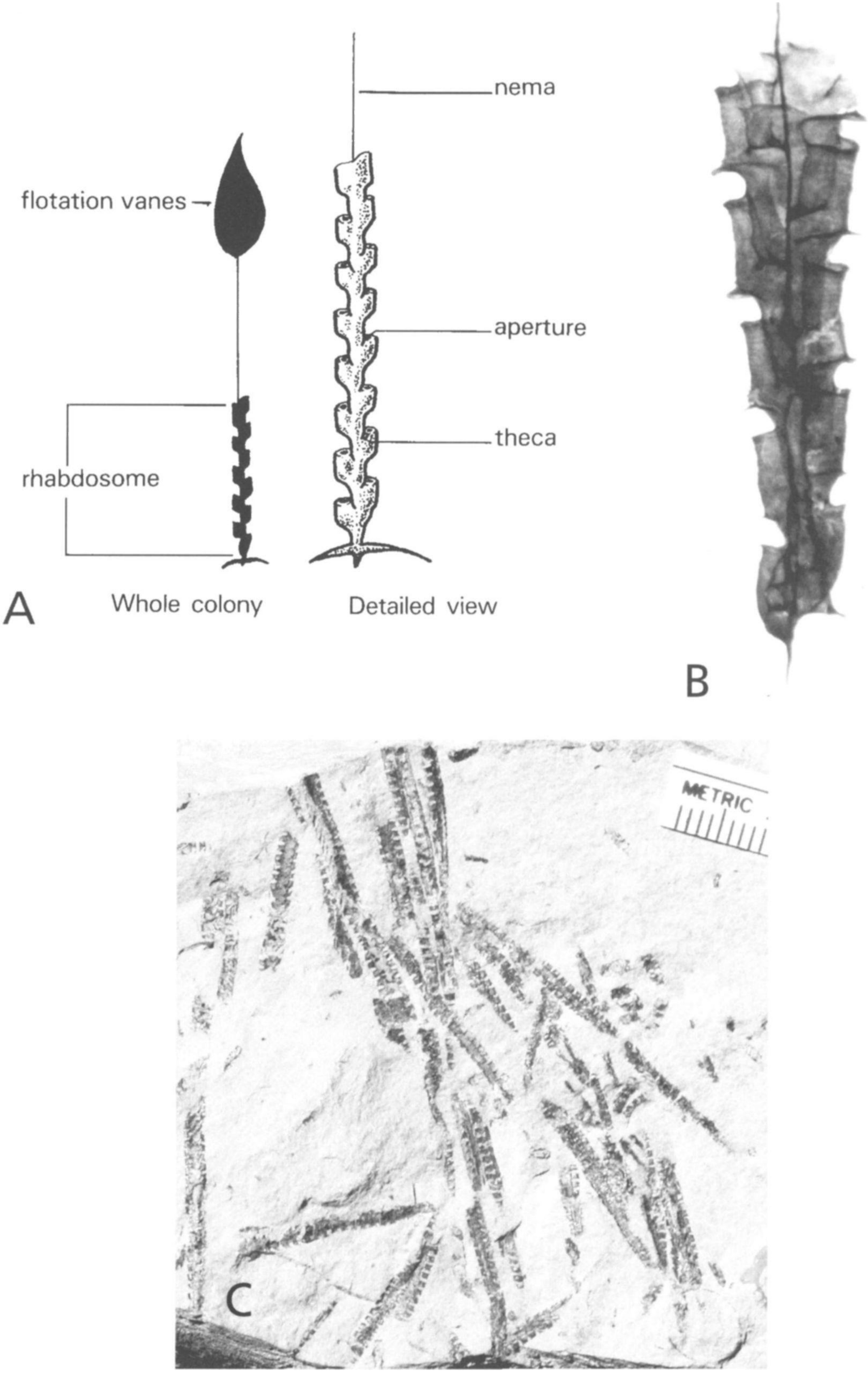
The cyclocystoids are among the rarest and most enigmatic of Cincinnatian echinoderms. They can be easily mistaken for an edrioasteroid because they had a circlet of squarish, marginal plates, 7-20 mm in diameter, but lack the characteristic five curving ambulacra of edrioasteroids (Figure 12.16C). A comprehensive study of cyclocystoids by Smith and Paul (1982) provides the most up to date understanding of their complex morphology. The skeleton of a cyclocystoid consists of three parts: a central disk, a marginal ring, and a peripheral skirt. Usually only the marginal ring is found, consisting of eighteen to sixty squarish or blockv ossicles. Numerous small plates cover one surface of the disk: grooved radial plates, ungrooved interradial plates, and cover plates covering the grooved radial plates. There is a central opening on this surface, presumably the mouth. Small polygonal plates cover the opposite surface, with a small cone at the center, presumably surrounding the anal opening. Although some cyclocystoids have five-fold symmetry of the plating, others have four-fold or six-fold symmetry, breaking the stereotypical echinoderm pattern. The nature of the plating suggests that in life, there was very little body space between the two plated surfaces. The marginal ossicles have a distinctive form and are perforated by tiny canals. Each marginal has one to seven cupulcs, which are spoon-shaped depressions. Each cupule leads to a radial duct lying within a circumferential groove. The peripheral skirt consists of small, imbricate plates that covered the ring of cupules in life.

Because there appears to have been very little space between the plated surfaces of the living cyclocystoid, the animal somewhat resembled a tambourine rather than a drum. Lacking internal space for organs, cyclocystoids were restricted to feeding on minute organic particles. Smith and Paul conclude that the particles were collected at the cupules by ciliary action and conveyed via the ducts to the radial grooves that converged on the central mouth. Although tube feet are not preserved, Smith and Paul suggest that tube feet could have emerged from pores between plates on the ventral surface and provided a means of locomotion. The cyclocystoid thus moved over the substrate and gathered organic particles using ciliated cupules. Other specialists, however, do not accept the life orientation favored by Smith and Paul, and instead regard the opposite side as lowermost (Sprinkle, pers. comm.) Cyclocystoids first appeared in the Early Ordovician and last in the Late Devonian or Early Carboniferous (Smith and Paul 1982). A total of nine genera and forty-one species have been described. In the Cincinnatian, three genera and five species are known.

Stylophorans

For many paleontologists, stylophorans surpass even the cyclocystoids as some of the most bizarre fossil echinoderms. For a minority of specialists, stylophorans are considered not even to be echinoderms, but rather ancestors of the vertebrates belonging to a group called calcichordates. (The interested reader is referred to Gee (1996) for a blow-by-blow account of this debate.) This controversy, coupled with their exceeding rarity in Cincinnatian strata, make the stylophorans one of the most intriguing fossils ever to be found in the Cincinnati region. A single genus, *Enoploura,* is found in the Cincinnatian, with two species, E. *popei* Caster in the Maysvillian (Figure 12.17) and E. *balanoides* (Meek) in the Maysvillian and Richmondian (Caster 1982; Parsley 1991).

Enoploura is typical of the stylophorans, an extinct echinoderm class that ranges from the Middle Cambrian through the Early Pennsylvanian, with about eighty genera in all. ***Enoploura*** has a flattened, plated theca that is roughly rectangular; the plating has no radial or pentameral symmetry whatsoever, but rather is bilaterally symmetrical. A pair of spines is attached at one end, and at the opposite end, a single, segmented appendage is attached. This appendage has a very complex structure and its function has been vigorously debated. It was once thought to be a stalk-like holdfast, but those favoring the echinoderm affinity of the stylophorans consider it to be a feeding appendage, called the aulacophore. The basal part of the aulacophore is made up of a series of thin elements each consisting of four components; it was probably flexible. Following this flexible region is the so-called styloid, bearing a pair of bladelike flanges that presumably dug into the sediment. The terminal part of the aulacophore has a tapering series of sharply keeled ossicles bearing a groove with covering plates. Two possible feeding positions have been postulated for the aulacophore: held up into the water or arched slightly above the substratum. In any case the food consisted of very fine organic particles. Particles taken in along a food groove entered an internal mouth, and wastes were emitted through an anal opening between the spines. Proponents of the ealcichordate interpretation of stvlophorans regard the appendage to be a true, wriggling tail, with the mouth located at the opposite end of the theca. Study of well-preserved skeletal microstructure in Cincinnatian *V.noploura* by Carlson and fisher (1981) revealed close similarity to typical echinoderm stcreom, further supporting the classification of stvlophorans with echinoderms. Some enigmatic fossils called maehaeridians might also be related to stvlophorans (see chapter 10).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GRAPTOLITES AND CONODONTS: OUR CLOSEST RELATIVES?

13

Graptolites

Graptolites are among the most distinctive fossils found in Cincinnatian strata and are also uniquely significant. Craptolites are commonly preserved in shales in a highly flattened condition, appearing like black pencil markings with a saw-toothed margin (the name graptolite in fact means "written stone"; Figure 13.lC). In some Cincinnatian limestones graptolites can be preserved in an uncompacted, three-dimensional condition. Because their skeletal structure (periderm) is organic these "inflated" graptolites can be etched free of the matrix using acid to reveal exceptional structural details (Figure 13.1B). Graptolites represent the skeletal sheath of a colonial, soft-bodied marine invertebrate whose soft parts are not preserved. Graptolite colonies existed as free-floating plankton (order Graptoloidea) or as branching, benthic colonies (order Dendroidea). The colonial skeleton (rhabdosome) housed many soft-bodied zooids each within a cup-like theca (Figure 13.1A). The walls of the thecae are constructed in a unique way that is of great importance in establishing the nature of the graptolite organism: narrow half-rings (fusellae) alternate to form a zigzag suture along the thecal tube. An outer cortical layer of collagen fibrils reinforces the fusellar layer by criss-crossing the surface; hence these are called cortical bandages. In planktic graptoloids, thecae are arranged as branches or stipes either in a single linear series (monoserial), a double Series (biserial), or even triserial or quadriserial. Stipes were attached singly or in multiples by the thread-like nema to vane-like structures or possibly to gas-filled bulbs that provided flotation. Although it was once thought that graptoloids attached by means of the nema to other floating material like seaweed, it is now generally accepted that planktic graptoloids used their own means of flotation, but there is debate as to whether flotation was actively or passively maintained (Rigby and Fortey 1991).

Figure 13.1. A. *Graptolite morphology. Drawing by Kevina Vulinec.* B, C. *Geniculograptus typicalis (Hall).* B. *Single rhabdosome, courtesy of Daniel Goldman.* C. *Cluster of partly parallel-oriented rhabdosomes, MUGM 29469, Cincinnatian, Butler Co., Ohio, scale in mm.*

The floating ability of graptoloids caused them to be carried great distances by ocean currents. Consequently a single graptolite species can be found over a vast geographic area, even on separate continents. This wide distribution, coupled with their relatively rapid evolutionary change over time, make graptolites some of the most ideal index fossils for biostratigraphic zonation and correlation of strata. Graptolites first appeared in the Middle Cambrian and became extinct as a group in the Pennsylvanian, but for Ordovician and Silurian strata in particular, graptolites (along with conodonts) provide the essential basis for relative age dating and correlation worldwide. The Upper Ordovician of North America is divided into four graptolite biozones on the basis of overlapping ranges of several species (Goldman and Bergstrom 1997).

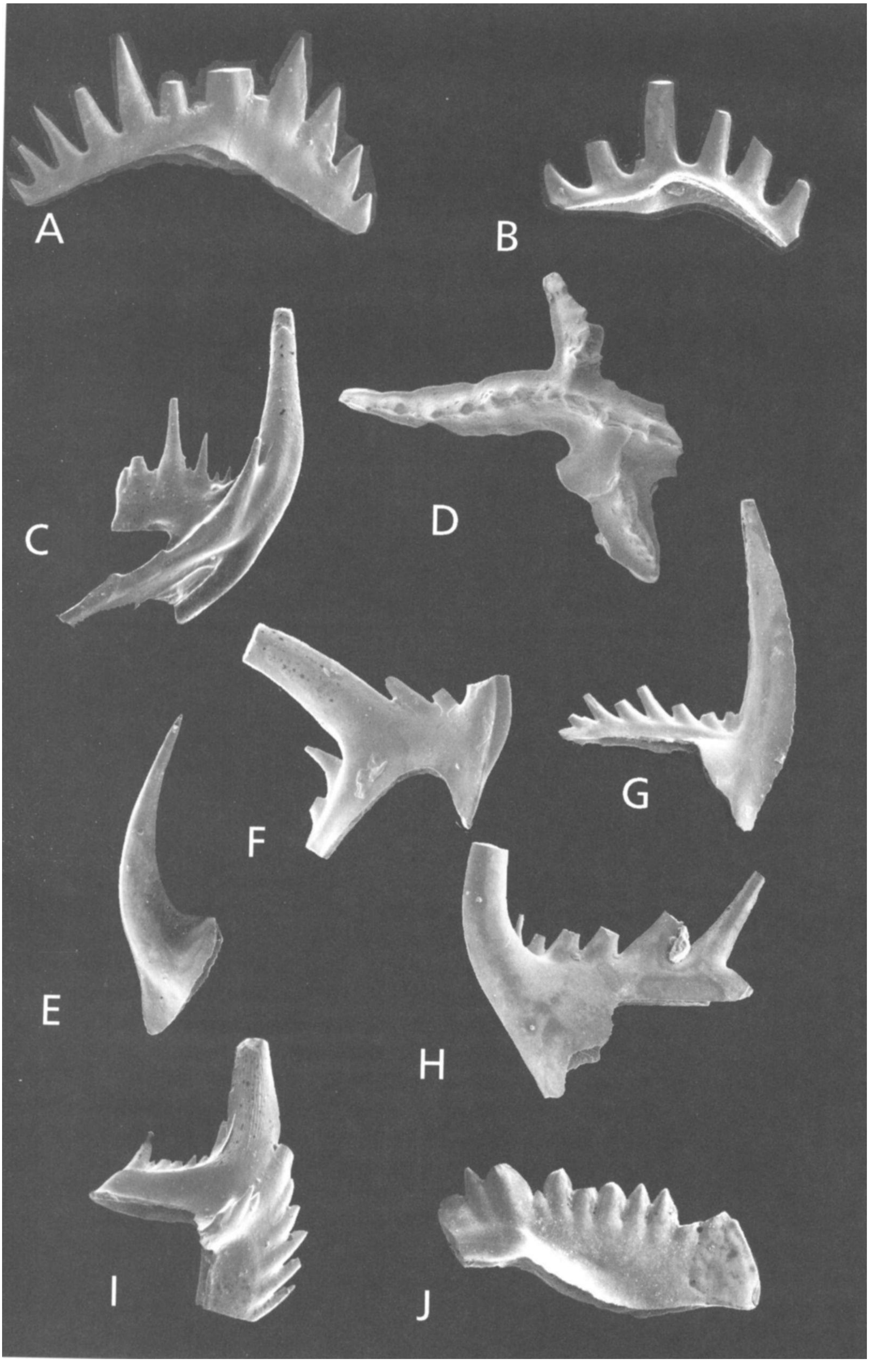
Figure 13.2. *Cincinnatian conodonts. Those shown are among the most common forms. All are from the lower Riehmondian Stage near Brookville, Franklin Co., Indiana.* A, G, H. *Plectodina tenuis (Branson and Mehl).* A. *Pb element.* G. *M element.* H. *Sc element.* B. *Oulodus oregonia (Branson, Mehl, and Branson), Pb element.* C, D. *Amorphognathus ordovicicus Branson and Mehl.* C. *Sc element.* D. *Pa element.* E. *Drepanoistodus suberectus (Branson and Mehl).* F. *Phragmodus undatus Branson and Mehl, S element.* I *Rhodesognathus elegans (Rhodes), Pb element.* J. *Aphelognathus grandis Branson, Mehl and Branson, Pb element. Scanning electron micrographs courtesy of Stig M. Bergstrom, approximately* x *130. P elements are principal elements, a and b denoting position in the apparatus, M elements are medial elements, and S elements are symmetry series elements, c denoting position in the apparatus.*

Although several species of graptolites occur in the Cincinnatian of the Cincinnati Arch region, only a few are common (Bergstrom 1997). The most common and characteristic Cincinnatian graptolite is ***Geniculogrciptus*** (identified as ***Climacograptus*** in older literature; figures 13.1B, C). This graptolite has a hiserial rhabdosome and is very characteristic of the Kope formation, where aggregations of stipes often occur in parallel alignment on bedding surfaces (figure 13.1C). Two species range from the Kope through Fairview formations (Bergstrom 1996a). 'Iwo hiserial graptolites occur in the Arnheim formation (Riehmondian): ***Orthogrciptus qucidrimucronatus*** and ***Arnheimograptus anacanthus*** (see Bergstrom 1996a). Several species of ***Mastigograptus,*** a delicate, bush-like dendroid graptolite, occur in the Kope, Arnheim, and Waynesville formations.

The zoological affinities of graptolites were for many years among the most challenging problems in paleontology. Graptolites were classified with several different groups, including cephalopods, cnidarians, bryozoans, and hemichordates, or were considered to be unrelated to any living group (Bulinan 1970). Research by the Polish paleontologist Roman Kozlowski (1966) noted several similarities between graptolites and the living hemichordates called pterobranchs that argue stronglv for a close evolutionary relationship. Pterobranchs are a group of small, marine, tube-dwelling invertebrates that are classed together with the acorn worms in the Phylum 1 lemichordata on the basis of embryological similarities; there are only three liv ing genera of pterobranchs (Barnes 19S7). The creeping tube constructed by the living pterobranch ***Rhabdopleura*** has the unique fusellar half-ring and cortical structure found in graptolites (Bulinan 1970). In addition, some encrusting types of graptolites have a black stolon preserved within the tubes that is verv similar to the structure of the stolon in pterobranchs that interconnects zooids within the colony. The identification of the protein collagen in the tubes of both graptolites and pterobranchs indicates not only their close relationship, but also affinity to chordates, in which collagen forms the connective tissue (Armstrong et al. 19S4). The extinct graptolites are thus generally treated as an extinct class within the 1 lemichordata. Although the soft part structure of the graptolite zooids remains unknown, hypothetical reconstructions suggest that the zooids probably had paired tentacle-bearing arms that were extended for purposes of suspension feeding and deposition of the outer cortical bandages of the thecal wall.

Conodonts

It is ironic that perhaps the most significant Cincinnatian fossils, in a geological sense, are also among the least conspicuous to most observers. These are the conodonts, tooth-like microfossils (< 1 mm), so unlike any other fossil or living organisms that they were regarded until recently as representing a distinct phylum. Conodonts can be found throughout the Cincinnatian by dissolving blocks of limestone in acetic acid, although they can also be found in disaggregated shales. Because conodonts have a calcium phosphate composition, they are insoluble in acetic acid. Conodonts are conspicuous in the acid-insoluble residue scanned under a dis-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secting microscope because of their unique forms and a beautiful amber color (Plate 5B).

Conodonts have a wide range of shapes, including single cones, multi-pronged "teeth," serrated blade-like shapes, and so-called platform-type forms (Figure 13.2). Most conodonts have a tooth-like appearance, leading to the assumption that they were used as teeth. However, conodonts also show regeneration. This suggests that at least some conodonts were embedded in soft tissue by which they were secreted. Individual conodonts, called elements, were given species names by earlier workers. However, the discovery of rarely preserved assemblages of different elements in rock matrix or fused together led to the recognition that elements were arranged in bilaterally symmetrical assemblages of pairs of elements, each of which is called an apparatus. Although few apparatuses are preserved intact, it has been possible to determine which elements found in a sample likely formed an apparatus on the basis of statistical analysis of the ratios of commonly associated elements. Modern taxonomists of conodonts attempt to include the six or seven different elements of a given apparatus under a single species name.

Because the tooth-like elements apparently were the only mineralized parts of the organism, the identity of the conodont-bearing organism and the nature of its soft part anatomy have been among the great mysteries of paleontology. A major breakthrough came in 1983 when a fossil of an eel-like, soft-bodied organism from the Lower Carboniferous of Scotland was shown to have a conodont apparatus at one end and fin-like structures at the opposite (Briggs et al. 11)83). This "conodont animal" is only 4 cm long and shows little of its internal anatomy, save for a midline suggesting bilateral symmetry. Although it bears similarities to both chaetognaths and chordates, the authors concluded that the conodont animal belongs to a distinct phylum. More recent phylogenetic studies based on more extensive data place the conodonts within the chordates, close to the living lampreys (Donoghue et al. 2000). Because conodont animals had mineralized calcium phosphate elements, among other characteristics, they are considered to be vertebrates, even though they lacked internal skeletons. The conodont animal could be considered to have been the fish of the Cincinnatian sea. However, given their small size and great differences from anything like present-day bony fish, the title of this book, A *Sea without Fish,* remains valid. The foregoing introduction is largely based on Clark (1987). For more information about the morphology and affinities of conodonts the reader should consult Aldridge et al. (1993), Aldridge and Purnell (1996), and Donoghue et al. (2000).

Conodonts of particular types are found in marine rocks over a very wide geographic range, even intercontinental in extent. This wide distribution suggested that the conodont organism was pelagic long before the fin-bearing conodont animal was discovered (Clark 1987). Conodonts apparently lived as swimming members of the marine nekton ranging from close to the sea floor to various positions in the water column. The tooth-like apparatus might have been used to seize or strain food items from the water.

In addition to their wide geographic range, genera of conodonts are restricted in their vertical (stratigraphic) ranges throughout their Middle

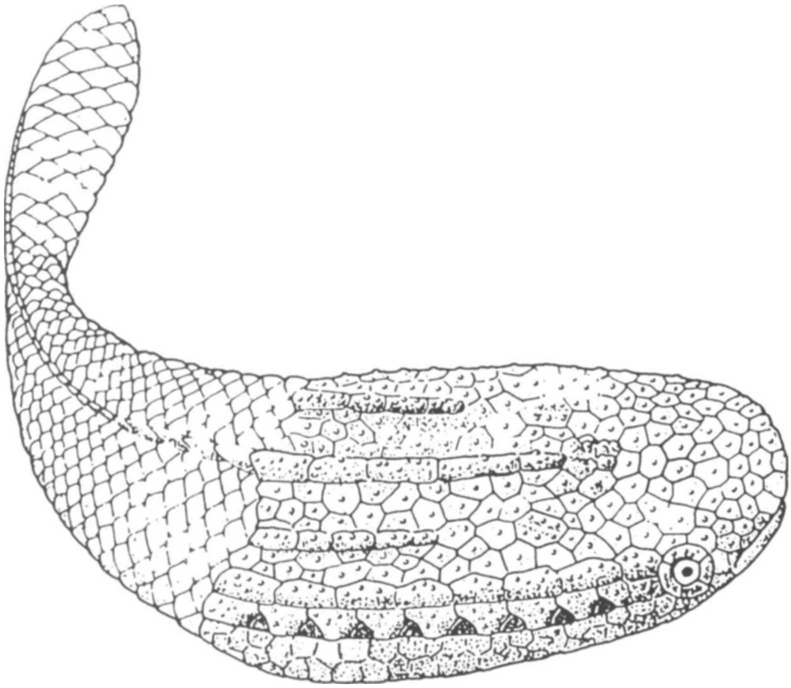
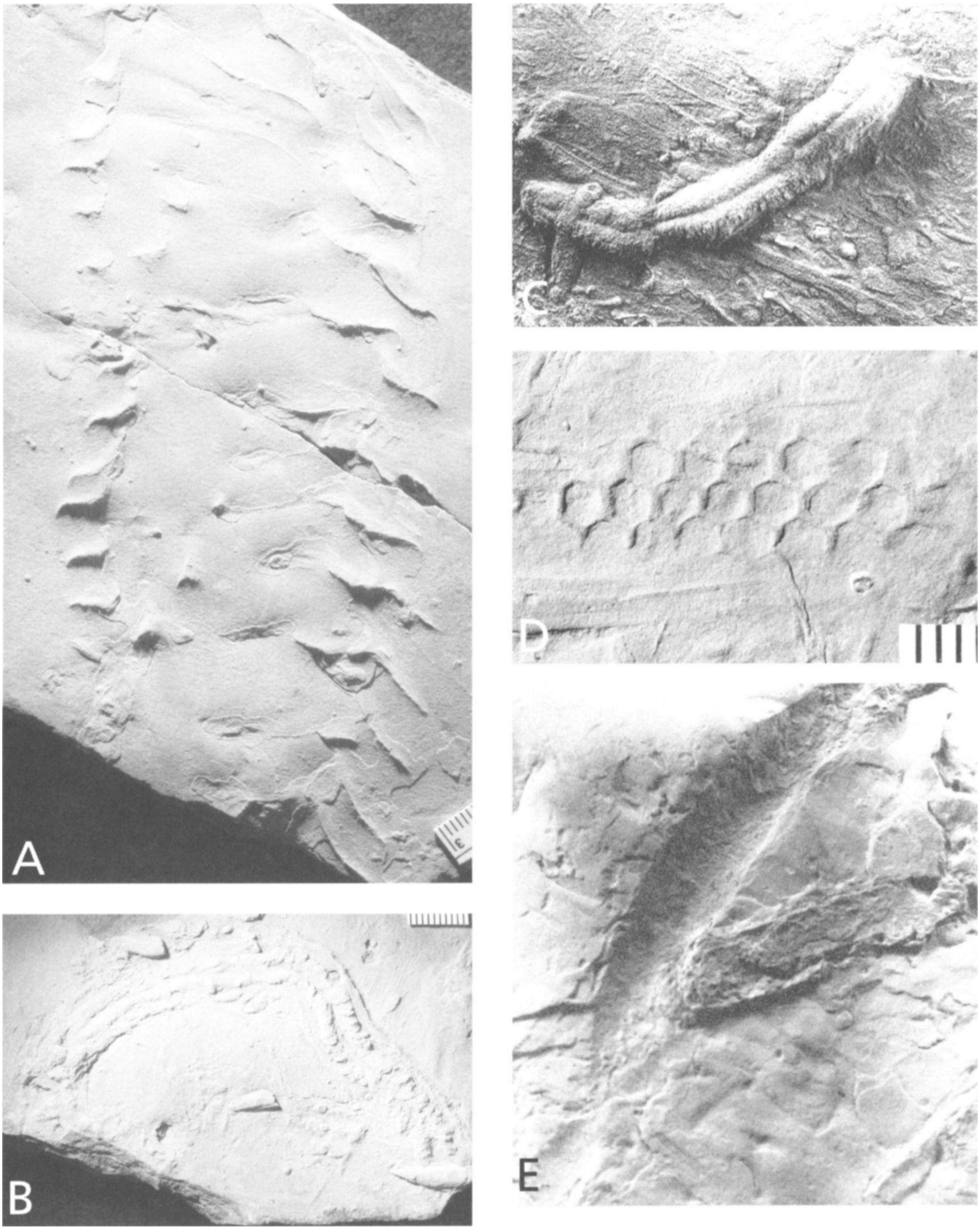


Figure 13.3. *Reconstruction of the Ordovician jawless fish, Astraspis desiderata Walcott, from the Harding Sandstone of Colorado. Length about 13 cm. From Cowen (2005, 86, figure 7.4). Reprinted with permission of Blackwell Publishing.*

Cambrian through Triassic geologic record. These attributes, together with abundance in marine strata as microfossils, make conodonts exceptionally useful for biostratigraphic subdivision of the Paleozoic sedimentary rock record. For the entire Upper Ordovician (above the base of the Lexington Limestone) in the Cincinnati region. Sweet (1979) recorded thirty-five conodont species representing twenty genera (Figure 13.2). Most genera occur also in Europe, Asia, Australia, or Africa, but species are more geographically restricted. Most Cincinnatian conodonts represent the North American Midcontinent Province, but some are components of the North Atlantic Province that is also represented in Europe. The type-Cincinnatian section spans all or parts of six conodont-defined biostratigraphy zones (Webby, Cooper, Bergstrom, and Paris 2004). Although many conodont taxa have long stratigraphic ranges within the Cincinnatian, variations in relative abundance are probably related to differing depth preferences among species (Sweet 1979, 1996).

Ordovician "fish"

Conodonts may have been the only representatives of the vertebrates in the Cincinnatian sea, but fossil evidence from many localities elsewhere shows that some of the earliest fish did indeed exist during the Ordovician Period. The Ordovician Harding Sandstone of Colorado contains abundant, tiny plates composed of an enamel-coated dentine, named *Astnispis desiderata* by Walcott in 1892. In 1997 Sanson) and others illustrated an extraordinary fossil from the Harding with a compressed, nearly complete, fish-like body that proved the long-held assumption that the tiny plates formed a head shield (Figure 13.3). Eyes and a series of openings probably related to respiration are preserved. A similar fossil fish from Ordovician rocks in Bolivia shows that these early fish had blunt, rounded heads, an elongated fish-like shape with a tail fin, but lacked bony jaws and separate fins. These jawless fish are called agnathans, but other Ordovician fossils represent the earliest jawed fish or gnathostomes (Sansom et al. 2001). Thus, a variety of early fish had already evolved by Cincinnatian time, but they are unknown from the Cincinnati region. Had these early fish been present in the Cincinnatian sea, it would seem reasonable to expect their mineralized plates to be preserved in the limestones or shales. Although their absence may indicate that then preferred an environment not represented in the type-Cincinnatian, the potential for their eventual discover) should not be overlooked.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14

TYPE-CINCINNATIAN TRACE FOSSILS: TRACKS, TRAILS, AND BURROWS

The Cincinnatian is renowned for its abundance of well-preserved shells and skeletons of Ordovician marine invertebrates, and because these fossils represent the remains of long-dead organisms, at first glance one would not expect them to yield much information about the activity and behavior of these animals during life. Of course, we can deduce a great deal about the life habits of Ordovician animals directly from the morphology of shells and skeletons (body fossils) by comparisons to their living relatives, but a vast range of evidence about ancient behavior also comes from a completely different source, namely the trace fossils that are both abundant and diverse in Cincinnatian strata.

Trace fossils are evidence of the activities of ancient organisms preserved in sedimentary rocks in the form of tracks, trails, burrows, borings, and other fossils such as **coprolites** (fossil feces). Most trace fossils were formed as organisms disrupted loose sediments before lithification, although borings are the results of drilling, rasping, or etching into hard substrata such as shells or already-lithified hardgrounds. The study of trace fossils (also known as ichnofossils or ***Lebensspuren***) has become a specialized field of geology known as ichnology. Cincinnatian trace fossils with their exquisite preservation have long fascinated students of these rocks. Among them were S. A. Miller, who described many Cincinnatian trace fossils but regarded them to be the remains of marine plants (so-called fucoids), and J. F. James, who was one of the earliest proponents of the correct organic interpretation of trace fossils (Osgood 1975a). Richard C. Osgood, jr., who completed his doctoral dissertation at the University of Cincinnati in 1905 (Osgood 1970), conducted a thorough systematic review of Cincinnatian trace fossils and thereby contributed much to the development of modern ichnology.

Trace fossils greatly enhance the ability of the paleontologist to reconstruct the life of the past (Osgood 1975). In rare cases a trace fossil can be preserved in close association with the body fossil of the actual tracemaker (figure 14.2). Usually the identity of the tracemaker is unknown, often because the tracemaker was soft-bodied and unpreservable. Different organisms and different preservational processes can sometimes produce a similar type of trace fossil. Consequently, trace fossils are not identified by a genus and species name of a body fossil, but instead are given genus and species names of their own. The need for this approach is further indicated because a single organism can produce several different types of traces, depending on its behavior. Thus, a one-for-one correspondence between a tracemaking biological species and a given type of trace fossil cannot be established. The

Figure 14.1. A. *Repichnia of the trilobite Isotelus, Asaphoidichnus trifidum Miller, CMC IP 37569, Edenian, Kope Formation, Cincinnati, Ohio,* x 7. B. *Repichnia of the trilobite Cryptolithus, similar to Cruziana, CMC IP 37622, horizon and locality unknown,* x 7. C. *Trilobite trail, intermediate between Rusophycus and Cruziana, Maysvillian, Corryville Formation, Clermont Co., Ohio (from Osgood [1970, plate 66, figure 3[),* x *0.8.* D. *Paschichnia, ?Paleodictyon, CMC IP 17431, Edenian, Kope Formation, Cincinnati, Ohio,* x *3.* E. *Fodinichnia or domichnia, the "turkey track," Trichophycus venosum Miller, CMC IP 37575, Campbell Co., Kentucky,* x *0.4. From Osgood (1970, plate 60, figure 7). C,* E *reprinted by permission of the Paleontological Research Institution.*

Linnaean binomial system was developed for trace fossils because they were once thought to be body fossils, and this procedure has persisted (Simpson 1975). Ideally, the ichnogenus might be defined to represent a particular behavioral pattern while the ichnospecies represents variations on this pattern, although this procedure has not been uniformly applied (Bromley 1990). Trace fossils provide information about unpreservable soft part structures of animals that are known as skeletal fossils. In the Cincinnatian, good examples of this are the varieties of *Rusophycus,* the resting trace of trilobites, with impressions formed by the digging activities of the legs (Figure 14.2A). Trace fossils also augment our record of diversity by preserving activities of entirely soft-bodied species that are otherwise unknown in the record.

The greatest significance of trace fossils is, however, the information they yield about the behavior of long-dead animals. The German paleontologist Rudolf Richter pioneered the analysis of ancient behavior from trace fossils by studying traces made by shallow marine organisms in Recent sediments of the North Sea. In many cases modern tracks and trails could be compared to fossilized traces. A remarkable book by Wilhelm Schafer (1972) summarizes the work of Richter and many subsequent German students of the North Sea traces in English. Adolf Seilacher (1964) classified trace fossils into behavioral categories that facilitated the interpretation of ancient environments on the basis of trace fossil assemblages.

Behavioral Categories of Trace Fossils

Repichnia are traces made by the directed locomotion of benthic organisms. These are the most common traces in the Cincinnatian, with seventeen ichnospecies recorded by Holland (2005). The appendages of trilobites or other arthropods digging into the substratum during crawling formed several repichnial traces. *Asaphoidichnus trifidum* (Miller) (Figure 14.1A) and *Allocotkhnus dyeri* Miller represent different forms of the crawling trace of the trilobite *lsotelus* (Osgood 1970). *Trachomatichnus numerosum* Miller is the crawling trace of the trilobite *Cryptolithus,* and *Petaliclmus multipartitum* Miller is the crawling trace of a medium-sized, unidentified trilobite (Osgood 1970). Other common repichnial traces *(Palaeophycus)* are tubular, usually unbranched burrows that run slightly oblique to bedding, preserved either as convex hyporeliefs or trough-like concave epireliefs. (A hyporelief is preserved on the base or sole of a sedimentary bed; epireliefs are preserved on the upper surface of a bed.) Osgood described three forms of *Palaeophycus* and indicated that modern counterparts are produced by infaunal burrowing of polychaete worms or molluscs.

Pascichnia are meandering traces made by the grazing activities of deposit feeders (animals that feed on particulate organic matter either on or within the bottom sediment). Although no actual meandering traces are found in the Cincinnatian, one very peculiar trace questionably referred to ***Paleodictyon,*** is classified by Osgood as a pascichnial trace (Figure 14.1D). This trace is a remarkably regular network of ridges as a convex hyporelief. It resembles the impression of a honeycomb or chicken wire. Osgood described only two known specimens from the Cincinnatian, and discussed the many varying interpretations that workers have proposed for the origin of *Paleodictyon* from other localities. Although it may be the impression of a patterned object being rolled along the substratum, Osgood concluded that the Cincinnatian *Paleodictyon* is a trace fossil. Seilacher (1977) interpreted patterned traces of this type to represent complex burrow systems rather than grazing patterns. These burrow networks are used by some infaunal organisms for the "fanning" of microbes beneath the sea floor.

Fodinichnia are feeding traces of deposit feeders operating from a fixed burrow. The most common Cincinnatian fodinichnia are the varieties of the branching burrow *Chondrites* as described by Osgood. *Chondrites,* type-A appearing on the vertical edges of beds of fine-grained carbonates, resembles narrow rootlets (0.8 mm average diameter), sometimes penetrating the entire thickness of a bed (Figure 14.3A). On bedding planes, this form occurs as a circular pattern of closely spaced holes. *Chondrites,* type-B can be seen on both bedding planes and vertical sections. Compared to *Chondrites,* type-A, type-B has tubes of greater diameter (1-4 mm), and branches that propagate to a greater extent horizontally than vertically (Figure 14.3B). *Chondrites,* type-C occurs as densely interwoven radiating branches, either parallel or oblique to bedding (Figure 14.3C).

Another common and interesting Cincinnatian trace classified by Osgood as fodinichnia, or possibly domichnia, is *Trichophycus venosum* Miller (Figure 14.1F). The most common expression of this trace, found throughout the Cincinnatian, is a shallow elongate depression with rounded ends on the upper surface of calcisiltite beds. Beds covered with these scoop-like depressions, oriented in random fashion, give the appearance of overlapping tracks of large birds; hence local collectors refer to these features as "turkey tracks." Osgood's careful study of "turkey tracks" revealed that they represent only a part of a U-shaped burrow structure with branches in the vertical plane. The depressions are often filled with thin lamellae of finer-grained sediment that indicate the burrowing organism dug through a mud layer until it reached coarser silt, whereupon it turned back toward the surface. After completing its deepest penetration the burrowing organism repositioned itself by working upward, forming the stacked lamellae and digging new tunnels upward, possibly reaching the surface. In most cases subsequent erosion removed the softer mud, leaving the more resistant silt with only the basal floor of the burrow as the "turkey track." by this interpretation, Osgood rejected the fascinating earlier idea put forth by Rousseau H. Flower (1955) that "turkey tracks" represented "touchdown" impressions left by nautiloid cephalopods. The large size of the "turkey tracks" (width 2.5-3.5 cm) indicates the activity of a large organism, but its exact identity remains conjectural. Fine striations parallel to the length of the depressions were formed by appendages of an arthropod or chaetae of a polychaete worm (chaetae are bristles extending from the body segments of a worm). Because the burrows are not bilobed, they were most likely not produced by a trilobite with paired appendages. "Turkey tracks" may well represent the only evidence we have of a rather large, soft-bodied infaunal organism that was quite common on the Cincinnatian sea floor.

Domichnia are permanent dwelling traces formed by benthic animals feeding by predation, scavenging, or suspension feeding. The "U-tube"

Diplocraterion is the most common domichnial trace fossil of the Cincinnatian. Osgood (1970) recognized three ielmospccies of *Diplocraterion.* As seen on vertical joint surfaces, /). *cf. luniformis* (Blanckenhorn) has a plain I l-shape with a rounded base. Narrow, elongated slots on the upper surface of a bed represent the base of the 11. In the more common /). *cincinnatiensis* (Osgood) the U expands with depth in different ways (figures 14.3A, 14.4 \i. faint downward-curving striations *(Spreiten)* connect the arms of the U. These so-called protrusive *Spreiten* may represent the downward propagation of the burrow as the organism grew. Alternatively, the organism may have burrowed deeper in order to maintain a constant depth below a constantly eroding sediment-water interface. The reason for the basal expansion is unclear. Some expansions occur at an interface with coarser material, yet others expand within the silt-sized layer (figure 14.4A). This led Osgood (1970) to suggest that the organism may have sensed a chemical change in the sediment before encountering a change in grain size. We speculate that the expansion of the U might have developed after the worm-like organism burrowed to its preferred depth. Lateral expansion of the U enabled the worm to grow in length while maintaining its depth.

The third *Diplocraterion* ichnospecies, *D. biclavata* (Miller), has a pair of short extensions developed at the base of the U as blind pouches. This form also occurs as concave epireliefs in what are commonly called "dumbbells" (figures 14.4B, C). Osgood showed that dumbbells represent the basal penetration of the D-tube with paired extensions into a coarser substratum that usually remains after erosion stripped off the upper parts of the U. All three ichnospecies of *Diplocraterion* can be found in the same bed, suggesting that a single type of organism could have produced all three expressions. The tracemaking organism was probably some type of worm that used the U-tube as its dwelling structure, while suspension feeding near the sediment-water interface.

Many borings found in Cincinnatian stromatoporoids, corals, bryozoans, brachiopods, molluscs, and hardgrounds represent domichnia. Pits on the underside of a Riehmondian stromatoporoid contain the tracemaking bivalve *Corallidomus scobina* Pojeta and Palmer as the oldest-known case of hard substrate boring by a pelecypod (see Figure 9.8A; Pojeta and Palmer 1976). The same elongate pits, now referred to the ichnospecies *Petroxestes pera,* are also found in calcareous nodules and the bases of bryozoans (Wilson and Palmer 1988). Cincinnatian rugose corals of the genus *Grewiugkia* commonly show borings called *Trypanites* (see figure 6.5K; flias 1986). Although it is usually impossible to determine whether the borings occurred during the life of the coral, Klias found some borings encased within swellings of the coral septa. Flias inferred that a boring worm penetrated the septa of a living coral, resulting in the secretion of the septal swelling. In other cases borings did not come into contact with the living coral polyps, but were probably located on corals in life position so as to expose the worms to ambient current flow.

A distinctive type of boring called *Sanctum laurentiensis* frickson and Bouchard occurs as isolated, round tunnels on the interior of branching Cincinnatian bryozoans (Krickson and Bouchard 2003). The interior of the excavation is elongate or sack-shaped and 1 mimed. The trace-maker was likely

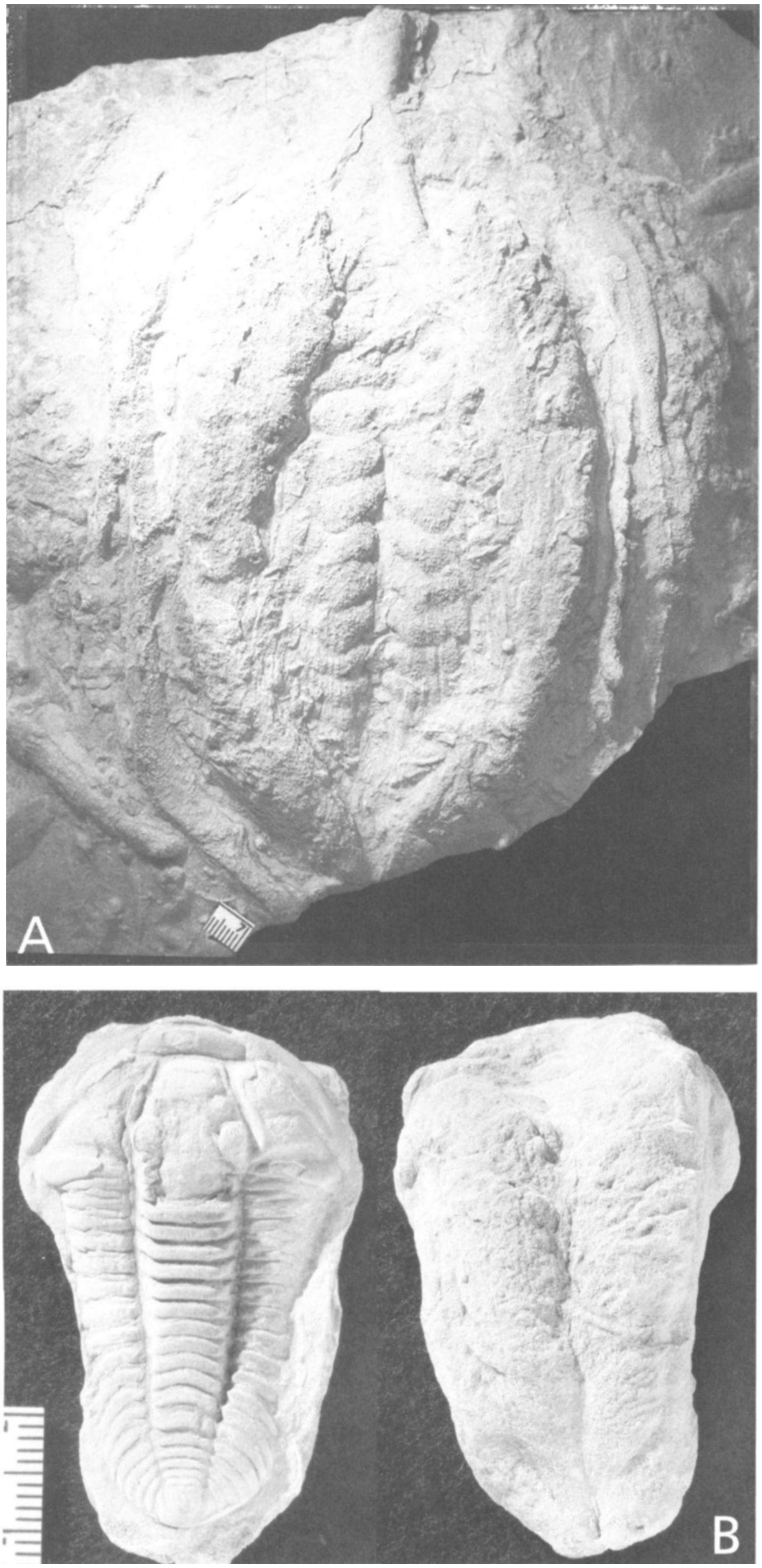


Figure 14.2. A. *Cubichnia and sderite impressions of trilobite Isotelus, Rusophycus carleyi (J. F. James), CMC IP 46411, Maysvillian, Corryville Formation, Clermont Co., Ohio,* x *0.6. Note impressions of cephalic margin, genal spines, pleurae, pygidial margin, as well as coxae (medial paired lobes, flanked by crescentic impressions made by legs. Also, at top, note Paleophycus burrow terminating at approximate position of trilobite mouth, with superimposed scratchmarks.* B. *Flexicalymene meeki (Foerste), CMC IP 37574, Maysvillian, Corryville Formation, Clermont Co., Ohio,* x *1.4.* Right: *Reverse side of specimen shown in* B, *cubichnia Rusophycus pudicum Hall, convex hyporelief, identifying trilobite as tracemaker. This exceptional specimen is one of the very few known with both trace and tracemaker preserved together.*

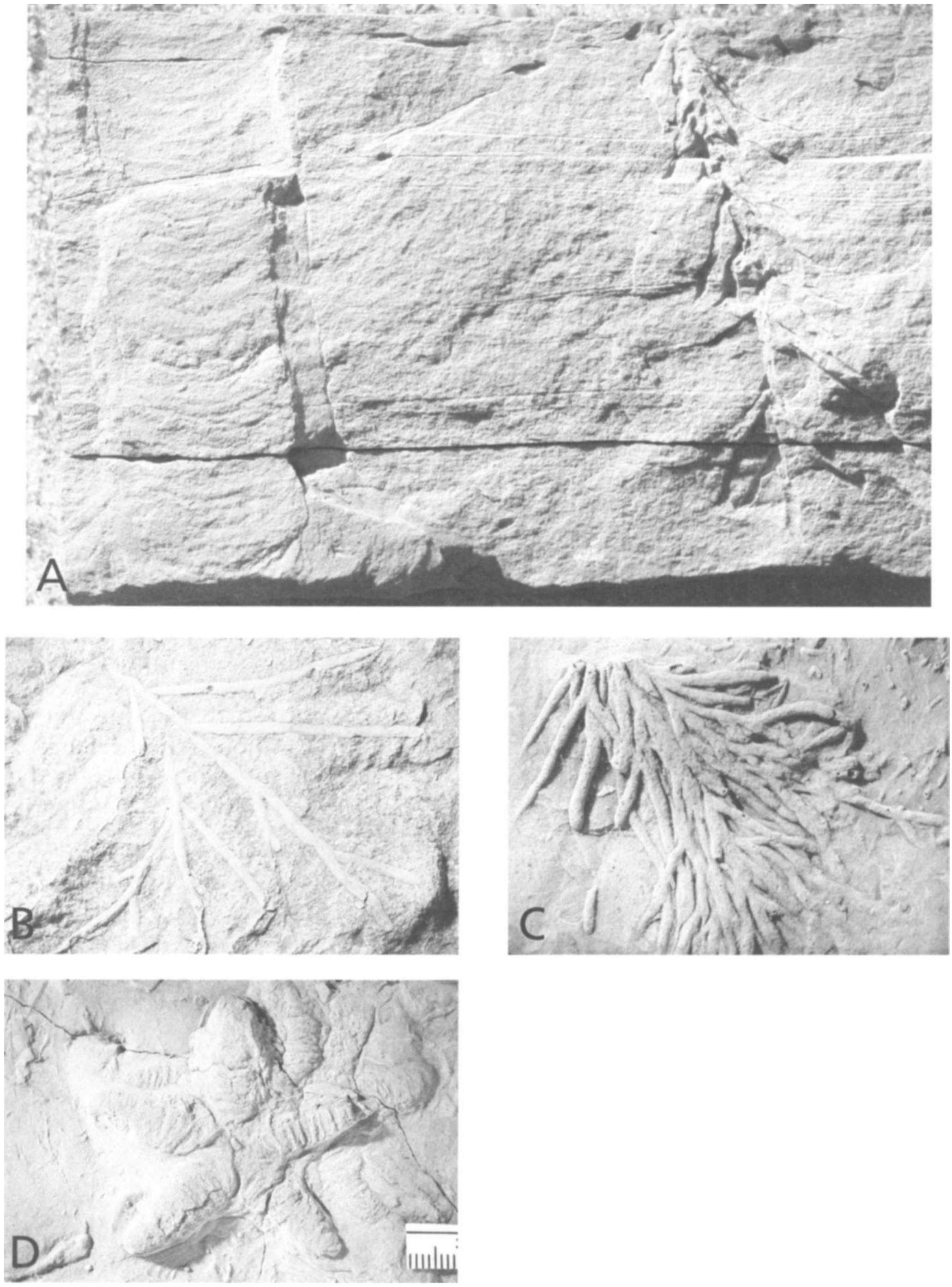


Figure 14.3. A. *Vertical joint surface showing two commonly associated trace fossils: at left, domichnia, Diplocraterion cincinnatiensis Osgood; at right, fodinichnia, Chondrites, type-A, CMC IP 37607, Edenian, Kope Formation, Cincinnati, Ohio,* x *1.3.* B. *Fodinichnia, Chondrites, type-B, CMC IP 37623, Maysvillian, Corryville Formation, Clermont Co., Ohio,* x *0.9.* C. *Fodinichnia, Chondrites, type-C, CMC IP 37678, Richmondian, Whitewater Formation, Wayne Co., Indiana,* x *1.2.* D. *Cubichnia of sea star, Asteriacites stelliforme (Miller and Dyer), CMC IP uncatalogued, Maysvillian, PCorryville Formation, Cincinnati, Ohio,* x 7.

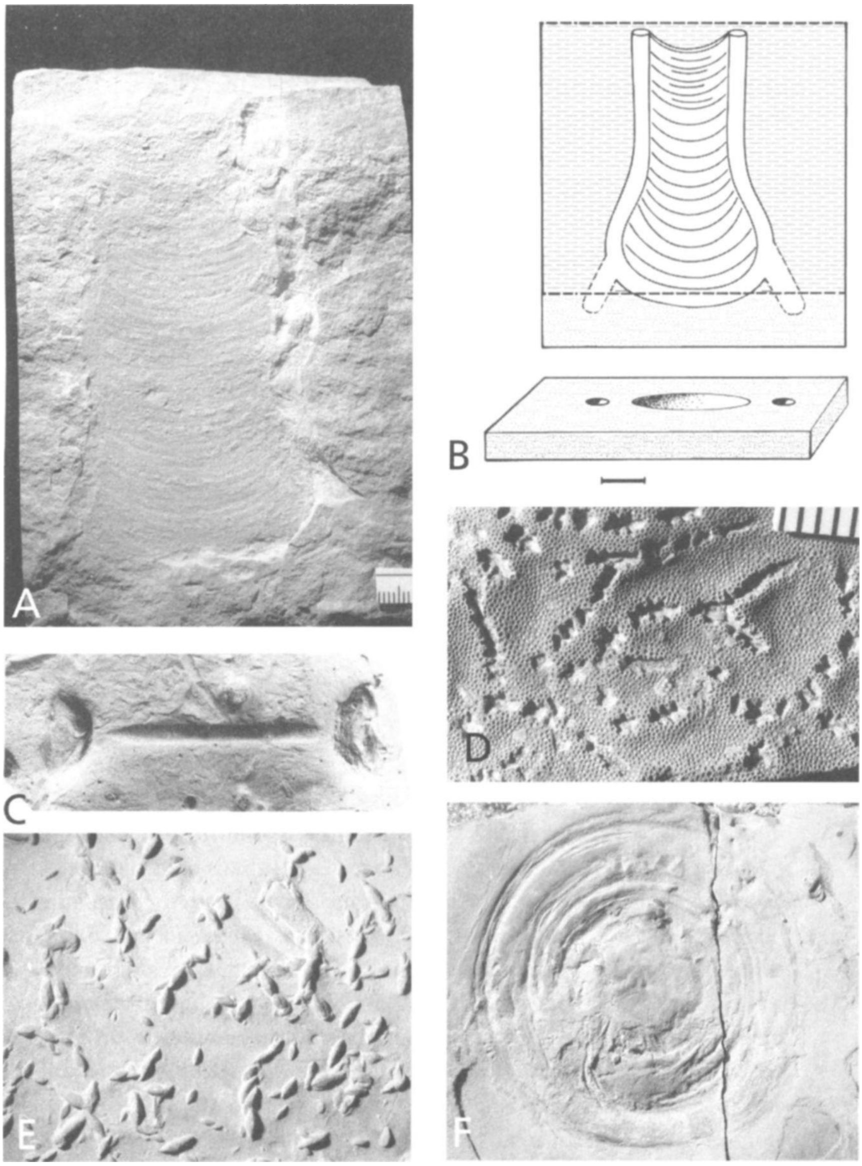


Figure 14.4. A. *Vertical joint surface showing domichnia, Diplocraterion cincinnatiensis Osgood, CMC IP, uncatalogued, Edenian, Kope Formation, Campbell Co., Kentucky,* x *0.8.* B. *Reconstruction of Diplocraterion biclavata (Miller), showing U-tube and spreiten constructed in upper shale (dashed pattern) with base of U and paired lateral extensions in underlying calcisiltite (stippled pattern). When shale is eroded away, a "dumbbell" impression remains on the upper surface of the calcisiltite, as shown in lower diagram. Modified from Osgood (1970).* C. *Domichnia Diplocraterion biclavata (Miller), "dumbbell" on upper surface, CMC IP 37657, Maysvillian, Corryville Formation, Clermont Co., Ohio, (from Osgood [1970, plate 61, figure 3]),* x *0.4.* D. *bioimmuration structure in bryozoan, Catellocaula vallata Palmer and Wilson, University of Cincinnati collection, Edenian, Point Pleasant Formation, Bracken Co., Kentucky, x.2.3.* E. *Cubichnia of pelecypods, Lockeia siliquaria U. P. James, CMC IP 37597, Edenian, Kenton Co., Kentucky,* x *0.5.* F. *Palaeoscia floweri Caster, holotype, CMC IP 24079, Maysvillian, Corryville Formation, Clermont Co., Ohio. Although originally interpreted as the impression of a porpitid jellyfish, this impression was considered by Osgood (1970) to be either a feeding trace or of inorganic origin as a result of rotatory sweeping of an agglutinated tube,* x *0.6.* B, C *reprinted by permission of the Paleontological Research Institution.*

a crustacean that took advantage of the bryozoan host for protection as well as for an elevated feeding position. Excavation of the interior of the bryozoan branches probably reduced the structural integrity of the colony and rendered it more susceptible to breakage during storms. *Trypanites* borings on bryozoans usually occur in clusters and were probably formed when dead, broken colonies were exposed on the sea floor (Erickson and Bouchard 2003).

Another type of trace found in Cincinnatian bryozoan colonies is not actually a boring but rather records the presence of a soft-bodied organism that lived as an endosymbiont within the bryozoan skeleton, termed bioclaustration by Palmer and Wilson (lcjHS) (figure 14.40; see Figure 11.6E). After settlement by a larva of the endosymbiont onto the living colony, bryozoan zooecia grew around the organism In conformation to its shape, resulting in distinctive pits arranged in rows, named *Catellocaula vallata* by Palmer and Wilson (19S8). tinlike borings, the margin of these pits is lined by zooecial walls. The morphology of the pits and their arrangement in rows suggested a colonial, stoloniferous organism, most likely a tunicate. Tapanila (2005) has proposed that a new behavioral category, Impedichnia, be used for such cavities that locally inhibit the normal skeletal growth of the host. *Catellocaula vallata* represents one of the oldest known examples of this endosymbiotic behavior.

Cubichnia are temporary traces made by mobile animals. Although they are often regarded as "resting" traces, there is also the possibly that some cubichnia represent feeding or predation burrows. Trilobite "resting" traces, represented by three ichnospecies of *Rusophycus,* are among the most common cubichnial traces in the Cincinnatian. Osgood (1970) recognized *R. pudicum* I lall as the trace of *Flexicalymene* on the basis of its size and a few exceptional occurrences of the tracemaker preserved with the trace directly beneath it (figure 14.2B). Occasionally clusters of *R. pudicum* are found that suggest the activity of several trilobites, although a single individual could also produce multiple burrows in close proximity. *R. carleyi* O. f. James) is a large burrow attributable to the largest Cincinnatian trilobite *Isotelus.* In a few exceptional specimens, casts of the cephalic and pygidial margin, genal spines, and pleurae are present along with impressions formed by the walking legs (figure 14.2A; Osgood 1970; Brandt et al. 1995). hi even rarer specimens, intersection by the trilobite trace of a worm burrow suggests that the burrow was formed for the purposes of predation (Figure 14.2A; Brandt et al. 1995; Fortey and Owens 1999). Small, ovoid *Rusophycus (R. cryptolithi)* are consistent with formation by the trilobite *Cryptolithus* (Osgood 1970). Other cubichnial traces for which the tracemaker is identifiable are *Lockeia siliquaria* U. P. James, formed by shallow-burrowing pelecypods (figure 14.4F) and *Asteriacites stelliforme* (Miller and Over) formed by sea stars (Figure 14.3D; Osgood 1970).

Ichnofacies and Paleoenvironmental Interpretation

Seilacher (1964) proposed that the relative abundance of trace fossils belonging to the behavioral categories varied according to the submarine environment, chiefly in relation to depth. Trace fossil assemblages (ichnofacies) dominated by domichnia] and cubichnial traces characterize shallow, nearshore marine environments because conditions of high turbulence cause vagile organisms and suspension feeders to seek shelter in burrows. As depth increases within the shallow nearshore zone, conditions of lower water movement permit food particles to settle, and thus deposit feeding activity increases, resulting in fodinichnial traces. In deep sea environments there is little need for permanent shelter, and so dwelling and resting traces are not formed; instead, organisms tend to graze the sediment surface for food, creating the meandering pascichnial traces. Repichnial traces are found in all submarine environments, because organisms are always going somewhere and leaving trails, no matter what the setting! Seilacher's original concept of trace fossil facies distribution has been widely tested, substantiated, and expanded to include assemblages characterizing non-marine environments and particular substrata such as hardgrounds and wood (Bromley 1990). Can the ichnofacies concept be applied to Cincinnatian trace fossils, and what can this tell us about the Late Ordovician marine environment?

Osgood (1970) listed thirty ichnogenera and forty-four ichnospecies from the Cincinnatian. Recent additions and revisions bring the total to thirty-four ichnogenera and forty-seven ichnospecies (Holland 2005; Tapanila 200^). The following list shows the distribution of these ichnospecies.

Cubichnia	5
Domichnia	6
Repichnia	17
Fodinichnia	9
Pascichnia	1
Impedichnia	2
Borings	2
incertae *sedis*	5

The high diversity in the categories domichnia, cubichnia, and fodinichnia, compared to the single (and rare) occurrence of pascichnia, led Seilacher (1964) and Osgood (1970) to conclude that the Cincinnatian as a whole coincides with the ***Cruziana*** ichnofacies, reflecting a shallow, open marine environment. Osgood suggested that the Cincinnatian marine environment was m i deeper than about 35 m.

Very little work has been done to refine paleoenvironmental analysis of the Cincinnatian using trace fossils. Osgood noted that a "subassociation" of three trace fossils, ***Diplocraterion,*** *Chondrites,* and ***Trichophycus*** is found in single beds near the top of the Kope Formation and recurs in the Corryville and again in the Liberty Formations, suggesting a recurrence of similar conditions. High resolution stratigraphic work has demonstrated that these ***Diplocraterion*** beds in the upper Kope are widely traceable over the Greater Cincinnati region (Jennette and Pryor 1993; Brett et al. 2001b), but there has been no detailed study of the trace fossil association.

"Traces" of Inorganic or Indeterminate Origin

Several sedimentary structures in Cincinnatian strata were named as "fucoids" but are likely to have an inorganic origin or remain problematic.

These are usually preserved as hyporeliefs. One such structure, *"Blastophycus,"* probably represents castings of impressions left by enrolled trilobites and current scour around them (Osgood 1970). Another, *"Dystactophycus,"* is a fan-shaped pattern of fine concentric ridges and grooves, and was once thought to be an algal frond. Osgood concluded that it formed by rotation of a crinoid stem as it was buried. At several Cincinnatian localities, perfectly circular impressions of concentric rings occur on the upper surface of a bed (Figure 14.4F). Caster interpreted these to be body fossil molds of a porpitid jellyfish and described them as *Palaeoscia floweri* (see Caster 1942). However, Osgood examined additional specimens and considered that these concentric rings could have formed under the influence of currents by rotational sweeping of some kind of organic dwelling tube embedded in the sediment. Alternatively, some living polychaetes create a feeding trace that resembles *Palaeoscia,* and thus Osgood relegated these most peculiar Cincinnatian "traces" to *incertae sedis.* Stanley (1986) supported Osgood's assessment that *Palaeoscia* is a trace fossil, but controversy continues over interpretation of *Palaeoscia* and similar concentric ring-like structures in the geological record (Ewing and Davis 1967, 274-275). Bell et al. (2001) listed Cincinnatian *Palaeoscia* as a jellyfish, and asserted that Osgood was incorrect in regarding it as a trace fossil, but gave no basis for this evaluation.

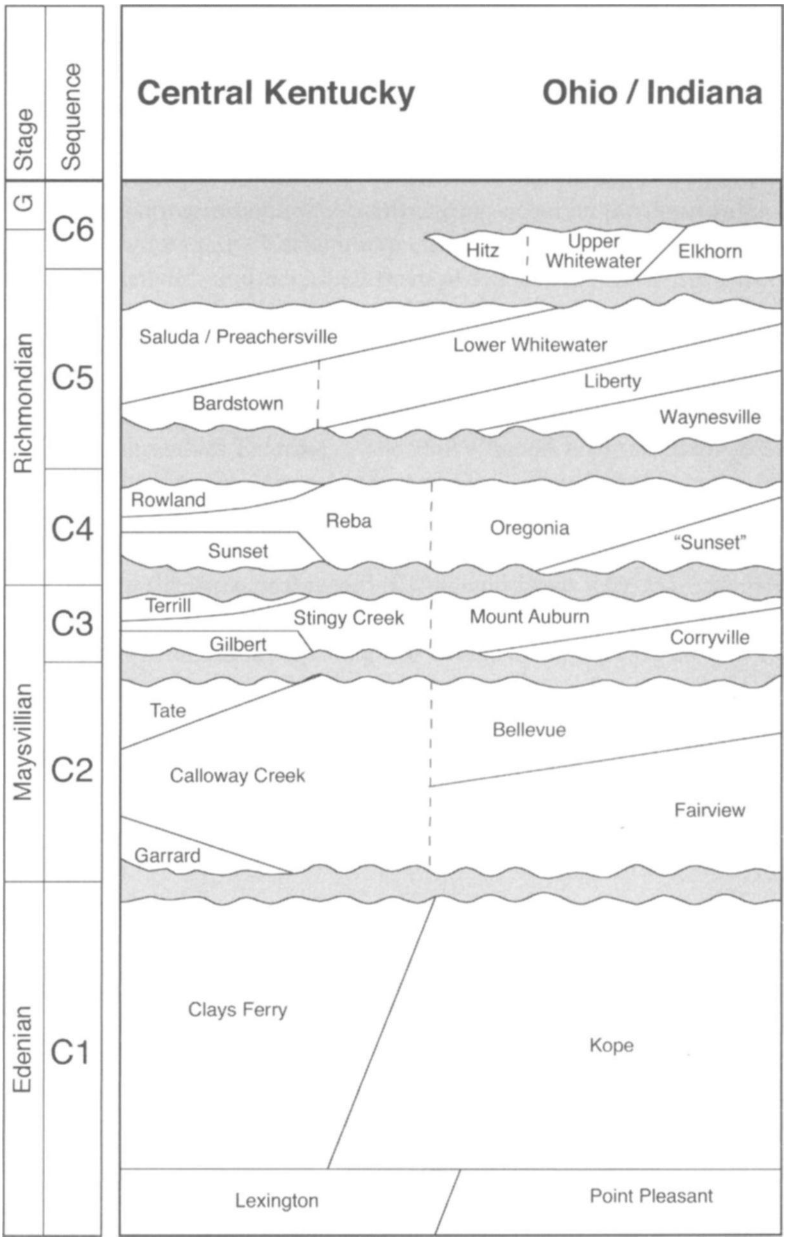


Figure 15.1. *Divisions of type-Cincinnatian strata. Geologists have traditionally defined sedimentary rocks on the basis of time, usually inferred from fossil assemblages, and on the basis of rock type. The Cincinnatian has been traditionally divided into three stages, shown at the far left, and there is currently disagreement over the relative durations of these three stages. A fourth stage, indicated by "G" and called the Gamachian Stage, is not present in the Cincinnati area. The divisions based on rock type are shown at the right. Most of those in modern usage are shown, but dozens of different named divisions have been proposed over the years and are not shown. The names currently used by the Ohio and Kentucky geological surveys differ, and dashed vertical lines indicate these "stateline stratigraphic divisions." The Indiana Geological Survey recognizes the Kope, Whitewater, and Saluda Formations, and assigns all strata between the Kope and Whitewater to the Bull Fork Formation (not shown). Type-Cincinnatian strata have also been divided into six units that reflect cycles of sedimentation produced by the rise and fall of sea level. These depositional sequences, numbered C1-C6, are bounded by unconformities shown in gray that reflect falls in sea level that drained the seas from the Cincinnati area, resulting in no deposition of sediments. The actual duration of these unconformities is poorly known.*

PALEOGEOGRAPHY AND PALEOENVIRONMENT

15

Steven M. Holland

Earth scientists reconstruct conditions during the ancient past from a wide variety of clues from minerals, rocks, and fossils. Although no place on Earth today is exactly like the Cincinnati area during the Late Ordovician, comparisons with modern environments offer valuable insights into the interpretation of these clues. Of modern environments, the Persian Gulf is perhaps the most similar to the Late Ordovician of the eastern United States in terms of its climate, the size of the sedimentary basin, the gently dipping sea floor, the mix of carbonate sediment and clay, and the occurrence of storms that rework and deposit sediment.

Geography

> "When Cincinnati Was in the Southern Hemisphere"
>
> (Title of a presentation by Kenneth E, Caster for the Cincinnati Historical Society, 1974)

Global geography during the Ordovician has been reconstructed primarily through studies of the magnetic properties of Ordovician rocks. When sediments are deposited, iron-bearing minerals tend to align with the Earth's magnetic field. As the sediments become cemented together and undergo lithification to become rocks, these miniature magnets are locked in place. By careful measurement of the orientations of these iron-bearing minerals, geophysicists reconstruct the latitude at which the sediments were originally deposited.

Four large continents dominated the globe during the Ordovician (Plate 1). Stretching from the South Pole into the northern hemisphere, Gondwana was the largest of these continents and consisted of modern day South America, Africa, Arabia, Antarctica, Australia, India, southeast Asia, and parts of China. Laurentia included most of present-day North America, except for New England and Maritime Canada, parts of the southeastern United States, and the west coast of the United States and Canada, all of which were added to Laurentia during subsequent tectonic collisions. Laurentia straddled the equator during the Ordovician and was rotated 45° clockwise from its present-day orientation. As a result, Cincinnati was situated at 20-25° south of the equator for the entire Late Ordovician. To the east of Laurentia along the equator sat the continent of Siberia-Kazakhstan, which consisted of present-day portions of central Asia. The fourth continent, Baltica, lay to the south at roughly 60° and was composed of northern Europe and Scandinavia.

Three major oceans separated these continents. The Iapetus Ocean separated Laurentia and Siberia-Kazakhstan from Baltica to the south. The Paleotethys Ocean lay between Gondwana and the continents of Baltica and Siberia-Kazakhstan to the west. The massive Panthalassic Ocean covered almost all of the Northern Hemisphere and would have dwarfed today's Pacific Ocean.

Global sea level was high during the Ordovician, and although its position is difficult to constrain, the current consensus is that it was 100 to 200 meters higher than present-day sea level (see Figure 1.3). Several factors contributed to such a high position of sea level. Rates of sea floor spreading were high following the breakup of an older, Late Proterozoic supercontinent called Rodinia, causing the average elevation of the sea floor to be higher than normal. This raising of the "bottom of the bucket" forced ocean waters to spill onto the continents. In addition, the lack of polar ice caps in most of the Ordovician also would have raised sea level relative to today because water in modern glacial ice caps such as Antarctica and Greenland is produced from snow generated by evaporation from the ocean. Because of this high sea level, low-lying areas on the continents were flooded with ocean waters, much like the flooding of the present-day continental shelves, but to a much greater extent. During much of the Ordovician, most of Lamentia was submerged, with the exception of parts of the Canadian Shield, a low mountain range running from Minnesota toward Colorado, the Ozark region of Missouri, and the uplifting laconic Mountains along the southeastern edge of Laurentia (Plate 1).

The eastern United States was divided into several geographic regions during the Late Ordovician (Plate 12). Extending from central Kentucky northward into Ohio and Indiana was a shallow marine carbonate area known as the Lexington Platform. Water depths on the Lexington Platform deepened to the north. The Lexington Platform was bounded on the west by a deeper water trough known as the Sebree Trough. Far to the east rose the Taconic Mountains, produced by the collision of Laurentia with a small plate or island are, such as the modern-day islands of Japan and the Aleutians. This collision warped the southeastern margin of Laurentia to form a deep water trough called the Appalachian Basin that separated the laconic Mountains from the Lexington Platform. Into this trough, sediments shed from the eroding Taconic Mountains built a Series of northwest ward-advancing deltas called the Queenston Delta. "Red-bed" tidal flat sediments typical of the Queenston can be seen in the latest Ordovician strata on the eastern side of the Cincinnati Arch in Adams County, Ohio.

Climate

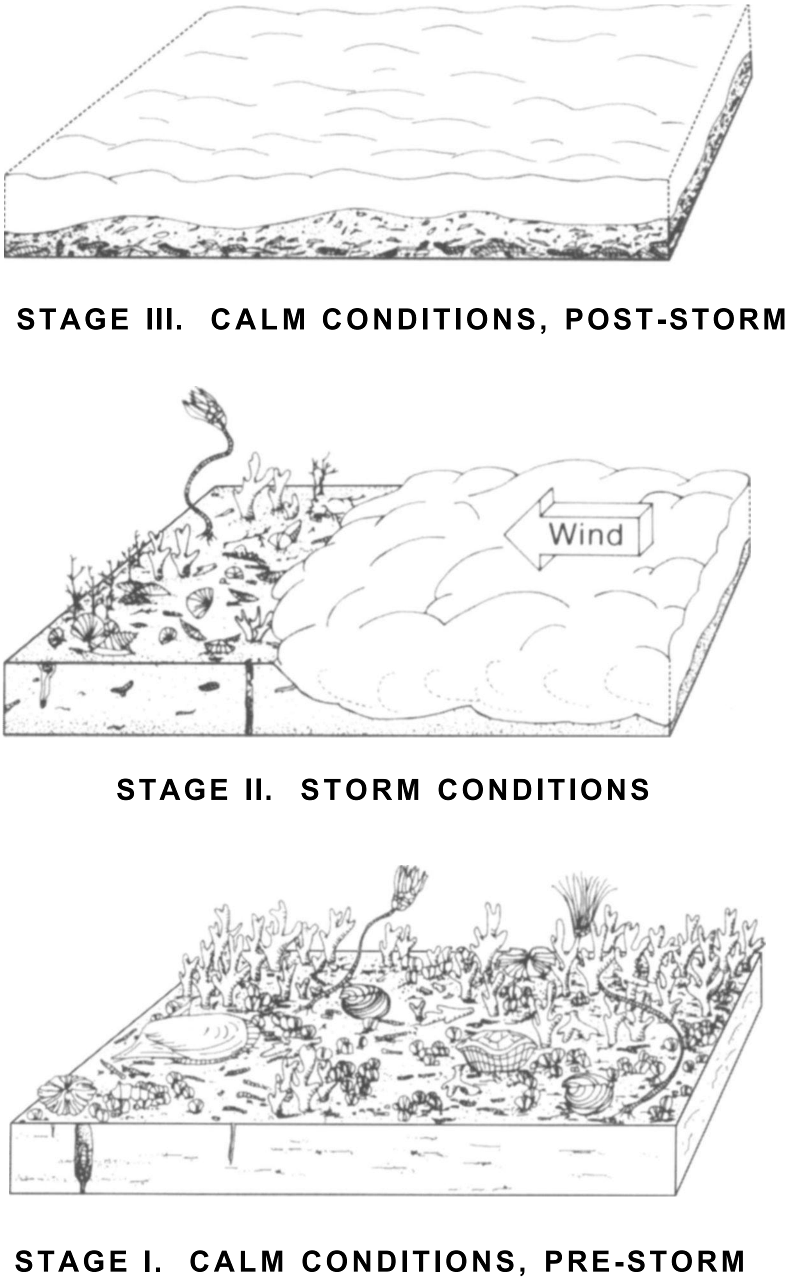
The climate of the Late Ordovician was warm, with much more even temperatures from the pole to the equator than seen today. High concentrations of carbon dioxide in the atmosphere (referred to as the partial pressure of carbon dioxide, or $p\text{CO}_2$,) caused these warm conditions. Computer models and limited geochemical data from Ordovician soil deposits suggest that levels of atmospheric $p\text{CO}_2$, were nearly sixteen times greater than today, compared to the 20 percent increase in $p\text{CO}_2$,witnessed in the past half-century.

Warm temperatures at the poles inhibited the formation of ice caps, such as today's continental glaciers on Antarctica and Greenland and the sea ice over the Arctic Ocean. In the last million years of the Ordovician, atmospheric pCO_2, levels dropped precipitously, triggering the rapid growth of polar glaciers and a geologically brief 160 meter global sea level fall. This fall in sea level drained the seas from the Cincinnati area, producing an erosional division between the Ordovician and Silurian strata called an unconformity.

In addition to this end-Ordovician fall in sea level, evidence for six cycles of global sea level change is preserved in the Ordovician near Cincinnati (figure 15.1). The evidence for these cycles comes from packages of rock known as depositional sequences, which are bounded by unconformities, or surfaces that record the erosion and weathering of sediments. Each depositional sequence begins with a relatively thin interval of rock that records local deepening of the oceans and ends with a much thicker interval of rock that records progressive shallowing of the oceans. These same sequences can be recognized across the United States and in Estonia. The fact that these sequences are not just local features is strong evidence that they reflect global sea level changes rather than local tectonic changes. In the Cincinnati area, these six depositional sequences also contain evidence of shorter-term variations in sea level, but it is currently unclear whether these represent global or regional changes in sea level.

from studies of todays geography and climate, as well as direct evidence from Ordovician strata, geologists have reconstructed the Ordovician climate of the Cincinnati area. Today, regions near 30° north and south of the equator are characterized by deserts, which form as air rising near the equator descends and forms a series of high pressure cells that inhibit rainfall. In Ordovician rocks of the Cincinnati area, direct evidence of such a semi-arid climate can be seen in the finely laminated dolomitic tidal flat deposits of central Kentucky. Similar deposits occur in semi-arid regions today, where high tides deposit thin laminae of sediment, but high salinity and temperature exclude animals that might burrow and disrupt the sediment. Dolomite itself can have a variety of origins, but the texture and occurrence of dolomite in Cincinnatian rocks matches that found in modern semi-arid settings with high rates of evaporation. Trade winds characteristic of subtropical latitudes would have blown westward across the Cincinnati area during the Ordovician.

The Cincinnati area was subjected to frequent hurricanes, which produced the distinctive alternations of limestone and mudstone, often called shale, although few true shales exist in the Cincinnati area (Figure 15.2; see figure 4.6). Although there is considerable variation in individual storm deposits as a result of differences in sediment supply, water depth, proximity to the hurricane, and the strength of the hurricane, most of these deposits contain at least some of the characteristic features produced by storms. Storm-generated deposits are well known not only from sediment cores on modern continental shelves, but also throughout the geologic record. Storm beds typically have an erosional base, which reflects progressively intensifying currents and waves as the storm approaches. This ero-



STAGE III. CALM CONDITIONS, POST-STORM

STAGE II. STORM CONDITIONS

STAGE I. CALM CONDITIONS, PRE-STORM

Figure 15.2. *Destruction of benthic communities by storm-generated waves and currents. During calm, pre-storm conditions, benthic communities of organisms develop on the sea floor. Under storm conditions, high winds generate large waves that stir up fine-grained bottom sediments into suspension. Stronger wave and current forces can displace benthic organisms, and suspended sediment can clog feeding and respiratory mechanisms of organisms, and even smother entire benthic communities. Mobile organisms can escape if burial is not too severe, but storms can be lethal for many immobile benthic organisms. Following a storm, barren sediment can cover the bottom until benthic communities again develop from larval settlement or immigration. Modified after Hinterlong (1981). Courtesy of Wayne D. Martin.*

sional base is often overlain by a shell-rich limestone, in which the size of shell fragments decreases upwards, which may in turn be overlain by laminated siltstone and burrowed mudstone. Such an upward decrease in shell and sediment grain size is called normal grading by sedimentologists and reflects deposition during the waning phase of a storm when storm-generated waves and currents weakened and deposited the sediment they carried. Laminated siltstone may display horizontal planar laminations, hummocky cross-lamination, or wave-ripple lamination, all of which can be produced by strong storm-generated waves and currents.

Cyclical changes in the character of storm beds are well developed in some Cincinnatian deposits, such as the Kope formation. At a broad scale, these roughly meter-thick cycles consist of a mudstone-rich unit and a limestone-rich unit (see Figure 4.6). The mudstone-rich unit consists of 3–5 cm beds of normally graded mudstone, with uncommon thin laminated siltstone beds. Limestone-rich units consist of shelly limestone beds, with a lesser amount of thin mudstone and siltstone beds. The alternation between these two units was originally thought to reflect changes in sea level, but recent studies suggest that these cycles may instead reflect changes in the average frequency and intensity of hurricanes over tens of thousands of years.

Oceanography

Compared to many modern carbonate settings, Ordovician limestone of the Cincinnati area is unusual in several regards. Most modern and ancient warm water carbonate deposits contain a wide variety of grain types, including skeletal grains (the shells of organisms), ooids (small, spheroidal, concentrically laminated grains), peloids (ovoid grains produced primarily as fecal pellets), and intraclasts (pieces of semi-cemented carbonate sediment that have been eroded and redeposited). In the type-Cincinnatian, ooids are absent, peloids are uncommon, and intraclasts occur sparingly and only in particular horizons. In contrast, skeletal grains of brachiopods, bryozoans, echinoderms, molluscs, and trilobites dominate most limestone in the Cincinnatian (see figure 4.2). Most modern warm water carbonate deposits contain abundant lime mud, called micrite, produced primarily by the photosynthetic activities of algae. In comparison, most limestone in the Cincinnati area contains only minor amounts of micrite. Sediments in modern warm water carbonate environments are prone to undergo cementation within a few centimeters below the sediment surface, and if currents or waves strip away the overlying uncemented sediment, this exposes a hard concrete-like surface on the sea floor, known as a hardground. Hardgrounds can be important substrata upon which encrusting organisms such as bryozoans and corals may attach. Although hardgrounds do occur in the type-Cincinnatian, they are relatively uncommon compared to warm water settings both today and in the past. The features that typify limestone of the Cincinnati area—abundant skeletal grains, a lack of ooids and peloids, minimal micrite, and uncommon hardgrounds—are typical of carbonates deposited today in cool temperate to polar waters.

The presence of cool water carbonates at tropical latitudes at first seems like a paradox, but such conditions occur today where coastal upwelling brings cool water up to the surface from depths of less than 200 meters. These cooler waters also contain abundant nutrients, which generate phosphate deposits. Indeed, the type-Cincinnatian is rich in phosphate, particularly in strata of Maysvillian age. Phosphate is also found in abundance in Upper Ordovician strata near Nashville, Tennessee, suggesting that the entire carbonate platform from Cincinnati to Nashville was a site of upwelling of cool, nutrient-rich water during much of the Late Ordovician. Upper Ordovician rocks of the Cincinnati area contain a greater amount of lime mud, more hardgrounds, and less phosphate, which collectively suggest a decrease in the intensity of upwelling in the latest Ordovician.

Additional evidence from the rich fossil faunas supports the interpretation of cool waters, followed by a return to warm water in the latest Ordovician. During the Late Ordovician, the western United States and Canada straddled the equator. Their carbonate sediments are typical of modern warm water settings, so their faunas are interpreted to reflect warm water conditions. These areas contain abundant corals and stromatoporoids, with a diverse array of brachiopods and trilobites. In particular, colonial rugosan and tabulate corals (for example, *Tetradium),* solitary corals *(Grewingkia, Streptelasma),* several brachiopods *(Glyptorthis, Plaesiomys, Rhynchotrema, Hiscobeccus, Lepidocyclus, Holtedahlina,* and *Leptaena,* for example), trilobites *(Ceraurinus),* and diverse cephalopods are characteristic of this warm water fauna. These organisms are absent from Edenian and Maysvillian strata in the Cincinnati area, but appear in the Richmondian as the limestones begin to reflect a return to warm water, low-nutrient conditions.

Type-Cincinnatian rocks differ from typical carbonate platform deposits in another significant aspect: the abundance of terrigenous mud, that is, clay produced by the weathering of silica-rich minerals such as feldspar. The earliest influx of this mud closely coincides with the beginning of nutrient-rich, cool water deposits at the base of the Lexington Limestone, which underlies type-Cincinnatian strata. The arrival of cool water, nutrients, and siliciclastic mud appears to have been triggered by the uplift of the Laconic Mountains to the east. Fine-grained terrigenous clay and silt were supplied by the Queenston Delta, as such sediments could easily have stayed suspended in the water across the Appalachian Basin until deposition in the Cincinnati area. These muds were best able to accumulate in relatively calmer deep water environments that were less disturbed by storms.

The Persian Gulf is similar in many respects to eastern Laurentia during the Ordovician. Both were developed as foreland basins, that is, deep water troughs adjacent to uplifting mountains. Both possess a carbonate platform that dips gradually into deep water. The sedimentary basins are similar in size and climate, and both sit at subtropical latitudes prone to storms. Large deltas supplied by abundant terrigenous sediment advanced into both basins. The Persian Gulf is notably different in that it lacks upwelling of cool, nutrient-rich water, which underscores that no modern setting is exactly analogous to Cincinnati during the Ordovician. Some have suggested the modern Bahama platform was similar to the Cincinnati area during the Ordovician, but the Bahama platform is flat-topped rather than gently dipping, is not a foreland basin adjacent to uplifting mountains that feed abundant terrigenous sediment to advancing deltas, and lacks upwelling of cool, nutrient-rich waters.

Marine Environments of the Cincinnati Arch

Four major sedimentary environments were present during the Late Ordovician of the Cincinnati Arch (Figure 15.3). Today, distinctive features of the rocks and fossils characterize these environments. Each of these environments is interpreted based on distinctive rock types and sedimentary structures that are found in similar settings today.

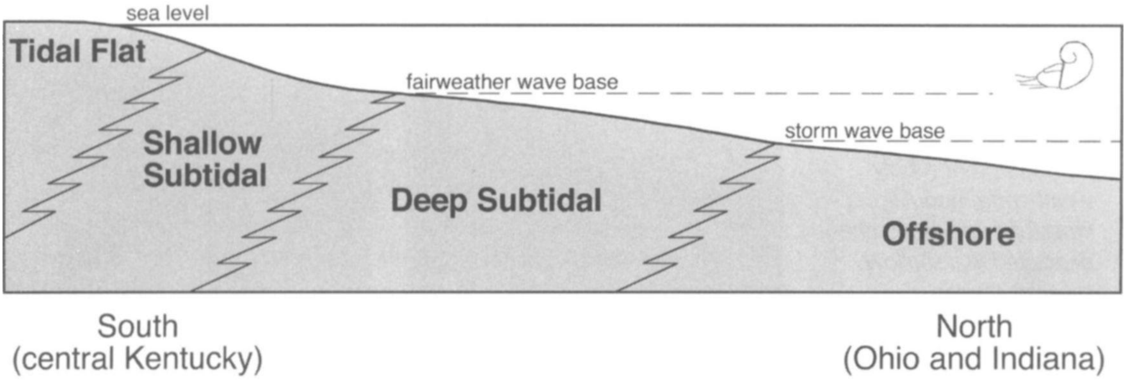


Figure 15.3. *The four principal sedimentary environments of the type-Cincinnatian. Cincinnatian seas generally deepened northward from shallow water environments in central Kentucky to deeper water environments in Ohio and Indiana. The boundaries between these four environments correspond to sea level, fairweather wave base, and storm wave base. Wave base reflects the depth at which waves can move sediment on the sea floor and this depth increases with the height and period of waves, both of which increase during storms. The locations of these environments changed over thousands to millions of years, with environments shifting northward (as shown in figure) during times of slowly rising sea level and retreating southward during times of rapidly rising sea level. Falls in sea level resulted in the draining of the seas from the Cincinnati area.*

Tidal flat environments today are flat, nearly featureless areas that form between the low tide line and the high tide line. These areas are covered daily by tides, but are subjected to extreme variations in salinity and temperature on a daily basis.

In Upper Ordovician rocks of the Cincinnati Arch, tidal flat environments are preserved as laminated to burrowed dolomite and dolomitic limestone containing small amounts of clay (Figure 15.4A). The presence of dolomite suggests strong levels of evaporation, which would have drawn magnesium-rich brines through fine-grained limestone and converted it to dolomite. Although such conditions form today in relatively arid settings, the lack of other evaporite minerals such as halite or gypsum in these tidal flat facies argues more for a semi-arid environment. Wave-formed ripple-marks attest to the shallow water environment in which these rocks were deposited, and desiccation cracks ("mud cracks") indicate the drying and shrinking of the mud when it was exposed during prolonged low tides. Some of these strata contain numerous closely spaced planar laminae that record the deposition of individual layers of carbonate mud during incoming tides and storms on the highest part of the tidal flat, which remained above average high tide. In places, these laminae are penetrated by short, vertical burrows, which suggest areas somewhat lower on the tidal flat where burrowing organisms would not have been killed by drying out and overheating during low tides. Elsewhere in the Cincinnati region, tidal flat deposits lack planar lamination and are thoroughly burrowed by soft-bodied organisms such as polychaete worms and arthropods. Such extensive-burrowing would require more frequent and persistent submergence during a tidal cycle, as on the lowest portions of the tidal flat. Many of these burrows are filled with the distinctive green iron mineral glauconite. Tidal flat deposits are most common in central Kentucky, but some tidal flats advanced as far northward as southern Indiana, as can be seen in exposures of the Saluda Dolomite near Madison, Indiana.

Most tidal flat deposits in the Cincinnati region are unfossiliferous, but locally the burrowed deposits contain a sparse fauna of bryozoans, and more rarely ostracods, brachiopods, stromatoporoids, and rugosan and tabulate corals. This restricted group of organisms presumably would have been capable of tolerating fluctuations in salinity and temperature. Preser-

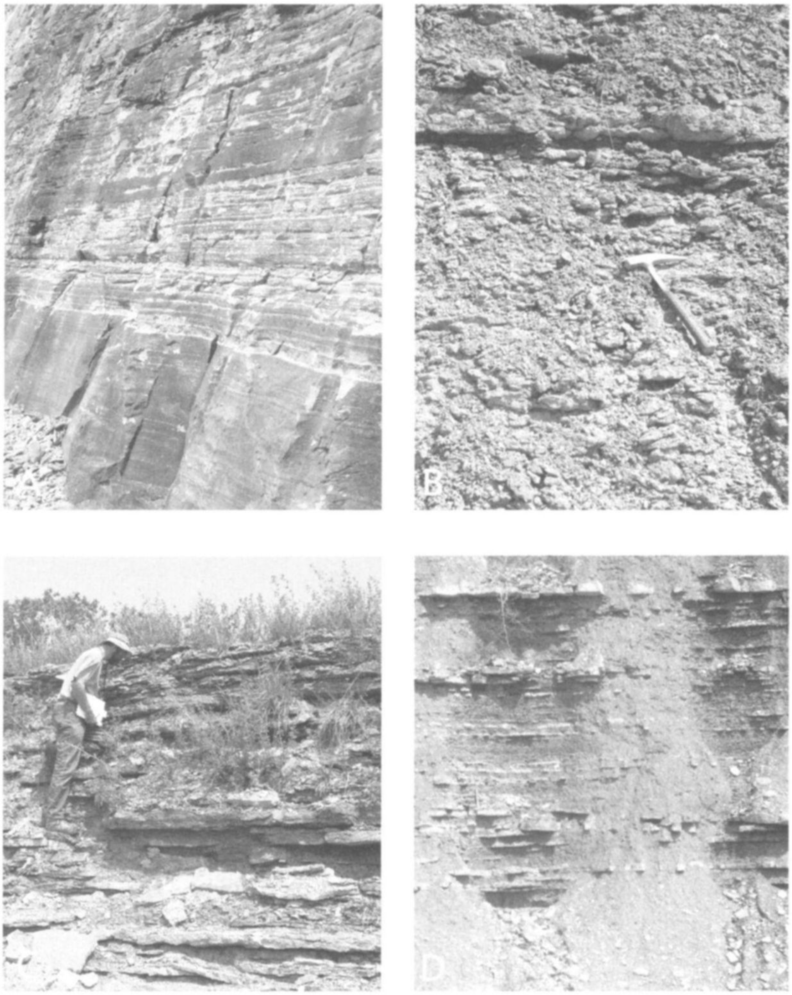


Figure 15.4. A. Outcrop *photograph of finely laminated dolomite deposited in a tidal flat environment.* B. *Outcrop photograph of rubbly weathering, nodular limestone and mudstone deposited in a shallow subtidal environment.* C. *Outcrop photograph of interbedded limestone and mudstone deposited in a deep subtidal environment, with the limestone beds recording deposition during hurricanes.* D. *Outcrop photograph of mudstone with thin beds of limestone and siltstone, all deposited in an offshore environment.*

vation of these fossils is typically poor, as a result of dolomitization, which tends to destroy fine details.

Shallow subtidal environments today are shallow marine environments below the low tide line, but above fair weather wave base, the depth to which waxes can stir the sediment during calm weather. Fair weather wave base is typically only a few meters on coasts protected from large oceanic waves. In modern carbonate settings, shallow subtidal environments are adjacent to tidal flats and are characterized by intense burrowing by soft-bodied organisms such as worms and arthropods.

Behind the history of every sedimentary rock there lurks an ecosystem, but what one first sees is an environment of deposition.

Edward S. Deevey
1965, 592

Shallow subtidal deposits are found in the type-Cincinnatian and are likewise characterized by highly burrowed shallow marine deposits that grade upwards into tidal flat deposits, indicating that the two were deposited in laterally adjacent environments. In the type-Cincinnatian, shallow subtidal deposits consist of nodular to very thin wavy-bedded shelly limestone and fossiliferous mudstone (Figure 15.4B). Because of the thinness and waviness of the limestone beds, these rocks weather to a characteristic rubble of fist-sized limestone nodules. This distinctive bedding results from the pervasive burrowing of the sediment by soft-bodied organisms. Although storms certainly reworked the sediment and deposited the characteristic well-sorted layers of shells overlain by layers of mud that are preserved in some places, subsequent burrowing mixed these layers, producing pods of shell-rich and shell-poor material. Preferential cementation of these churned sediments produced pockets of well-cemented shells material surrounded by non-cemented zones rich in clay.

Shallow subtidal limestone in the Cincinnati area is locally rich in phosphate, particularly in the Maysvillian. Much of this phosphate occurs as infillings of bryozoan zooecia, the porous skeletons of echinoderms, and the larval shells of pelecypods, gastropods (such as ***Cyclora),*** and monoplacophorans. The presence of this phosphate indicates large amounts of decaying organic matter within the sediment. By dissolving pieces of shallow subtidal limestone in vinegar or dilute hydrochloric acid, one can see the rich fauna preserved by this phosphatization. Shallow subtidal rocks are broadly distributed over the Cincinnati Arch and occur from the southern edge of the Ordovician outcrop belt in southern Kentucky to the northern limit of Ordovician rocks in central Ohio and Indiana. The Bellevue, Mt. Auburn, Oregonia, and Whitewater Formations all accumulated within shallow subtidal environments.

Shallow subtidal rocks are exceedingly fossiliferous in most places, reflecting the abundance of life in this shallow marine habitat. Most commonly, shallow subtidal rocks are packed with large brachiopods, such as ***Platystrophia,*** *Hebertella,* and ***Rafinesquina.*** Many of these have thick or coarsely ribbed shells, presumably for protection against waves and currents. *Platystrophia,* in particular, has a greatly thickened pedicle valve near the hinge, which would have increased the stability of the shell on the sea floor. Disarticulation, breakage, and abrasion of these shells are widespread and attest to the damaging effects of waves and currents. Large bryozoans are often abundant and include branching, encrusting, sheet-like, and massive forms. As is true for the brachiopods, these robust bryozoan skeletons reflect the intensity of waves and currents in this shallow water environment. Molluscs are present in shallow subtidal rocks, particularly the byssally attached pelecypods *Ambonychia* and *Caritodens,* the carnivorous cephalopod T*reptoceras,* and the gastropods ***Lophospira*** and *Cyclonema. Cyclonema* is commonly associated with crinoids, on which it may have been a parasite. *Lophospira* has been interpreted as a scavenger. Crinoids and trilobites occur, but most specimens are disarticulated rather than whole, presumably owing not only to waves and currents, but also burrowing organisms.

Deep subtidal environments today are those that lie below fair weather wave base, but above the wave base of all but the most powerful storms or hurricanes, which would have extended to depths of a several tens of meters. In these settings, the sedimentary deposits are characterized by the alternation of sandy and shelly beds deposited during storms and muddy beds that reflect quiet water deposition during weak storms or during periods between storms. Deep subtidal environments are adjacent to and slightly deeper than shallow subtidal environments.

As on modern shelves, storm deposits are the most conspicuous feature of the deep subtidal environment in the type-Cincinnatian, with roughly equal proportions of thin to medium-bedded shelly limestone, laminated siltstones, and mudstone (Figure 15.4C). Burrowing is much less intense here than in deep subtidal environments, resulting in thicker and more laterally continuous limestone beds. Beds of siltstone are commonly rippled or display internal planar or hummocky lamination generated by strong storm currents and waves. At times, storms occurred with sufficient frequency that they commonly eroded through the mudstone layer capping the deposit from the previous storm, such that the shelly layer from one storm was deposited directly on the shelly bed of the previous storm. This phenomenon, known as amalgamation, produces thick layers of limestone with subtle internal erosion surfaces that separate individual storm beds, thereby producing what are known as multi-event beds. In some cases, a one-foot thick bed of limestone may record half a dozen storm events. Deep subtidal rocks are as broadly distributed over the Cincinnati Arch as shallow subtidal rocks. The Fairview, Corryville, Sunset, and Liberty Formations accumulated in deep subtidal environments.

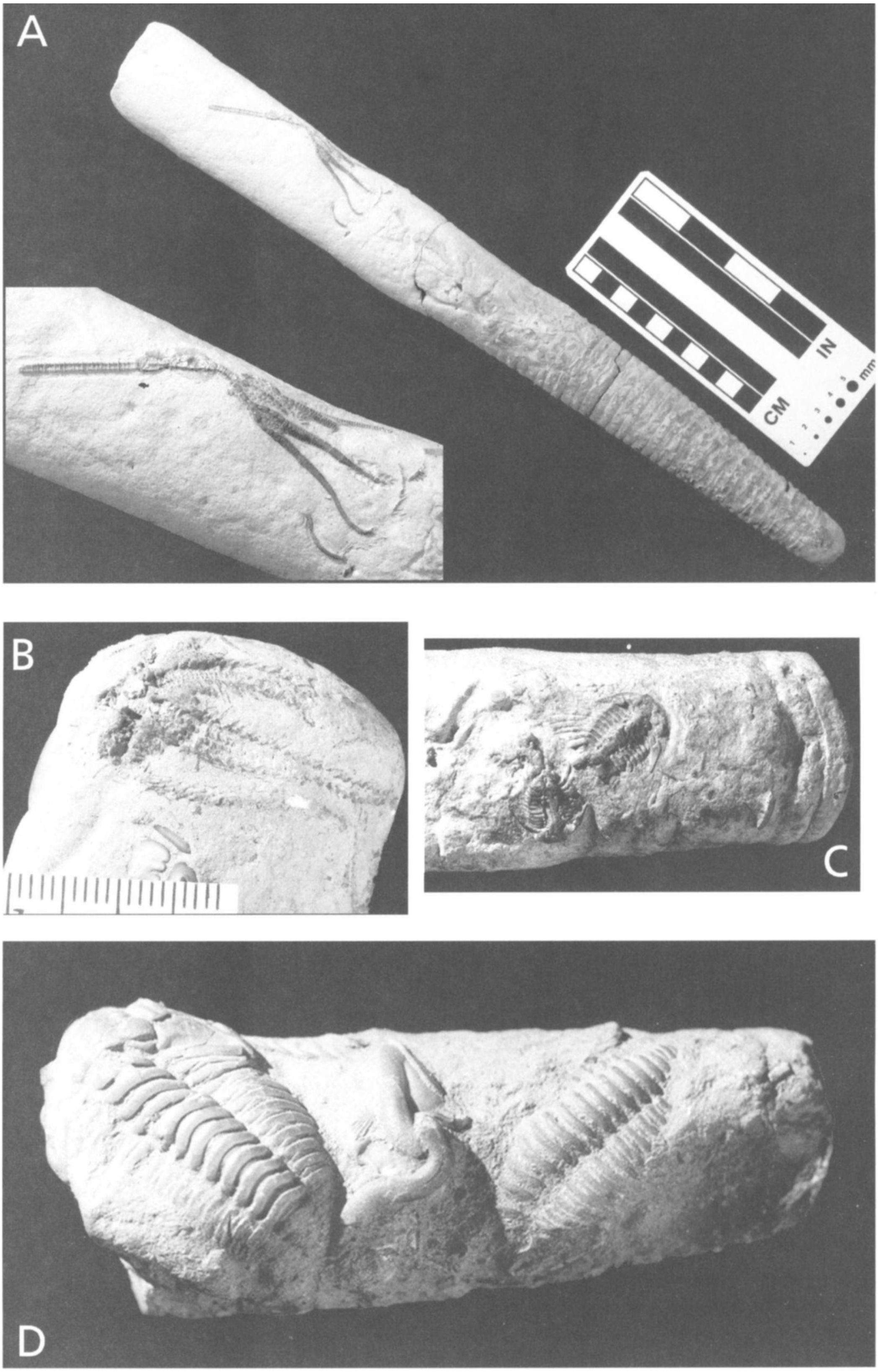
Deep subtidal rocks of the type-Cincinnatian contain an abundant and diverse fauna. Preservation is commonly better than in shallow subtidal rocks, with less overall disarticulation, breakage, and abrasion, suggesting less exposure to the damaging effects of waves and currents. Many brachiopod genera may be present, including *Rafinesquina, Strophomena, Leptaena, Hiscobeccus, Platystrophia, Plectorthis, Glyptorthis,* and *Plaesiomys.* All have shells that are thinner and finer-ribbed than those in the shallow subtidal. Bryozoans can be abundant and also tend to be thinner and less massive than in the shallow subtidal. Molluscs are common, with similar forms as in the shallow subtidal, as well as the byssally attached pelecypod *Modiolopsis.* Crinoids *(Glyptocrinus, Pycnocrinus,* and *Iocrinus)* and edrioasteroids *(Carneyella, Isorophus,* and *Streptaster)* are locally abundant, and beds and pockets containing fully articulated specimens are not unusual. Trilobites *(Isotelus* and *Flexicalymene)* are common both as individual sclerites and as articulated specimens. The frequency of articulated crinoids and trilobites suggests early burial and less frequent disturbance by waves, currents, and burrowing organisms. In the uppermost Cincinnatian, solitary corals *(Grewingkia* and *Streptelasina),* and the encrusting tabulate coral, *Protaraea,* are conspicuous additions to the deep subtidal fauna. Trace fossils are common in the siltstone beds. *Chondrites* and *Trichophycus* were the burrows of deposit feeding worms or arthropods. The U-shaped burrows of *Diplocraterion* were the homes of a polychaete worm, but whether it was a suspension feeder, a stationary deposit feeder, or an ambush carnivore is uncertain, as modern examples of all such U-tube builders are known. *Paleophycus* records the horizontal burrowing of another scavenging or deposit feeding worm.

The thick, tabular limestone beds of the deep subtidal are well suited as building stones. Many old quarries were established in deep subtidal rocks and many of those stones can now be found in old building foundations and rock walls. Two intervals of deep subtidal rocks frequented by quarrymen were the River Quarry Beds (now called the Point Pleasant Formation) and the Hill Quarry Beds (now called the Fairview Formation). Although the River Quarry Beds near Cincinnati are now largely under the Ohio River, whose level was raised during the construction of dams, they can still be seen near Point Pleasant, Ohio, along the crest of the Cincinnati Arch. Many of the Hill Quarries can still be seen in the bluffs south of the University of Cincinnati and flanking the Mill Creek Valley.

Offshore environments on modern coasts lie below the wave base of most storms, but are sometimes affected by the most severe storms and extend to depths of several tens of meters. In these modern settings, deposition is dominated by muds, which can accumulate when currents and waves are weak. Rare, exceptionally strong storms are capable of moving shells and sediments even at these depths and produce thin storm beds, although these make up a minority of the deposits. Offshore environments are adjacent to and somewhat deeper than deep subtidal settings.

In the type-Cincinnatian, offshore rocks contain a greater proportion of mudstone (commonly near two-thirds), but in other regards are quite similar to the deep subtidal (Figure 15.4D). The less frequent occurrence of storm beds in offshore deposits indicates less frequent disturbance by storm-generated waves and currents. As a result, amalgamation is much less common in the offshore, and most limestone beds are single-event beds and record the passage of a single hurricane. Many of the thick mudstone layers found in the offshore are also the result of storm deposition, as indicated by the presence of multiple 2-3 cm fining-upward mudstone beds, each with a slightly silty interval at its base. Each of these thin layers records the minor disturbance of the sea floor by a hurricane, with settling of silt and then clay following the storm. Frequently, such mud layers would blanket the bottom, smother the fauna living on the sea floor, and preserve articulated crinoids and trilobites. Offshore rocks occur as tar south as north-central Kentucky but extend beyond the northern limit of Ordovician exposures in central Ohio and Indiana. The Kope and Waynesville Formations largely reflect offshore settings.

Offshore strata contain an abundant and diverse fauna, characterized by small, thin, and delicate fossils, suggesting generally quiet water conditions, except during rare, severe storms. Common brachiopods include the highly gregarious *Dalmanella* and *Sowerbyella,* and the burrowing inarticulates *Pseudolingula* and *Leptobolus,* which are sometimes found preserved inside their vertical burrows. Although sheet-like bryozoans do occur, thin branching forms and flat disc-shaped forms are more common. Molluscs are diverse and abundant in a few widely traceable horizons, which are conspicuously poor in brachiopods and bryozoans. Common molluscs include the byssally attached pelecypods *Ambonychia* and Modi*olopsis,* the burrowing pelecypods *Deceptrix and Rhytimya,* the scavenging gastropods *Lophospira* and *Liospira,* the monoplacophoran *Sinuites,* and the cephalopods *Treptoceras* and *Cameroceras.* Trilobites are numerous and frequently fully articulated. The burrowers *Flexicalymene, Gravicalymene, Cryptolithus,* and *Isotelus* are the most common, but the spiny swimming *Acidaspis* can be abundant in some crinoid-rich layers. Suggestive of deep water settings is the presence of the blind trilobites *Cryptolithus* and *Triarthrus* in offshore strata. Crinoids are also numerous and are frequently articulated. The most common genera are *Cincinnaticrinus* and *Fxtenocrinus,* whose ossicles may comprise entire beds of limestone. Given the tens of kilometers over which such beds can be traced, the number of crinoid individuals must have been astronomical. As in the deep subtidal, trace fossils are numerous in beds of siltstone. *Chondrites, Diplocraterion, Trichophycus* and *Paleophycus* are all common. The trilobite burrow *Rusophycus* is also common, and examples of *Rusophycus* made by *Isotelus* and *Cryptolithus* have been reported, but ones produced by the calymenids *Gravicalymene* and *Flexicalymene* are much more common.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LIFE IN THE CINCINNATIAN SEA

16

The Ecological Theater and the Evolutionary Play

G. E. Hutchinson 1965

The Ecological Theater and the Evolutionary Play is a book of fascinating essays about the complex interactions between the environment and the organisms inhabiting it. It was written by the ecologist G. E. Hutchinson in 1965. Hutchinson's title, an extrapolation of the Shakespearean metaphor, provides a useful analogy by which to view the Cincinnatian as a Series of acts in the evolutionary play. In chapters 5-14 of our book we introduced the cast of characters, the players on the stage, of the Late Ordovician sea that covered the Cincinnati Arch region. Having read these chapters, the reader should be able to recognize the characters and know something of their roles—in particular their modes of life and feeding habits.

In scientific terms, this is the realm of autecology, the relationship of organisms of a single species with the environment, assessing the influence of chemical, physical, as well as biological factors. Given that we are dealing with organisms long since extinct, perhaps we should add the prefix for "ancient" and enter the ancient realm of paleoautecology.

For marine organisms, major inorganic factors include temperature, salinity, oxygen content of the water, nature of the sea bottom, water movement (both currents and wave-induced turbulence), and turbidity (sediment content of the water). Changes in hydrostatic pressure associated with water depth do not exert a major influence except in organisms like fish with air bladders or air-breathing, diving marine vertebrates. However, all of the other factors listed can vary significantly with water depth, and, hence, depth itself often is correlated with changes in the distribution of species. Biological factors include the mode of feeding, food availability, and a host of potential interactions with organisms of other species such as predator-prey interactions, commensalism, and parasitism.

In chapter 15, Steven M. Holland described the stage settings for the Cincinnatian play, the paleogeography and environments of the Late Ordovician sea in which the organisms lived. In order to understand the entire play, we now must consider the (Cincinnatian players as an assembled cast on that stage. How did the cast change with each act, and how did the players interact with one another as the plot unfolded?

Reassembly of the cast of characters and the interplay between them brings us to the subdiscipline of synecology (or, in this case, paleosynecology), the relationships of the animals of the many Cincinnatian species that lived together with their chemical, physical, and biological environment. In order to determine how extinct species were influenced by other species and their environment, a paleoecologist must first grapple with a very difficult question: what species actually lived together at a given time in the past?

Figure 16.1. A. *Internal mold of nautiloid, Treptoceras duseri (Hall and Whitfield), with crinoid Xenocrinus baeri (Meek) preserved within body chamber. Richard Arnold Davis collection, Waynesville Formation, Adams Co., Ohio, collected by Thomas T. Johnson.* B. *Ophiuroid, Taeniaster spinosus (Billings), MUGM 28187, preserved on internal mold of nautiloid, Waynesville Formation, Butler Co., Ohio, scale in mm.* C. *Trilobites, Acidaspis sp., preserved on internal mold of nautiloid, ?Treptoceras sp., CMC IP 2257, Cincinnatian, vicinity of Cincinnati, Ohio,* x 0.9. D. *Trilobites, Flexicalymene meeki (Foerste), preserved on internal mold of nautiloid, ?Treptoceras sp., OSU 50329, Cincinnatian, vicinity of Cincinnati, Ohio,* x *2.6. C,* D *from Davis et al. (2001, figures 2, 5), and reprinted by permission of Blackwell Publishing.*

What cast was on stage for a given act? An ecologist can observe and sample living organisms in the field, but the paleoecologist must deal with assemblages of dead remains preserved in sedimentary rock. Factors affecting fossil preservation discussed in chapter 1 are of the utmost importance here. Are these assemblages representative of actual life assemblages or are they death assemblages representing mixtures of organisms that lived at different times or places and accumulated gradually over time (time-averaged assemblages) or suddenly in some quick event? How much information is missing from the fossil record because of preservational bias? Fossil assemblages are biased in favor of organisms with preservable remains with hard parts like shells, skeletons, and exoskeletons, and they are biased against organisms lacking hard parts. Criteria such as those presented in Table 1 in chapter 1 can be applied to answer these questions. Throughout this book, examples of Cincinnatian fossils preserved in life position or in direct association with organisms of other species provide evidence by which to distinguish life assemblages from death assemblages. Keeping these issues in mind, we can proceed to examine how fossil assemblages vary through the Cincinnatian and what this reveals about Cincinnatian paleosynecology.

Ever since some of the earliest studies of Cincinnatian fossils and strata, paleontologists have recognized that assemblages of organisms of extinct species change markedly through the section and show a close relationship to the character of the rock (see chapter 5). The quotation from Nickles (1902) in chapter 4 demonstrates that he recognized the paleoenvironmental significance of the lithologies and their associated fossil faunas. Paleontologists compiled lists of fossils characteristic of each formation. Fossils of organisms of some species occur in many formations and thus have long stratigraphic ranges; fossils of other species are restricted to single formations or thinner intervals within a formation. Elizabeth Dalve (1948) compiled faunal lists for each Cincinnatian rock-unit based on many previous studies, but her paper is not widely available. The well-known biostratigraphic zonation of the Cincinnatian that is still widely used (Caster et al. 1955; Davis 1985, 1992) expresses these faunal changes. Using this kind of information on fossil distribution one could predict what species might be found in a given formation, but the assemblages of species in a formation and their relative abundance were less well known.

Beginning in the late 1960s, the burgeoning subdiscipline of paleoecology focused the attention of paleontologists on assemblages of fossils occurring together and their relationship to the enclosing sedimentary matrix. To what extent did fossil assemblages represent ecological communities comparable to present-day marine benthic communities? Marine ecologists recognized communities as recurrent assemblages of species inhabiting particular environments characterized by particular water depth, bottom type, temperature, salinity, or other chemical or physical attributes. They delimited assemblages on the basis of statistical analysis of samples recovered from the sea floor. Communities were named for dominant or characteristic species.

The existing faunal lists of Cincinnatian fossils were inadequate for this type of analysis, so paleoecologists collected new samples in which the abundance as well as simple occurrence of fossil species was recorded from censuses of bed surfaces or bulk samples of rock. One of the pioneering studies of this type was that of Peter Bretsky (1970), who recognized a series of fossil communities of Cincinnatian age in the Appalachian Basin. Bretsky's communities were characterized by brachiopods, molluscs, and animals of other taxa and were distributed according to depth in parallel bands close to the shoreline of the same epicontinental sea that extended westward to the Cincinnati Arch region. Other studies focused on community paleoecology of the Cincinnati Arch region, such as the work of Fox (1962, 1968), Lorenz (1973), Oldroyd (1978), and Harris and Martin (1979) (see chapter 8). Subsequently, use of the term fossil community became less frequent, because increased understanding of taphonomic processes showed that most of the time-averaged assemblages of fossils are not directly comparable to present-day communities.

In recent quantitative studies of Cincinnatian fossil assemblages, fossil specimens of individuals from extinct taxa (either species or genera) are treated as variables taken from samples restricted to a single bed surface or disaggregated from a thin bed of limestone or shale. In each sample, the abundance of fossil specimens of each taxon is counted and tabulated.

In the study of fossil assemblages in the C1 (Kope Formation) depositional sequence, Holland, Miller, Meyer, and Dattilo (2001) collected samples from every fossiliferous bed through a seventy meter stratigraphic section—1949 samples in all. In each sample, the relative abundance of fossils was recorded in the field as rare (1-2 specimens per 1000 cm^2 of bedding surface), common (3-10 specimens per 1000 cm^2), or abundant (>10 specimens per 1000 cm^2). Fossils were identified to genus, and included brachiopods, crinoids, trilobites, pelecypods, cephalopods, and gastropods. Some distinctive bryozoans were identified to genus, whereas others were classified on the basis of colony morphology as thin bifoliate (<5 mm), thick bifoliate (>5 mm), thin ramose or branching (<5 mm), thick ramose (>5 mm), or encrusting. Fifty-seven taxa were tabulated from the 1949 samples. After removal of all taxa occurring in just a single sample, as well as the removal of all samples containing specimens of just a single taxon, the final dataset formed a matrix of forty-six taxa or colony forms and 1337 samples.

Large datasets of this type can be analyzed using several kinds of computer-driven, multivariate statistical techniques. In the work of Holland, Miller, Meyer, and Dattilo (2001), a technique called detrended correspondence analysis (DCA) was used, although other techniques, for example, cluster analysis, factor analysis, and polar ordination, produce similar results. DCA calculates a numerical score for each taxon and each sample and plots them along graphical axes that reflect similarity of taxa as grouped in samples or similarity of samples based on their taxa. Ecologists have found that techniques like DCA are very useful to examine how taxa are arrayed along these axes, which commonly correspond to some environmental parameter or gradient. In the analysis of the Kope Formation, numerical values of taxa along one DCA axis displayed a shift from lower values in the lower parts of the section, toward higher values moving up-section. As noted in chapters 4 and 15, analyses of lithologic features such as the shale-to-limestone ratio and bedding thickness demonstrates that water depth decreased from the base to the top of the formation. The DCA showed that the composition of fossil assemblages also reflects this trend and may even provide a more sensitive measure of depth changes than the character of the rock reveals.

In fossil assemblages from the lower Kope (deeper water), the most abundant fossils are the slender crinoids *Ectenocrinus* and *Cincinnaticrinus,* the small, thin-shelled brachiopod *Sowerhyella,* and the trilobites *Cryptolithus* and *Acidaspis* (see Figures 11.5,11.6). Higher in the Kope, the larger brachiopod *Dalmanella,* branching bryozoans, and the trilobites *Flexicalymene* and *Isotelus* become the most abundant taxa. The brachiopods Zygospira an *Dalmanella* assemblage at higher levels. At the lop of the Kope, the larger concavo-convex brachiopods *Rafinesquina* and *Strophomena* are the most abundant brachiopods, and the larger crinoid *Glyptocrinus* replaces the smaller crinoids. In an earlier study of the Kope to Fairview to Bellevue Formations, Diekmeyer (1998) found similar transitions from taxa of smaller, more delicate animals in the Kope to larger, more thick-shelled and robust animals (*Platystrophia,* more massive bryozoans) in the overlying Fairview. She interpreted this to be a result of a continuation of the shallowing initiated during the deposition of the Kope sequence.

Recent research by Holland and Patzkowsky (2007) provided similar faunal analyses for each of the Cincinnatian depositional sequences, C1-C6. In Figure 16.3 we present a time environment diagram for the entire Cincinnatian based on the work by Holland and Patzkowsky. In this diagram we show the major taxa of depth-related assemblages in each sequence. The transition from taxa of smaller, more delicate animals in deeper parts of a sequence to taxa of larger, more robust organisms in the shallower parts that was found in the C1 sequence by Holland, Miller, Meyer, and Dattilo (2001) was confirmed and found to be repeated in the succeeding C2 and C3 sequences. In other words, in each of these sequences the fossil assemblages reflect a depth gradient from deeper to shallower water. they also identified a second environmental gradient corresponding to the nature of the substratum. Animals of taxa along one end of this gradient characterize soft substrata and tend to be smaller and thinner-shelled, whereas animals of taxa arrayed toward the other end of the gradient characterize firm substrata, tend to be larger and more robust, and commonly are attached or encrusting in growth habit.

The Richmondian Invasion

Within the upper division of the Cincinnatian, the Richmondian Stage, the stable patterns of distribution of fossil assemblages found in the lower Cincinnatian are disrupted and reorganized by the influx of organisms of many new taxa, including species, genera, and classes. This influx is termed the Richmondian Invasion. These invaders did not replace pre-existing taxa but instead increased Cincinnatian diversity to its highest level. There is an initial phase of the Richmondian Invasion within the C4 sequence, but the influx culminates within the C5 sequence where fossils of over fifty new genera of corals, brachiopods, bryozoans, molluscs, trilobites, and echinoderms appear (Holland 1997; Holland and Patzkowsky 2007; figure 16.3; see chapters S and 9). many of the new taxa were not present during the Edenian and Maysvillian Stages of the Cincinnatian, although some newcomers represent speciation within long-ranging Cincinnatian taxa such as the brachiopods *Platystrophia* and *Strophomena* (Holland 1997). New taxa appeared in all depositional environments across the spectrum of the Cincinnatian depth gradient, and the animals occupy the entire range of feeding types and life habits (Holland 1997).

The invasion was not limited to particular facies, trophic groups, or life-habit groups; rather the Riehmondian Invasion was a major ecological revolution affecting all aspects of the Cincinnatian seas.

Steven M. Holland 1997, 320

In the C4 sequence, some elements of the older, depth-related assemblages, such as *Hebertella* and *Platystrophia,* are present in the shallow subtidal zone, and *Rafinesquina* and *Zygospira* in the deeper subtidal zone (figure 16.3). In the C5 sequence, a *Dalmanella* brachiopod assemblage is again present in the offshore environments, but specimens of *Zygospira* also are present. Specimens *of Rafinesquina, Platystrophia,* and branching bryozoans occupy the deeper subtidal zone, but the *Hebertella-Platystrophia* assemblage is gone from the shallow subtidal zone, where an assemblage of colonial corals appears for the first time. The depth gradient is re-established in the C5 sequence, but it is much more crowded with taxa and has a different character than in older sequences (Holland and Patzkowsky 2007). The C6 sequence is represented only by shallow water assemblages including corals and robust brachiopods and bryozoans.

There has been considerable debate about the causes of the Riehmondian Invasion. Because main of the invasive taxa occur in the Middle and Upper Ordovician of the western United States and Canada as far north as the present-day Arctic, it is most likely that the invasion originated from the west and northwest, tropical, warm water latitudes during the Late Ordovician (see chapter 15). The invasion was a large-scale immigration event rather than an evolutionary burst within the Cincinnati Arch region itself (Holland 1997).

Returning to the theater analogy, we find that many players (species) in the Riehmondian final act of the Cincinnatian appeared in earlier acts recorded by pre-Cincinnatian formations of the Appalachian region. These include brachiopods like *Leptaena, Glyptorthis,* and *Plaesiomys* (Holland 1997), as well as stromatoporoids and corals like *Tetradium.* Likewise the scene during pre-Cincinnatian time featured widespread limestone deposition in Kentucky suggesting a warmer water environment conducive to carbonate deposition.

As the Edenian act of the Cincinnatian play opened, the scene changed with the influx of muds derived from tectonic activity offstage in the Taconic region of the Appalachian orogenic belt, and cooler waters swept in as circulation patterns changed (Holland 1997). Many players made their exits, to return only when the scene again altered in Riehmondian time

The Cincinnatian Ecosystems: A Sea without Fish!

Further understanding of the Cincinnatian evolutionary play also depends on the interplay between characters. How the members of the cast interacted with one another was of fundamental importance in determining the plot and outcome of the play. Interactions between organisms are of major importance in ecology and lead to the concept of an ecosystem.

For an ecologist, an ecosystem encompasses all the chemical, physical, and biological aspects of the environment, including the sources of energy and nutrients entering the environment and the way living organisms use this energy to survive and reproduce. The Sun is the primary energy source for the vast majority of ecosystems on Earth, the only known exceptions being the recently discovered deep sea vents, where hydrothermal fluids rich in nutrients sustain microbial life that is, in turn, the basis for unique ecosystems. In shallow seas like that of the Cincinnatian, we can assume that planktonic as well as benthic algae harnessed solar energy as the primary producers. Individuals of all of the animal groups constituted consumers, feeding either directly on the primary producers or on other consumers. In order to understand the nature of Cincinnatian ecosystems, we must understand how the consumers were interrelated in what ecologists call a food chain or, more realistically, a food web. How did Ordovician marine ecosystems compare to those of the present-day shallow sea? Did the nature of the interrelationships among organisms and the form of the food web play a role in determining the diversity and abundance of organisms in the Cincinnatian sea? In our analogy, did the interplay among characters actually determine the cast on stage during any particular act?

For an ecologist, interpretation of a food web requires detailed knowledge of the feeding habits and diets of organisms of species living together at a given time. An ecologist can directly observe predator-prey interactions and can sample gut contents of animals and their droppings. An ecologist can gauge the flow of energy through an ecosystem by measuring the caloric content of organisms at different levels in the food chain. However, a paleoecologist working with fossils preserved in rock cannot observe or sample the living ecosystem directly and thus faces some severe limitations in reconstructing a "fossil" ecosystem. It often is hard to determine with certainty whether all fossils preserved in a single bed were alive at the same time, because many fossil assemblages are time-averaged amalgamations of organisms of many generations. Moreover, organic remains can be moved into an area or out of an area, for example, by currents. Despite these limitations, it is rather surprising to find how much information the fossil record of the Cincinnatian sea does provide, information that can be used to answer many questions about the nature of the ecosystems.

The most direct evidence for interactions between organisms of Cincinnatian species comes from a compilation of close associations among different types of organisms. Associations are essential because the\ can provide evidence for predator-prey relationships as well as evidence that two different species lived at the same time and possibly affected one another in various ways. Besides predator-prey relationships, other common interspecific interactions include host-parasite associations, competitive interactions, mutualisms, or commensalisms. In competitive interactions, individuals of both associated species are in some way inhibited or harmed by the association; in a mutualistic interaction, both individuals derive some benefit from the association; in a commensalistic interaction, one species derives some benefit, whereas the "host" is unaffected by the presence of the **symbiont.** In some cases a living animal of one species might be associated with non-living remains of another species, as in the case of hermit crabs occupying shells of dead snails (Davis, Mapes, and Klofak 1999; Davis, Fraaye, and Holland 2001).

We compiled available information on associations of fossils of Cincinnatian species into two summary tables. Table 2 shows potential predator-prey associations derived from direct fossil evidence, and Table 3 shows all other associations reported among individuals of Cincinnatian species or other groups.

Predator-Prey Interactions

The list of potential predator-prey associations in the Cincinnatian is quite short (Table 2), and the nature of the evidence is variable. Throughout the fossil record there are rare but notable cases of fossilized stomach contents that are the strongest evidence for the diet of an extinct animal. The only possible instance of this in the Cincinnatian is the occurrence of ostracodes preserved within the coralla of the rugose corals *Grewingkia* and *Streptelasma* (Elias 1984). The ostracodes are mostly articulated and located near or within the alar and cardinal fossulae of the coral's calice. The fossulae are expanded regions between the septa that probably functioned in water circulation within the polyp and thus were related to ingestion of food and/or ejection of waste. Although it is possible that the coral ingested the ostracodes as prey, Elias favored an alternative hypothesis that the ostracodes entered the calice when the polyp became detached from the side of the calice and eventually became trapped beneath newly secreted tabulae. In this scenario, the ostracodes might have lived symbiotically within the coral calice.

The most direct evidence of a predator-prey relationship is the remarkable specimen of a sea star *Promopalaeaster* preserved with its arms wrapped around a specimen of pelecypod tentatively assigned to genus Cu*meamya* (see Figure 12.15E; Blake and Cuensburg 1994). This specimen is probably one of the most extraordinary fossils ever to be found in the Cincinnatian. It provides strong evidence that some Cincinnatian sea stars had acquired the ability to open pelecypods seen in living asteriid sea stars, even though the present-day forms are not direct descendants of *Promopalaeaster* (Blake and Cuensburg 1994).

The predatory behavior of some individuals of Cincinnatian trilobite species was discussed in chapter 11. *Rusophycus* trace fossils that intersect burrows suggest that individuals of the trilobite *Isotelus* preyed on some burrowing, probably soft-bodied organisms. Babcock (2003) inferred that both eurypterids and cephalopods were potential predators on trilobites during the Ordovician, although there is no direct evidence available.

Specimens of Cincinnatian brachiopods such as *Rafinesquina* and several other genera provide evidence for predation in the form of characteristic breakage and shell repair (Alexander 1986). Alexander considered possible predators among sea stars, eurypterids, gastropods, and nautiloid cephalopods. He concluded that the beaks of nautiloids were most likely to have inflicted the type of damage found in the brachiopods.

Cincinnatian crinoids also show evidence of damage and regeneration of the calyx, arms, and column that is very likely the result of predation (Ausich and Baumiller 1993; Donovan and Schmidt 2001; Baumiller and Gahm 2004). However there is no evidence as to the specific predator responsible. We speculate that nautiloids might be the most likely culprits, in view of their abundance and potential behavior.

Other Interspecific Interactions

Table 3 shows that virtually all the major invertebrate groups found in the Cincinnatian have recorded associations of individuals of taxa belonging to a wide variety of groups. The type or nature of the associations ranges from the use of either a living host or dead remains as a substratum for encrustation, boring, or habitation (Figure 16.1), to possible commensalism or parasitism. To the extent that a host was, by definition, living at the time of the association, it appears that interactions between individuals of Cincinnatian species were very common. Detailed discussion of the nature of the associations listed can be found in the chapters concerning the taxonomic group of each host.

We present Table 3 with a significant caveat. In cases in which a fossil specimen includes an organism of one species attached to an individual of another species, it is not always clear whether both animals were alive at the time of attachment. It is possible that the attached organism fastened onto the other after the hitter's death and, for example, was using the empty shell as a hard substratum. An added complication is that various biologists and paleontologists have not been consistent as to which terms are used for which associations. Take the term "epizoa," for example. For an association properly to be termed "epizoism," both parties must have been alive at the time of the association—both host and guest. However, the term "epizoa" not uncommonly has been used in cases in which the "host" clearly was dead at the time of attachment and in cases in which it is unclear whether the "host" was alive or dead at the time of the association. (Davis, Mapes, and Klofak 1999; Davis, Fraaye, and Holland 2001.)

Most of the cases cited in Table 3 have been gathered from published reports. The authors of those reports have not always been able to determine or state whether both "host" and "guest" were alive at the time of a given association. In cases where the type of association is recorded in Table 3 as epizoic, endozoic, or one involving boring, the putative host organism may or may not have been living at the time of the association; the entry in the table depends on the information and interpretations presented in the original publications. On the other hand, in cases entered as commensal or parasitic, there is evidence that the host was, in fact, living at the time of the association. Bioimmuration is also indicative of interaction between a living host and organisms of an associated species, because the associate modified the growth of the host in some way as to leave evidence that the associate was present. There are no known documented cases in the Cincinnatian of either competitive or mutualistic interactions, Liddell and Brett (19S2) reported evidence for competition between associated species of encrusting bryozoans from the Middle Silurian of Indiana.

Colonies of different species of bryozoans encrusting crinoid calyces sometimes formed raised margins where they grew into contact when encrusting crinoid calyces. The raised margins indicate some kind of "standoff" in which colonies of each species were unable to overgrow the other and both were thus inhibited. Bryozoans encrusting brachiopods in the Cincinnatian might also be expected to provide this kind of evidence although no instances have yet been reported. Evidence for mutual benefit to two associated species is even more difficult to establish from fossil material.

Cincinnatian Guilds

As a means of characterizing the complexity of an ecosystem, ecologists developed the concept of a guild. As applied to natural ecosystems, a guild is defined as "a group of species that exploit the same class of environmental resources in a similar way This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements" (Root 1967, 335). The paleoecologist Richard Bambach applied the guild concept to fossil communities and ecosystems in order to explain how the ecological structure and complexity of ecosystems has changed over evolutionary time (Bambach 1983,1993; Bush and Bambach 2004).

Bambach (19S3) first compared the major adaptive strategies of organisms comprising the three marine "Evolutionary faunas": Cambrian, Paleozoic, and Mesozoic-Cenozoic (Sepkoski 1981). Bambach classified adaptive strategies according to the mode of space utilization and feeding habit. Subsequently Droser and Sheehan (1997) called these broad categories "megaguilds" and assigned benthic taxa to megaguilds for the entire Ordovician. they found that the patterns established for epifauna and infauna during the Ordovician remained stable for the rest of the Paleozoic Era. We constructed megaguild diagrams for major groups found in the Cincinnatian, modified somewhat from those of Droser and Sheehan and including pelagic groups (Table 4a). Most of the groups are at the class level, but some are orders. It should be recognized that this compilation is cumulative for the entire Cincinnatian; thus the total number of guilds exceeds the total that would be expected in a single contemporaneous assemblage.

Comparison of megaguild structure of the Cincinnatian with that of the Mesozoic-Cenozoic reveals major contrasts (Table 4b). Among the epifauna, the Mesozoic-Cenozoic includes many suspension feeding taxa as does the Cincinnatian, but present-day groups have replaced many of those that were present during the Cincinnatian. Pelecypods became dominant, whereas brachiopods assumed a minor role. The bryozoans dominant in the Paleozoic, the trepostomes, became extinct and the cheilostomes became dominant. Stalked echinoderms (crinoids, blastoids, and cystoids) suffered major extinctions at the end of the Paleozoic, and stalked crinoids survived only in deep water. The number of taxa of mobile epifaunal animals, such as gastropods, crustaceans, and sea urchins increased markedly.

Exploitation of living space and food resources within the sediment by

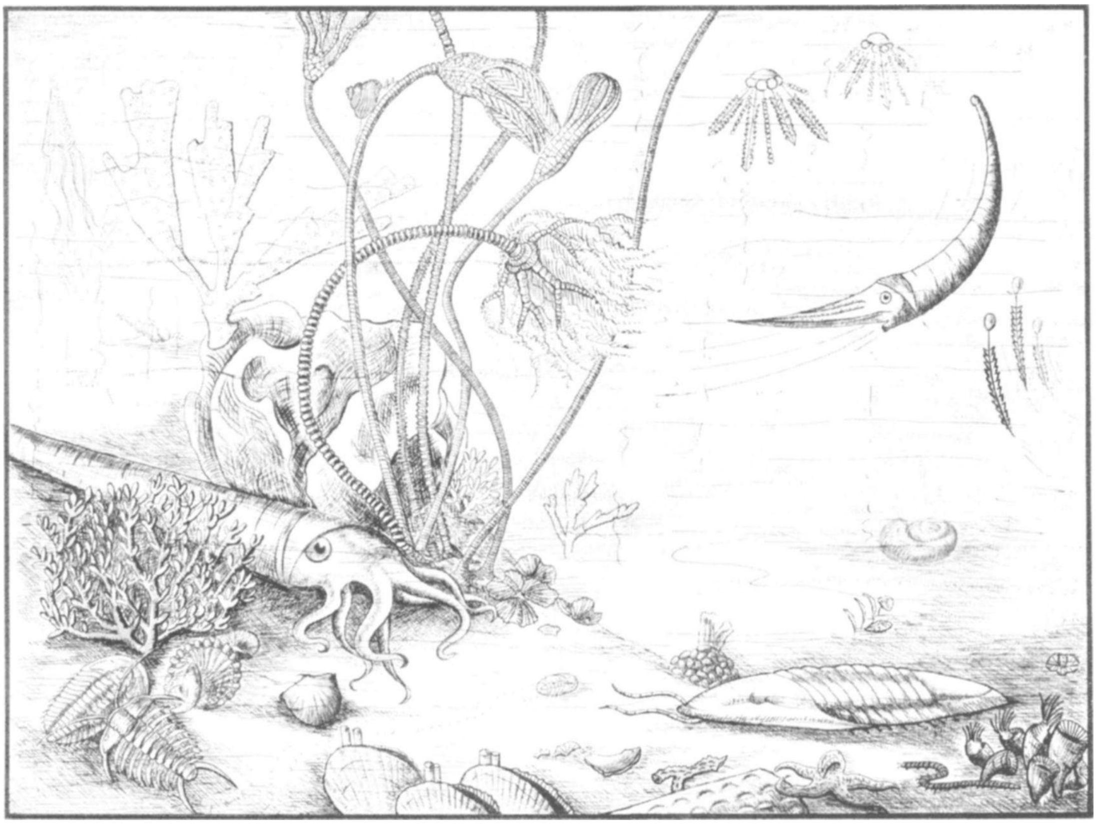

Figure 16.2. *Reconstruction of life on the Cincinnatian sea floor. Drawing by Anneliese Caster and Elizabeth A. Dalve. From von Engeln and Caster, Geology, 1952, figure 347, McGraw-Hill, and reprinted by permission of the McGraw-Hill Companies.*

infaunal organisms stands out as one of the major contrasts between the Ordovician guild structure and that of the post-Paleozoic. The diversification of burrowing pelecypods, gastropods, polychaetes, crustaceans, and echinoids populated blocks of the infaunal megaguild structure that were relatively empty during the Paleozoic (Table 4a).

Perhaps the most striking contrasts between the Ordovician and post-Paleozoic were in the pelagic realm, the open water above the sea floor. During Cincinnatian time few groups occupied the water column, and animals of those groups differed greatlv from those of the post-Paleozoic (Table 4b). It is astounding to realize that during the Cincinnatian there really was, in the region of Cincinnati, a sea without fish, where nautiloid cephalopods and some trilobites and eurypterids were the only large, actively swimming organisms (Plates 13, 14; figure 16.2). Only later in the Paleozoic did fish began to proliferate, but modern bony fish did not diversify as herbivores and carnivores until the late Mesozoic and Cenozoic. During the Cincinnatian and indeed for most of the Paleozoic, the shallow marine ecosystem was vastly different from anything resembling a present-dav selling. How can we explain these striking differences?

Was the Cincinnatian Sea a "Beggar's Banquet"?

Bambach (1993) argued that major changes in the structure of marine ecosystems, as seen in the fossil record, are a reflection of an increase in

THE primary productivity of the world's oceans during the Phanerozoic Eon. As mentioned earlier, we assume that primary production in the Cincinnatian sea was based on microphytoplankton as well as some benthic macroalgae. It is a paradox that despite the high abundance of benthic suspension feeding invertebrates in the Cincinnatian fauna the only preserved microphytoplanktonic organisms are the acritarchs. Were acritarchs the only suspended food source for a bottom fauna dominated by abundant and diverse suspension feeders? We can speculate that perhaps other microplanktonic algae existed—ones that lacked preservable organic cell walls or mineralized tests. Or, perhaps clay particles suspended in the water column served as substrata for bacteria that formed a "marine snow" that nourished benthic suspension feeders. But, speculation aside, the fossil record of marine plankton definitely indicates that the diversity of taxa of planktonic organisms in the Cincinnati region during the Cincinnatian was about fifty species (Colbath 1979), reached a Paleozoic maximum of three- to four hundred species of acritarchs, then suffered a decline during the late Paleozoic and early Mesozoic. It then began to increase during the Jurassic and Cretaceous, with the appearance of present-day groups such as dinoflagellates, calcareous nannoplankton, and diatoms (Tappan and Loeblich 1973). If the diversity of planktonic organisms is correlated in some way with abundance and productivity, then the fossil record of marine plankton indicates a marked increase in productivity during the Phanerozoic (Bamhaeh 1993). The Cincinnatian sea, despite its seeming organic abundance, may, in fact, have been poor in food resources compared to present-day settings.

Although the earliest spores of land plants date from the Ordovician, terrestrial regions of the Earth remained essentially devoid of widespread plant cover until the late Devonian (Bamhaeh 1993). Bamhaeh suggested that the rise of land plants had a profound effect on marine ecosystems, because rivers began to carry vast amounts of organic matter and nutrients into the sea. This organic matter provided a major new food resource for benthic marine organisms and contributed to the great diversification of infaunal guilds in the post-Paleozoic. (These had been poorly developed in the Cincinnatian.) Increased organic input from the land also increased the supply of nutrients to coastal marine environments, in turn enhancing overall marine productivity. Bamhaeh argued that increasing levels of marine productivity enabled an increase in marine biomass, diversity, and functional versatility that is reflected in the fossil record of post-Paleozoic marine ecosystems.

The vastly different, seemingly alien world of the Cincinnatian sea can thus be understood as the product of a period in Earth history when the capacity of the sea to support life was a mere fraction of what it became through subsequent Phanerozoic time. The modes of life, body size, and overall abundance of marine life in the Cincinnatian of the Cincinnati region were all limited by the amount and quality of food resources available. The "beggar's banquet" may have defined the running plot of the Cincinnatian play.

The ultimate outcome of this plot is hidden from view in the Cincinnati region because the evidence of the closing acts of the Ordovician re-

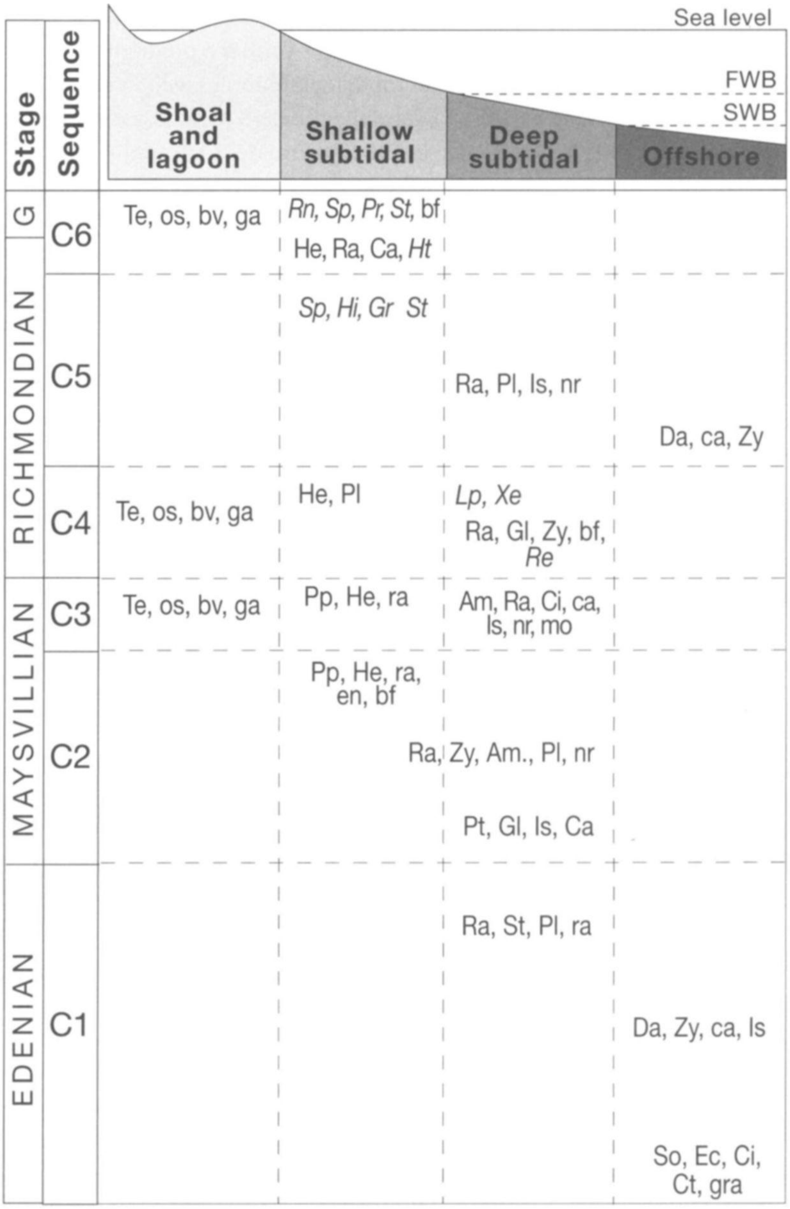

Figure 16.3. *Time-environment diagram for the Cincinnatian Series. The vertical axis shows the timescale and six major shallowing-upward sequences of the Cincinnatian (see chapters 4 and 15).* G *= Gamachian Stage (not preserved in Cincinnati region). The horizontal axis shows the major environments of the Cincinnatian (see chapter 15). Offshore environments are located towards the present north in Ohio and westward in Indiana, and shoal and lagoon environments are located toward the present south in Kentucky (see Plate 12). FWB = fairweather wave base, SWB = storm wave base. Letter-codes indicate major fossils characteristic of assemblages found in each sequence and environment, defined as fossils occurring in >20% of samples from each setting. Letter-codes as follows:* corals: *Gr = Gewingkia, Sp = Streptelasma, Te = Tetradium, Pr - Protaraea;* bryozoans: *bf = bifoliate forms, en = encrusting forms, nr = thin ramose forms, ra = ramose forms;* brachiopods: *Da = Dalmanella, He = Hebertella. Hi = Hiscobeccus, Ht = Holtedahlina, Lp = Leptaena, PI = Platystrophia, Pp = Platystrophia ponderosa, Pt = Plectorthis, Ra = Rafinesquina, Re = Retrorsirostra, Rn = Rhynchotrema, So = Sowerbyella, St =*

Strophomena, Zy = Zy-

cord was obliterated by subsequent erosion. The missing script, as read elsewhere, tells us that sweeping environmental changes brought about mass extinctions of many Ordovician players worldwide. The causes of these extinctions are debated. They apparently were complex and seem to have involved a global ice age, along with changes in sea level and ocean chemistry (Hallam and Wignall 1997). The shallow seas that again covered the region of the Cincinnati Arch during the ensuing Silurian act were populated with many familiar players and roles, yet the cast of characters represents a clearly different troop of players on a new stage setting.

When we search the seas of the present day for anything resembling the Cincinnatian ecosystems, a revival of the Cincinnatian play, we are hard pressed to find main good analogues. Of course, extinction has swept away virtually all the taxa of the organisms that inhabited the Cincinnatian sea, including entire major groups such as graptolites, conulariids, trilobites, eurypterids, and edrioasteroids. However, today we can find rather restricted regions where the sea floor is covered with bryozoans, such as the shelf off South Australia (Bradstock and Cordon 1983; Hageman et al. 2000). New Zealand, isolated in the southwestern Pacific, harbors the greatest diversity of living brachiopods; elsewhere these animals are but minor components of shallow water communities. Closer to the area of the Cincinnatian, the San Juan Islands in the Pacific Northwest support a diverse and abundant fauna that includes many Paleozoic elements such as echinoderms, bryozoans, brachiopods, solitary corals, and sponges. However, these relicts are a mere fraction of a more diverse fauna rich in molluscs, crustaceans, and fish—all groups that proliferated in the post-Paleozoic. Present-day tropical reefs far surpass those of the Ordovician in diversity and abundance, and yet there are certain reef-related habitats that mirror, to some extent, the Paleozoic. In Australia's Great Barrier Reef, deeper, soft sediment bottoms located below the coral-dominated shallow reefs have a Paleozoic aspect, rich in algae, sponges, solitary corals, bryozoans, and crinoids (Messing et al. 2006). Individuals of the chambered *Nautilus,* the only living descendants of the nautiloid cephalopods of the Paleozoic, also survive at depths of 100 m below the tops of the reefs of the Pacific. Likewise, the only living stalked crinoids are restricted to depths greater than 100 in (Meyer 1997). Collectively, these examples of present-day survivors from the past and Paleozoic-like communities share the characteristics of existence in some isolated or restricted settings where dominance by the more typical shallow marine fauna is, to some degree, relaxed. It is only under such anomalous conditions that organisms of many ancient groups can flourish and provide us with a fleeting glimpse of the ancient Ordovician sea that once covered the Cincinnati region.

gospira; trilobites; ca = *calymenid, Ct = Cryptolithus, Is = Isotelus;* ostracodes = os; gastropods = *ga;* pelecypods; *Am = Ambonychia, by = indeterminate pelecypod, Ca = Carotidens, mo = modiomorphid pelecypod;* crinoids. *Ci = Cincinnaticrinus, Ec = Ectenocrinus, Gl = Glyptocrinus, Xe = Xenocrinus;* graptolites = *gra. Italicized fossils are those invading region during the Richmondian invasion. Information derived from Holland and Patzkowsky (2007); see this publication for distribution of additional fossils.*

Table 2. *Predators and Prey among Cincinnatian Taxa*

Predator	**Prey**	**References**
Rugose corals	ostracodes?	Elias 1984
Nautiloids	brachiopods	Alexander 1986
	trilobites	Babcock 2003
Unspecified	crinoids	Ausich and Baumiller 1993; Donovan and Schmidt 2001; Baumiller and Gahn 2004
Trilobites	worms	Babcock 2003; Brandt et al. 1995
Eurypterids	trilobites	Babcock 2003
Asteroids	pelecypods	Blake and Guensburg 1994

Table 3. *Associations among Individuals of Cincinnatian Taxa*

ARRANGED BY "HOST"			
Host	**Associate**	**Type of Association**	**References / [Annotations]**
PROTISTA			
foraminifers	bryozoan	bioimmuration; epizoism	Wilson, Palmer, and Taylor (1994)
PORIFERA			
stromatoporoids	pelecypods	boring	Pojeta and Palmer (1976); Wilson and Palmer (1988)
CNIDARIA			
hydrozoan	bryozoan	encrustation (post-mortem); dwelling inside empty shell	Wilson, Palmer, and Taylor (1994)
corals	algae, fungi	boring	Elias and Lee (1993)
	corals	epizoism	Elias (1983)
	bryozoans	encrustation: epizoism	Bassler(1953)
	bryozoans	encrustation: epizoism	Elias (1983)
	worms	boring (at least some during life of host)	Elias (1983) *[Trypanites* in *Grewingkia]*
	worms	boring	Elias (1986)
BRACHIOPODA			
brachiopods	algae	boring	Kobluk and Risk (1977)
	corals	epizoism	Elias (1983)
	brachiopods	post-mortem attachment	Shrake(1989)
	bryozoans	encrustation; epizoism	Nicholson (1875)
	bryozoans	bioimmuration; epizoism	Wilson, Palmer, and Taylor (1994)
	bryozoans	"boring"; presumably post-mortem	Anstey and Wilson (1996)
	bryozoans	"boring"	Pohowsky (1974, 1978)
	bryozoans	post-mortem attachment	Shrake(1989)

ARRANGED BY "HOST"

Host	Associate	Type of Association	References / [Annotations]
	bryozoans	encrustation; ? epizoism	Anstey and Wilson (1996) *[Corynotrypa* on interior of brachiopod shell]
	bryozoans	encrustation; ? post-mortem	Anstey and Wilson (1996) *[Cuffeyella* on interior of brachiopod shell]
	bryozoans	encrustation	Ulrich (1879)
	bryozoans	encrustation	Ulrich (1883)
	brachiopods	epizoism	Alexander and Scharpf (1990)
	Cornulites	? commensalism	Morris and Rollins (1971)
	crinoids	post-mortem attachment	Shrake (1989)
	edrioasteroids	epizoism	Richards (1972)
		epizoism or commensalism	Meyer (1990)
	gastropods	borings	Fenton and Fenton (1931)
		borings	Bucher (1938)
	Sphenothallus	epizoism	Neal and Hannibal (2000)
	stromatoporoids	epizoism	Richards (1972); Alexander and Scharpf (1990)
ECTOPROCTA			
bryozoans	corals	epizoism	Elias (1983)
	brachiopods	epizoism	Richards (1972)
	brachiopods	aegism; epizoism	Shrake (1989)
	bryozoans	encrustation; epizoism	Nicholson (1875)
	bryozoans	encrustation	Ulrich (1879a)
	bryozoans	encrustation	Ulrich (1883)
	bryozoans	aegism; epizoism	Shrake (1989)
	bryozoans	bioimmuration; epizoism	Wilson, Palmer, and Taylor (1994)
	Catellocaula	bioclaustration; parasitism; epizoism	Palmer and Wilson (1988)

Host	Associate	Type of Association	References / [Annotations]
	Cornulites	epizoism; ? commensalism	Morris and Rollins (1971)
	cornulitids	encrustation and intergrowth	Baird, Brett, and Frey(1989)
	pelecypods	boring	Wilson and Palmer (1988)
	Sanctum	boring	Erickson and Bouchard (2003)
	Sphenothallus	epizoism	Bodenbender et al. (1989)
	trilobites	aegism	Shrake(1989)
	"worms" — *Trypanites*	borings	Palmer and Wilson (1988)
CORNUUTIDS			
cornulitids	bryozoans	encrustation and intergrowth	Baird, Brett, and Frey (1989)
cornulitids	bryozoans	bioimmuration; epizoism	Wilson, Palmer, and Taylor (1994)
MOLLUSCA			
Mollusca — gastropods	brachiopods	epizoism	Morris and Felton (1993)
Mollusca — gastropods	*Cornulites*	encrustation; ? commensalism	S. A. Miller (1874c)
Mollusca — gastropods	*Cornulites*	commensalism	Morris and Rollins (1971); Morris and Felton (1993)
Mollusca — gastropods	*Cornulites*	? epizoism: ? commensalism	Richards (1974)
Mollusca — gastropods	trilobites	? endozoism ?	Brandt (1993)
Mollusca — monoplacophorans	bryozoans	encrustation	Ulrich (1883)
	Cornulites	epizoism or commensalism	Morris and Rollins (1971)
Mollusca — nautiloids	brachiopods — (inartic.)	encrustation	Davis and Mapes (1996)
Mollusca — nautiloids	bryozoans	encrustation; epizoism	Nicholson (1875)

ARRANGED BY "HOST"

Host	Associate	Type of Association	References/ [Annotations]
Mollusca "nautiloids" — actinoceroids endoceroids nautiloids	bryozoans	epizoism; ? commensalism	Frey (1988, 1989); Baird et al. (1989)
	bryozoans	encrustation presumably epizoism; ? commensalism	Davis and Mapes (1996)
	bryozoans	encrustation	Ulrich (1879a)
	bryozoans	encrustation	U. P. James (1884b)
	bryozoans	encrustation	Ulrich (1883); Bassler (1953)
	bryozoans	encrustation (post-mortem); dwelling inside empty shell	Wilson, Palmer, and Taylor (1994)
	Cornulites	? epizoism ? commensalism	Richards (1974)
	hydrozoan	encrustation (post-mortem); dwelling inside empty shell	Wilson, Palmer, and Taylor (1994)
	stromatoporoid	encrustation	J. F. James (1886)
	stromatoporoid	encrustation	Baird, Brett, and Frey (1989)
	trilobites	? incolenism	Davis et al. (2001)
Mollusca — pelecypods	*Cornulites*	epizoism or commensalism	Morris and Rollins (1971); Morris and Felton (2003)
ARTHROPODA			
trilobites	bryozoans	epizoism	Brandt (1996)
trilobites	*Cornulites*	epizoism	Morris and Rollins (1971); Brandt (1996)
ECHINODERMATA			
Echinodermata — crinoids	brachiopods	aegism; epizoism	Shrake (1989)
Echinodermata — crinoids	brachiopods — *Zygospira*	commensal	Sandy (1996)
Echinodermata — crinoids	bryozoans	encrustation	Ulrich (1883)
Echinodermata — crinoids	bryozoans	encrustation: epizoism	Bassler (1953)

ARRANGED BY "HOST"			
Host	**Associate**	**Type of Association**	**References/ [Annotations]**
Echinodermata — crinoids	byroniids	parasitism	Warn (1974); Welch (1976); Malinky et al. (2004)
Echinodermata — crinoids	*Cornulites*	commensalism	Morris and Rollins (1971); Morris and Felton (1993, 2003); Richards (1974)
Echinodermata — crinoids	gastropods	commensalism	Bowsher (1955); Morris and Felton (1993)
Echinodermata — crinoids	gastropods	? parasitism ?	Baumiller and Gahn (2002)
"WORMS"			
(see also: cornulitids)			

SUSPENSION	HERBIVORE	CARNIVORE	PRIMARY PRODUCERS
chitinozoans (?) conodonts graptolites trilobites (pt)		cephalopods eurypterids	acritarchs

EPIFAUNA

	SUSPENSION	DEPOSIT	HERBIVORE	CARNIVORE
MOBILE	trilobites (pt)	monoplacophorans gastropods trilobites ostracods ophiuroids, asteroids (pt)	monoplacophorans gastropods ostracods	trilobites (pt) asteroids
ATTACHED LOW	stromatoporoids (pt) tab., rugose corals (pt) bryozoans craniate brachs rhynch. brachs bivalves cornulitids edrioasteroids cyclocystoids			
ATTACHED ERECT	sponges conulariids stromatoporoids (pt) tabulate corals (pt) bryozoans rhombiferans crinoids			
RECLINING	rugose corals (pt) strophomenate brachs tentaculitids hyolithids stylophorans			

	SUSPENSION	DEPOSIT	CARNIVORE
SHALLOW PASSIVE	rostroconchs		
SHALLOW ACTIVE	Ungulate brachs bivalves *Diplocraterion*	bivalves polychaetes	polychaetes
DEEP PASSIVE			
DEEP ACTIVE			

Table 4A. *Type-Cincinnatian Marine Guilds Modified after Droser and Sheehan (1997).*

	SUSPENSION	HERBIVORE	CARNIVORE	PRIMARY PRODUCERS
PELAGIC	gastropods malacostracans mammals	bony fish mammals	cephalopods chondrichthyans bony fish reptiles mammals	dinoflagellates coccolithophores diatoms

		SUSPENSION	DEPOSIT	HERBIVORE	CARNIVORE
EPIFAUNA	MOBILE	bivalves crinoids ophiuroids (pt) asteroids (pt) holothuroids	gastropods ostracods malacostracans ophiuroids asteroids (pt) echinoids holothuroids	chitons gastropods ostracods malacostracans echinoids	gastropods cephalopods malacostracans asteroids
	ATTACHED LOW	sponges corals bryozoans brachiopods polychaetes bivalves barnacles			
	ATTACHED ERECT	sponges corals bryozoans crinoids			
	RECLINING	corals (pt) bivalves			

		SUSPENSION	DEPOSIT	CARNIVORE
INFAUNA	SHALLOW PASSIVE	gastropods bivalves echinoids	bivalves	bivalves
	SHALLOW ACTIVE	lingulate brachs bivalves polychaetes echinoids	bivalves polychaetes echinoids holothuroids	gastropods malacostracans polychaetes
	DEEP PASSIVE	bivalves		
	DEEP ACTIVE	bivalves polychaetes malacostracans	bivalves polychaetes	polychaetes

Table 4B. *Mesozoic and Cenozoic Marine Guilds Modeled after Bambach (1983).*

EPILOGUE: DIVING IN THE CINCINNATIAN SEA

many paleontologists, ourselves included, became fascinated with fossils and embarked on scientific careers long before we ever encountered living marine animals. For many of us, the greatest thrill has been our first encounters with living representatives of the animal groups we knew first only as grey, lifeless forms encased in rock. Both of us have been privileged to examine firsthand living relatives of animals of our favorite groups of fossils—crinoids for Meyer and nautiloid cephalopods for Davis. Our experiences have fueled a curiosity that affects practically anyone who contemplates the fossil richness of the Cincinnatian or other comparable fossiliferous strata. Many times, in the field, we stand on a Cincinnatian outcrop where fossils are abundant in almost every rock, and we wonder: what did the Cincinnatian sea actually look like? How did these creatures behave when alive? If we could travel back in time to dive into the Cincinnatian sea, what would we see?

In his book *The Crucible of Creation,* the paleontologist Simon Conway Morris (1998) takes the reader on a journey through time in an imaginary time machine that lands on the shores of the Cambrian sea in western Canada of 520 million years ago. The time machine then descends into the sea and enables time traveling scientists to view the varied and bizarre animals found as fossils in the famous Burgess Shale. Conway Morris recreated the environment of the Cambrian sea and the life within it from the evidence of the fossils and rocks, but he embellished the scenario with a measure of speculation and fantasy.

Were we to travel back to the Late Ordovician, would we need a deep-diving submersible to explore the Cincinnatian world in a similar, imaginary journey? Based on the evidence from the rocks and fossils (see chapter 15), the time traveler to Cincinnati in the Late Ordovician would have to land on the sea surface, because no dry land would be found. With no familiar landmarks—the Ohio River valley, the Suspension Bridge, or Carew Tower—breaking the horizon, we would be attracted to the area only by vast shallows appearing as varying shades of aquamarine, with occasional shoals marked by breakers.

Our time machine transforms into a small boat as we land, and we check our position. There is no Global Positioning System of satellites, so we use a sensitive dip-needle that indicates that we are at 25° south latitude, but we have no reliable indicator of longitude. The water feels cool, about 65°F, so we need wet suits for the dive. Breakers off to the south look menacing, so we keep our distance and drop anchor where we can see the bottom. Let's see what's down there!

We don masks and snorkels for a quick reconnoiter, and slip over the side. We have anchored over very shallow water, and the bottom appears only a meter or so beneath us. As we take a closer look at the bottom, we notice that it is irregular, with low mounds separated by patches that are more level. The mounds are actually clumps of large, ribbed brachiopods, ***Platystrophia ponderosa.*** Living animals with articulated shells are intermingled with separated valves, some broken and worn smooth. It is the environment that, millions of wars in the future, will be preserved as the Mt. Auburn Member of the Grant Lake Limestone. We easily scoop up a sample of specimens of ***Platystrophia*** because they have no pedicle attachments.

Clearly there is much of interest to see here, but we return to the boat because snorkel diving is not adequate for prolonged exploration. We have not been able to hold our breath during our dives as long as we normally do—we had to come up quickly, gasping for air. A check of our air quality monitor reveals the reason: the Late Ordovician atmosphere has only a fraction of the oxygen content of present-day air, perhaps as little as 1 percent. Fortunately we have brought along some sophisticated diving gear that will let us fill our diving cylinders with compressed air in which we have boosted the oxygen content to its present-day level, 21 percent. Because the rest of our compressed gas mixture is predominantly nitrogen, we still have to follow the dive tables that tell us how long we can dive at a given depth and resurface without suffering decompression sickness. We need to be really careful: we could not be farther away from a recompression chamber!

Equipped with collecting gear and cameras, we resume our dive using scuba gear. The water clarity actually is quite good: we can see perhaps 15 meters (50 feet) horizontally. However, there are patches of the mud and silt covering wide areas of the bottom that could be easily stirred up if surface waves picked up. Visibility could drop sharply. As we settle to the bottom right beneath the boat, we can feel some wave motion. Although the sea floor appears very flat, we can see that there is a gentle slope tailing off toward the north, so we swim slowly toward deeper water. We cover a lot of distance, but the depth changes very little. We see vast areas of the sea floor covered with bryozoans in dense thickets or folded sheets like a rumpled carpet. As we go deeper, more bush-like bryozoan colonies appear, some very delicate. It is amazing to see how similar the colony forms are to those of present-day bryozoans. But we know that, in the Ordovician, we are looking at trepostomes, not at animals of the groups that thrive in the seas of today. In places the sea floor is a hard, limestone pavement with a convoluted surface; depressions are filled with fine silt or shelly sand. Bryozoans and brachiopods are attached to the hard surfaces. The heart skips a beat as we spot for the first time a living edrioasteroid echinoderm, also attached like a present-day barnacle to the hardground. Because edrioasteroids became extinct in the Late Paleozoic, we have never been able to envision the living animal with confidence until now. A clump of tall, pillar-like specimens of *Streptaster* shows that Colin Sumrall had the right idea in suggesting that some edrioasteroids could inflate their thecae and telescope up or down from the substratum. Fine tube feet extending from the ambulacra] grooves recall the reconstructions made by Bruce Bell. With a rock pick we easily break off a piece of the hardground with edrioasteroids attached, and we bag it for study in the lab. The hardground gives way to an area covered with thin-shelled *Rafinesquina* bachiopods, forming shell pavements like those we found in rock units with names like Corryville, Bellevue, and fairview in the distant future from which we came. The concavo-convex brachiopods rest with the convex valve either down or up, and main are encrusted with small bryozoans or edrioasteroids. Brachiopods of taxa like *Zygospira* and pelecypods of genera like *Caritodens* are attached. Other clams, of taxa like *Modiolopsis,* poke up through the sediment between shells. Small *Flexicalymene* and *Acidaspis* trilobites glide over the surface, and here and there a crinoid has the stem coiled around a bryozoan. This is a diverse habitat.

But the water mass above the sea floor is surprisingly empty compared to the scene in present-day shallow seas. Today, fish are everywhere in the sea, filling a wide variety of ecological roles. Where are the fish in this Ordovician sea? Only small nautiloid cephalopods are jetting about, against a backdrop of pulsating jellyfish. At close range, we can pick out very small strings suspended in the water with clumps of minute tentacles arranged in vertical series. These are graptolites. Closer to the bottom some small, spiny trilobites, probably odontopleurids, swim above the bottom for short distances. Although early, jawless fish inhabit some Late Ordovician seas elsewhere, they had not yet spread to the Cincinnati region. It truly is a sea without fish! We do not have to worry about sharks either, because they will not evolve until the Devonian—millions of years in the future.

Our depth gauge shows that, as we swim farther away from the boat, the bottom gradually rises, and it becomes littered with brachiopods and bryozoans. Here and there mounds rise up as tall as a meter from the bottom. Although the mounds look somewhat like coral colonies, closer inspection reveals that they are heavily calcified colonics of bryozoans, whose fuzzy-looking surfaces are millions of oh-so-tiny tentacles extended into the water. They retract when we brush against the surface, and we can see the minute honeycomb-like skeleton beneath. Some colonies are rounded and boulder-like; others are branching or composed of complexly folded sheets. The patches between bryozoans are littered with broken fragments of bryozoans and brachiopods of genera like *Hebertella* and *Platystrophia,* including both living animals and dead, disarticulated shells. Here and there we see bryozoan colonies apparently turned upside down; we know that because the rounded side of each is on the bottom, or the branches do not radiate upward from a basal plate. These hefty, overturned colonies suggest that conditions can be far more turbulent than the placid calm in which, with great good luck, we landed. These waters sometimes must be raked by great storms. We feel stronger wave motion and soon we are breaking the surface on this shoal. Patches of dead, thin-shelled *Rafinesquina* brachiopods are turned on their edges and packed tightly together by wave action—what will be called "shingled *Rafinesquina*" beds in the far-distant future. Bryozoan branches and sheets are stacked into patches of coarse rubble. This is the environment of the Bellevue Limestone to be.

A gully leads us back into deeper water. Here we find vast areas covered with brachiopods of taxa like *Rafinesquina* and *Strophomena* or branching bryozoans. There are intervening patches of mud about equal in area to the shelly patches; this must be the environment of the Fairview, with continuous, even beds that will produce about 50 percent limestone and 50 percent shale.

In the distance we spot a ridge of bryozoans standing almost a meter above the surroundings, and we head toward it. Could we he approaching a sharp drop-off leading to deeper water? Approaching closer, we can see a richness of life around this ridge, and we sense a gentle current flowing along the bottom, parallel to the gradual slope, which intensifies as we reach the ridge. The depth gauge reads 15 meters (50 feet), and we have descended below the depth where the small surface waves stirred the bottom. Here, current flow takes over and follows the contours of the slope. The ridge is actually a mound built entirely of the branching bryozoan colonies of genus *Parvohallopora;* it projects outward from the slope, The current is diverted and gains velocity as it flows over the ridge. Crinoids forming a dense clump are of genus *Glyptocrinus;* their stalks are coiled around the bryozoan branches, and the crinoids stand above them like a forest canopy. Their crowns are splayed out in feathery filtration fans that are all aligned perpendicular to the current. Standing above them are a few gigantic crinoids of genus *Anomalocrinus,* with thick stems a meter or more in length and broad, dense filtration fans some 30 centimeters in diameter, also oriented by the current. Many other invertebrates make their homes in this intricate thicket. *Gyclonema* snails are attached to the calyces of practically every specimen of *Glyptocrinus* and clumps of small *Zygospira* brachiopods attach to the crinoid stems. Other brachiopods of genus *Platystrophia* and pelecypods of *Ambonychia* are nestled in among the bryozoan branches.

Suddenly we are startled by streaky shadows passing over us, and look up to see large, conical nautiloid cephalopods gliding above us, aligned like airplanes in formation. They behave much like schooling squid, but each has an outer shell, with a pattern of color banding. One is holding a large, wriggling trilobite in its tentacles. These cephalopods are the largest creatures we have seen, and some of these reach a meter or more in length, and their large eyes and numerous tentacles are more than a little menacing. We hunker down next to the ridge and point the camera upward as they shoot by overhead. If this picture does not make the cover of *Science,* it will at least be the hit of the next meeting of the Paleontological Society! In a flash they are gone, and our breathing rate settles down.

In a hollow of the ridge we find a large *Isotelus* trilobite, its pygidium (tail shield) folded neatly under its cephalon (head shield)—it must have seen us coming and rolled up for protection. It is a giant, about 25 centimeters between the sharp tips of the genal spines. The temptation to grasp a living trilobite is too great, and as we reach out for this prize, the animal suddenly unfolds with a snap and glides away, ventral side up, out of reach. It then flips back over and clings tightly to the bottom, pressing the dorsal carapace down into the sediment. Had this one not gotten away, it might have surpassed the world record specimen of *Isotelus* from the Ordovician of northern Canada! Nevertheless, we have managed to gather up several smaller trilobites, and maybe their DNA finally will resolve the question of how trilobites are related to other arthropods.

We venture out beyond the bryozoan ridge onto a seemingly level plain with patches of brachiopod pavement and bryozoans. The brachiopods are noticeably smaller forms like ***Dalmanella*** and ***Sowerhyella.*** Bryozoans are delicate, twig-like colonies with fewer sheet-like or massive forms. ***Flexicalymene*** trilobites are here, hut are smaller than those we found in shallower water; some new trilobites of genera like ***Cryptolithus*** and ***Triarthrus*** cruise on the muddy patches, leaving grooved trails. Extending upward from some bryozoan thickets are very slender yet long-stemmed crinoids of the taxa ***Ectenocrinus*** and ***Cincinnaticrinus.*** Although they have fewer arms than the other crinoids we have seen today, they splay them into conical filtration fans in alignment with the gentle current (not open into the flow but with the concave side bearing the food grooves downcurrent). Some sediment patches are sands entirely composed of fragments of disarticulated crinoids, with odd bundles of long, still-articulated steins. The sands have broad, sinuous ripple marks like those along a beach. How could such ripples form at our present depth of 30 meters (100 feet)? We sense no wave motion and only slight current; however, as experienced divers, we know that severe storm conditions at the surface, including hurricanes, can produce occasional, strong wave oscillation or currents along the deeper sea floor where normal, fair weather wave motions do not penetrate. We have an uneasy feeling that we have ventured into an environment that can turn violent very quickly, as we see around us the remnants of shattered bryozoans and current-winnowed shells. Areas of pure mud have now become wider than areas of shelly sediment, and we recognize the characteristics of what will conic to be known as the Kope Formation.

A glance at the dive computer shows we have almost exceeded our allowable bottom time at the maximum depth of 30 meters, so it is time to return to the shallows. We turn back on a reverse compass course, hoping we we will surface close to the boat. As we again approach the bryozoan ridge, we notice an overhang we had overlooked. Some kind of movement is apparent in the shadows beneath this ledge. Whip-like, spiny appendages are waving at us; this is something new—we must investigate! Using a long, slender pole with a hook at one end, we reach back under the ledge. After a few unsuccessful tries, we have snagged a large and bizarre creature. We recognize the flailing appendages of a eurypterid of genus ***Megalograptus.*** It is the size of a Maine lobster but has very strange and spiny, non-lobster-like appendages. The elongate, segmented tail section is flexible like a lobster tail. We do not have time to observe the eurypterids now, so we pop a few into a mesh hag for later study. The mystery of how they use their appendages will remain until then. Perhaps we will see whether one tastes like lobster!

After more finning toward the shallows, our dive computer beeps, and we must ascend. We break the surface and switch to snorkel because we are low on air. We spot the boat in the distance, perhaps 200 meters away. It is a long swim on the surface. We are laden with specimen bags and gear, and, by the time we reach the boat, we are exhausted from gulping the oxygen-poor air. We haul ourselves over the gunwale, peel off our wetsuits, and just lie in the boat, catching our breath, our minds racing with the sights we have seen. What a dive!

Suddenly, we sense the warmth of the afternoon sun, amid the coolness of a crisp autumn day. We are staring at the fossil-covered surface of a bed of Ordovician limestone littered with rusty autumn leaves. We are sitting on the banks of Stonelick Creek, in Clermont County, Ohio, having lunch on a field trip with our students—and maybe you!

APPENDIX 1. RESOURCES: WHERE TO GO FOR MORE INFORMATION

Paleontology textbooks

There are many textbooks in paleontology, but we restrict the following list to some of the most recent as well as one older, classic work.

Fossil Invertebrates (Boardman et al. 1987)
Principles of Paleontology, 3rd ed. (Foote and Miller 2007)
Invertebrate Fossils (Moore et al. 1952)
Invertebrate Palaeontology and Evolution, 4th ed. (Clarkson 1998)

Publications of Geological Surveys

Ohio Fossils (La Rocque and Marple 1955)
Fossils of Ohio (Feldmann and Hackathorn 1996)
Exploring the Geology of the Cincinnati/Northern Kentucky Region, 2nd ed. (Potter 2007)

Locally published books

Cincinnati Fossils (Davis 1985,1992) and its predecessors (Caster et al. 1955, 1961)

Encyclopedic works

Index Fossils of North America (Shinier and Shrock 1944)
Treatise on Invertebrate Paleontology

Internet websites

R. A. Davis's "The Type-Cincinnatian," http://inside.nisj.edu/acadeinics/facultv/davisr/cintian/index.htm. The College of Mount St. Joseph, Cincinnati, Ohio (accessed February 18, 2008).

The Dry Dredgers, http://drydredgers.org/, Dry Dredgers, Inc., Cincinnati, Ohio (accessed February 18, 2008).

EarthTime, http://www.earth-tiiue.org/about.html (accessed February 18, 2008).

"History of Life through Time," http://www.ucmp.berkeley.edu/exhibits/historyoflite.php. University of California Museum of Paleontology (accessed February 18, 2008).

Steven Holland's "The Stratigraphy and fossils of the Upper Ordovician near Cincinnati, Ohio," http://www.uga.edu/~strata/cincy/index.html,The University of Georgia Stratigraphy Lab (accessed February 18,2008).

Indiana Geological Survey; http://igs.indiana.edu/, Indiana University (accessed February 18, 2008).

International Geological Correlation Programme, IGCP 410, "The Great Ordovician Biodiversification Event. Implications for Global Correlation and Resources," http://www.es.mq.edu.au/MUCEP/igcp410/, Macquarie University, Sydney, Australia (accessed February 18, 2008).

Kentucky Geological Survey, http://wwvv.uky.edu/KGS/, University of Kentucky (accessed February 18, 2008).

Kentucky Paleontology Society, http://www.uky.edu/Otherorgs/KPS/ (accessed February 18, 2008).

Ohio Geological Survey, http://www.ohiodnr.com/geosurvey Division of Geological Survey, Ohio Department of Natural Resources (accessed February 18, 2008).

University of Cincinnati Department of Geology, http://www.uc.edu/geology/ (accessed February 18, 2008).

Field guides

These are guidebooks to field trips pertaining to the Ordovician geology of the Ohio, Indiana, and Kentucky regions. Most contain detailed roadlogs and directions to geological localities, as well as detailed descriptions of exposed stratigraphic sections. Localities listed in older guidebooks may no longer be accessible.

Caster 1961b; Hattin et al. 1961; Pope and Martin 1977; Hay et al. 1981; Meyer et al. 1981; Meyer et al. 1985; Davis 1986; Haneberg et al. 1992; Shrake 1992; Davis and Cuffey 1998; Algeo and Brett 2001; McLaughlin et al. forthcoming.

Museums

Behringer-Crawford Museum, Covington, Kentucky http://www.bcmuseum.org/bcmuseum/default.aspx (accessed February 18, 2008)

Cincinnati Museum Center http://www.cincymuseum.org/ (accessed February 18, 2008)

Limper Geological Museum, Miami University, Oxford, Ohio http://www.cas.muohio.edu/limpermuseum/ (accessed February 18, 2008)

Orton Geological Museum, Ohio State University, Columbus, Ohio http://www.geology.ohio-state.edu/facilities.php (accessed February 18, 2008)

Outdoor education areas

Caesar Creek State Park, near Waynesville, Ohio http://www.dnr.state.oh.us/tabid/720/default.aspx/ (accessed February 18, 2008)

At the Visitors' Center, there is an exhibit about the geology and fossils to be found at the overflow spillway, where fossil collecting is permitted in accordance with certain regulations available at the Visitors' Center.

Hueston Woods State Park, near Oxford, Ohio http://www.dnr.state.oh.us/parks/tabid/745/Default.aspx (accessed February 18, 2008)

Fossil collecting is permitted in certain areas of the park.

Cincinnati Nature Center, near Milford, Ohio http://www.cincynature.org/index2.asp/ (accessed February 18, 2008)

Although fossil collecting is not permitted, there are good exposures of Cincinnatian strata at several sites on the Nature Center properties.

Sawyer Point Geological Timeline, Cincinnati, Ohio http://www.cincinnati-oh.gov/crc/pages/-5708-/ (accessed February 18, 2008)

This timeline begins with the Late Ordovician and continues through the founding of Cincinnati with each pavement block representing one million years. Important geological events are engraved on blocks at appropriate intervals.

Trammel Fossil Park, Sharonville, Ohio http://www.sharonville.org/fossilpark.aspx (accessed February 18, 2008)

This park is dedicated to education about Ordovician geology and paleontology (see Figure 1.8).

Scientific societies and institutions

Paleontological Society. The Paleontological Society is the largest paleontological organization in the United States. It publishes both the *Journal of Paleontology* and *Paleobiology*. A series of educational brochures about fossils can be downloaded from their website http://paleosoc.org/ (accessed February 18, 2008).

Paleontological Research Institution, Ithaca, New York. PRI publishes both the *Bulletins of American Paleontology* and *Palaeontographica Americana,* as well as a popular magazine, *American Paleontologist.* Their website is http://www.priweb.org/ (accessed February 18, 2008).

Geological Society of America. The GSA is the leading geological organization in North America and it publishes both the *Geological Society of America Bulletin* and *Geology.* It sponsors many regional and national scientific meetings and field trips. Their website is http://www.geosociety.org/ (accessed February 18, 2008).

APPENDIX 2. INDIVIDUALS AND INSTITUTIONS ASSOCIATED WITH THE TYPE-CINCINNATIAN

The following is a list of the names of individuals and institutions associated with the Cincinnati region, and, especially, its geology and paleontology. Some of the individuals listed were members of the Cincinnati School; most were not.

There are some potential problems with this list. In some instances, there are two people with similar, but different names, but who may not be different people. For example, different sources refer to a J. H. Hall and a John W. Hall associated with the Cincinnati Society of Natural History, and there is I. Harris, I. H. Harris, and I. M. Harris, all of Waynesville, Ohio. George Vallandingham and George Vallandigham are almost certainly the same person, and the latter probably is the correct spelling, but maybe not.

In this volume, we present photographs of some of the people discussed. Many of the individuals portrayed are sufficiently well known that there is little question of identification. In some instances, however, a photograph is the only one of which we are aware that is supposed to represent the person in question. The identification may be based on a hand written notation on the photograph or on the album page that bears the photograph, with no independent verification. We hope that such identifications are correct.

Albers, H. E.

Listed as a local fossil collector by Nickles (1936).

Aldrich, T. H. (1848-1932)

Publications by Truman Heminway Aldrich on Tertiary and present-day molluscs appeared in early numbers of the ***Journal of the Cincinnati Society of Natural History*** (Coan, Kabat, and Petit 2007; Johnson 2002; the given name "Thomas" in Caster [1982] apparently was a typographical error).

Anderson, D. R.

D. R. Anderson collected one of the original specimens of the starfish, ***Palaeasterina approximata*** S. A. Miller, 1878.

Anthony, John Gould (1804-1877)

Anthony was elected recording secretary of the Western Academy of Natural Sciences on May 1,1838. In 1840, he was elected secretary of the Natural Science Section of the Cincinnati Society for the Promotion of Useful Knowledge, which merged with the academy later that year. He is recorded as having given some fossils to the academy, and he published on type-

Cincinnatian and other trilobites. Anthony was one of the hosts when Charles Lyell, probably the foremost geologist on Earth, visited the Cincinnati area in the 1840s. Anthony was author, along with U. P. James, of a paper on echinoderms in the local rocks, and he described an unusual specimen of a fossil cephalopod from the type-Cincinnatian. In 1854, he resigned from the academy, and, in 1863, he became curator of conchology at Harvard University, under Louis Agassiz. According to Clench (1936,69), Anthony's ". . . chief interest was in freshwater mollusks, and he built up a series of American freshwater forms that for its time was superior to any collection in this country" (Anthony 1838,1839a, 1839b, 1847,1848; Anthony and James 1846; Brandt and Davis 2007; Coan, Kabat, and Petit 2007; Hendrickson 1947; Johnson 2002; Lyell 1845).

Austin, George M.	Dr. Austin, a physician from Wilmington, Ohio, was listed as a local collector by Nickles (1936). His collection went to the United States National Museum, which published a paper by him on fossil zones in the Richmondian rocks of the type-Cincinnatian area (Austin 1927; Becker 1938; Nickles 1936; Shideler [1952] 2002).
Barnhart, W. C.	W. C. Barnhart collected the type-specimen of the starfish, *Palaeasterina speciosa* S. A. Miller and Dyer, 1878. He sold it to J. W. Harvey, who, in turn, sold it to C. B. Dyer (Miller and Dyer 1878a).
Bassler, Ray S. (1878-1961)	(See chapter 2)
Bean, W. H.	The bryozoan species, *Ceramopora ? beam,* was named after W. H. Bean, of Lebanon, Warren County, Ohio (U. R James 1884a).
Best, Robert	Dr. Best was the principal curator of the Western Museum at the time of its opening in 1820 (Drake and Mansfield 1827).
Braun, E. Lucy (1889-1971)	Emma Lucy Braun gained world fame as a botanist and plant ecologist, but prior to that she authored the first paleontology thesis at the University of Cincinnati, a master's thesis on Cincinnatian brachiopods that later was published by the Cincinnati Society of Natural History (Braun 1916; Caster 1981}.
Braun, Fred	Frederick Braun was listed as a local fossil collector by Nickles (1936), and a collection of his fossils went to Yale (Shideler [1952] 2002). Braun sold fossils as "Fred Braun and Co." and "the Western Naturalist's Agency" (Caster 1982,

25), and, in conjunction with Paul Mohr, another Cincinnati collector, undertook long-term and extensive excavations for crinoids from Carboniferous rocks at Crawfordsville, Indiana (Van Sant and Lane 1964).

Bridge, Josiah (1890-1953)

Dr. Bridge was born in Norwood, Ohio, adjacent to Cincinnati, and he received his bachelor's degree from the University of Cincinnati in 1913. His higher education was elsewhere, and professionally he was associated with the United States (Geological Survey and the United States National Museum in Washington, D.C. He was a long-time associate of Ulrich (Becker 1938; Croneis 1963).

Byrnes, Richard M. (1835-1892)

Dr. Richard Mahan Byrnes was a founding member of the Cincinnati Society of Natural History, and he served as its curator of mineralogy from 1871 until 1880, when he was thrice elected president and, thus, served three years in that position. He was a member of the society's Committee on Geological Nomenclature (S. A. Miller et al. 1879) and was a co-author of the eulogy of C. B. Dyer. He was listed as a local fossil collector by Nickles (1936), and he had a large collection of fossils, but was interested in minerals, in terrestrial and freshwater molluscs, in plants, and much more (Anon. 1876,1878,1892; Byrnes, Cotton, and Langdon 1883; Johnson 2002).

Carley, S. T.

S. T. Carley, of Bantam, Clermont County, Ohio, was an active member of the Western Academy of Natural Sciences, beginning in the 1830s, and he was one of the seven surviving members-of the academy when its assets were donated to the Cincinnati Society of Natural History in 1871 and the academy ceased to exist. In about 1846 David Dale Owen enlisted the help of the academy to improve the taxonomic nomenclature of the region's fossils; Carley and U. P. James "were appointed a committee to prepare a report on the naming of the ***Strophomena*** of the Cincinnati blue limestone. In this they said that they had 'carefully examined and compared a great number of specimens' and were 'satisfied that, by far, too many species have been made,' thus affirming Owen's contention." "This report was published in the ***Cincinnati Gazette,*** September 5, 1846" (Hendrickson 1947, 143). In 1849 there was published a catalogue of freshwater mussels, as recognized by the academy; the pamphlet was published anonymously, but according to Hendrickson (1947), it was largely the work of Carley, John Gould Anthony, U. P. James, and Joseph Clark (but see Johnson 2002).

Carley was one of the collectors whose specimens were used in the original description of the species of trace fossils, ***Licrophycus flabellum*** S. A. Miller and Dyer, 1878a. The well-known species of articulate brachiopods, ***Retrorsirostra carleyi,*** was named after S. T. Carley (Anon. 1878; Hendrickson 1947).

Christy, David

David Christy was a Cincinnati-area geologist, anti-slavery writer, printer, and newspaperman. His geological letters were published in 1848, originally in a newspaper, the *Cincinnati Gazette,* but then separately. In around 1858 his collection was sold to Miami University, Oxford, Ohio, for $2,200 (Becker 1938) or, according to Shideler ([1952] 2002, 2), for $5000, "an almost unheard of sum for such a purpose, in those days." The same collection must have been a financial benefit to at least one other party, too; again according to Shideler ([1952] 2002,4): "I have mentioned the Christy collection, acquired by Miami University. Some years ago when the University of Chicago was cleaning house we were given some of their unwanted material. Included were fossils distinctly marked 'Christy Collection.' The Christy collection had disappeared from Miami when that institution was closed between 1873 and 1885. Chicago had bought the collection from James Hall who operated out of Albany, N.Y. Just who swiped the collection and sold it to Hall hasn't been determined. Other material from the Christy collection has come back in similar ways" (Becker 1938; Christy 1848; Merrill [1924] 1964; Shideler [1952] 2002).

The Cincinnati Museum of Natural History

(See The Cincinnati Society of Natural History)

The Cincinnati Normal School

"Normal schools" were institutions that trained teachers and would-be teachers. The Cincinnati Normal School was established by the Cincinnati Board of Education in 1868 and housed in one of its school buildings; it was suspended shortly after the start of the twentieth century. John Mickleborough ***(q.v.)*** was principal of the Cincinnati Normal School for seven years, from 1878 until 1885 (Lathrop 1900,1902).

The Cincinnati Society for the Promotion of Useful Knowledge

(See Anthony, John Gould; The Western Academy of Natural Sciences)

The Cincinnati Society of Natural History

The Cincinnati Society of Natural History was founded in 1870 (Anon. 1878, 1902). In 1871 the remaining members of the Western Academy of Natural Sciences donated all the assets of the academy, including money, books, and their collection, to the Cincinnati Society of Natural History. Initially, the society rented rooms in the building of the Cincinnati College. In 1877 the society, using part of a bequest received from member Charles Bodman, acquired its own building at the southeast corner of Arch and Broadway. In 1934 the society moved to new premises in the building of the Ohio Mechanics Institute on Central Parkway, and in 1957 relocated to its own building on Gilbert Avenue, in the southwest corner of Eden Park (Anon. 1978). At the same time, the name of the organization was changed to the Cincinnati Museum of Natural History and, with the addition of a planetarium, the Cincinnati Museum of Natural History and Planetarium. With the abandonment of the Gilbert Avenue facilities and absorption into the Cincinnati Museum Center at Union Terminal in the 1990s, what was originally the Cincinnati Society of Natural History ceased to exist as a separate entity.

Cook, W. E.

Listed as a local fossil collector by Nickles (1936).

Cooper, Edward M.

Elected a member of the Cincinnati Society of Natural History in 1878 and served as curator of paleontology of the society (Anon. 1879,1885a).

Dalve, Elizabeth A.

Elizabeth A. Dalve, known to her friends as Bettina, was an illustrator and part-time museum assistant in the Department of Geology at the University of Cincinnati. She prepared a list of the stratigraphic occurrences of the fossils in the type-Cincinnatian (Brandt and Davis 2007; Dalve 1948,1951).

Deiss, Charles Frederick (1903-1959)

Deiss was born in Covington, Kentucky, and graduated from Miami University, Oxford, Ohio, where he was a student of Shideler. He was the head of the Indiana Geological Survey from 1945 until the time of his death (Becker 1938; Croneis 1963).

Dickhaut, Henry E.

Listed as a local fossil collector by Nickles (1936); he is presumably the same person as H. E. Dickhaut, listed by Ulrich (1879b, 30).

Dorfeuille, Joseph

The proprietor of the Western Museum from 1823 until sometime in the late 1830s (Drake and Mansfield 1827; Trollope 1832; Kellogg 1945).

Drake, Daniel (1785-1852)

Dr. Drake was the one of the most significant forces in the intellectual life of Cincinnati in the first half of the nineteenth century. He was the motivating force behind both the Western Museum and the Western Academy of Natural Sciences, and he was one of the "managers" of the Western Museum at the time of its founding (Caster 1982; Hendrickson 1947; Johnson 2002; S. A. Miller 1882a; [Silliman] 1819).

Dry Dredgers

The Dry Dredgers are a group of amateur fossil collectors founded in 1942 in the wake of a discussion and field trip series sponsored by the Depart-

	ment of Geology at the University of Cincinnati. They are still going strong (Brandt and Davis 2007; Dalve 1951).
Dyche, D. T. D.	(See chapter 2)
Dyer, Charles Brian (1806-1883)	(See chapter 2)
Embree, Jesse	One of the "managers" of the Western Museum at the time of its founding, about 1820 ([Silliman] 1819).
Faber, Charles (died 1930)	(See chapter 2)
Fales, J. C.	Professor J. C. Kales, of Centre College. Danville, Kentucky, was the person who provided the specimens on which *Monticulipora falesi* U. P. James, 1884 was based and after whom the species was named (U. P. James 1884b).
Fenton, Carroll Lane	Was the first Faber Curator in the Department of Geology at the University of Cincinnati (Caster 1982).
Findlay, James	One of the "managers" of the Western Museum at the time of its founding ([Silliman] 1819).
Foerste, August F. (1862-1936)	August Frederick Foerste was a long-time high school teacher in Dayton, Ohio. He was one of foremost workers on fossil nautiloid cephalopods. In addition, he worked extensively on the fossils and stratigraphy of the type-Cincinnatian. His collection went to the U.S. National Museum in Washington, D.C. It was Foerste who named the species of trilobite now known as *Flexicalymene meeki*. There is extensive biographical material on Foerste available (Bassler 1937, 1947; Becker 1938; Brandt and Davis 2007; Caster 1951,1981,1982; Holland 2000; Sandy 1994; Shideler [1952] 2002).
Foster, W. B.	Donated a "valuable collection of fossils and minerals" to the Cincinnati Society of Natural History in September of 1878. In about 1869 Schuchert's father took the young lad to visit". . . William Foster's geological museum which opened to me an unknown world" (Schuchert, quoted by Becker 1938,193); this could have been W. B. Foster (Anon. 1879; Becker 1938).

Franks' Museum

Toward the end of its existence, the Western Museum in Cincinnati was best known as a chamber of horrors; in that business it had a rival in the form of Franks' Museum (Tucker 1965, 32).

Fulton, Robert

Lawyer; listed as a local collector by Shideler ([1952] 2002).

Gault, Wm.

Listed as a local fossil collector by Nickles (1936).

Graham, George

(1798-1881)

George Graham was one of the original members of the Western Academy of Natural Sciences in 1835, and he was one of the seven surviving members of the academy when its assets were donated to the Cincinnati Society of Natural History in 1871. His collection of fossils, shells, and plants, unfortunately, was destroyed in a fire (Anon. 1878; Hendrickson 1947; James, Howe, and Norton 1881).

Grinnell, George Bird

Author of the species *Nereidavus varians* Grinnell, 1877, which was based on scolecodonts; Albert Gallatin Wetherby had sent Grinnell specimens of these jaws of annelid worms from the type-Cincinnatian (Knell, pers. comm.).

Haime, Jules

Henri Milne-Edwards and Jules Haime described the type-Cincinnatian bryozoans now known as *Parvohallopora rugosa* and *Dekayia aspera* (Cuffey, Davis, and Utgaard 2002).

Haines, M. P.

Mrs. M. P. Haines, of Richmond, Indiana, collected one of the specimens of the species of starfish, *Palaeasterina approximate* S. A. Miller and Dyer, 1878a.

Hall, J. H.

Listed as curator of paleontology of the Cincinnati Society of Natural History (Anon. 1876); almost certainly the same person as John W. Hall, Jr., listed below.

Hall, James

James Hall proposed the resolution for the establishment of the Western Academy of Natural Sciences on April 25, 1835 (Hendrickson 1947, 140). This is almost certainly not the same person as the James Hall (1811-1898) who was one of the most eminent paleontologists of the United States in the nineteenth century. The latter hailed from New York, but did paleontological work all over the country, including the Cincinnati region, and he had connections with various members of the Cincinnati School (Hall 1845,1861,1872a, 1872b, 1883a, 1883b; Hall and Whitfield 1875). Biographical information about James Hall of New York is voluminous and far flung (Becker 1938; Caster 1951, 1982, 1985; Croneis 1963; Merrill [1924] 1964; Sherborn 1940; Shideler [1952] 2002).

Hall, John W., Jr.

J. W. Hall, Jr., is listed as curator of paleontology of the Cincinnati Society of Natural History from 1874 to 1877, and as corresponding secretary of the society in 1877 and 1878 (Anon. 1878). Later that year, he donated some fossils to the society (Anon. 1879). He also served the society as curator of mineralogy (Anon. 1885b). He co-authored a paper with a number of members of the Cincinnati School and other local fossil collectors (S. A. Miller et al. 1879). J. W. Hall, of Covington, is listed as a local fossil collector by Nickles (1936).

Hammond, W. E.

Of Madison, so listed as a local fossil collector by Nickles (1936).

Harper, George W. (1832-1918)

(See chapter 2)

Harris, I. H.

The collection of I. H. Harris, of Waynesville, Ohio, provided specimens upon which a number of species originally were based, including some named after him (S. A. Miller 1878,1880,1881,1882b, 1882d, 1883b, 1884. At least part of his collection ended up in the National Museum of Natural History, in Washington, D.C. (Sandy 1996; Shideler [1952] 2002). The "I. M. Harris" listed as a local fossil collector by Nickles (1936) is probably the same person as "I. H. Harris," as is the "I. Harris" of Becker (1938).

Harvey, J. W.

J. W. Harvey bought the type-specimen of the starfish, *Palaeasterina speciosa* S. A. Miller and Dyer, 1878 from W. C. Barnhart and, in turn, sold it to C. B. Dyer (Miller and Dyer 1878a).

Hayden, F. V.

Ferdinand Vandeveer Hayden is most famous for his having been the leader of the United States Geological and Geographical Survey of the Territories, one of the great surveys of the American West, which employed Lesquereux (q.v.), among many other notable geologists of the day. In 1879 the Hayden Survey was one of three federal surveys consolidated to become the then-new United States Geological Survey. Meek and Worthen, along with F. B. Meek ***(q.v.),*** proposed the use of the term "Cincinnati Group" for the body of rocks in the Cincinnati region that hitherto had been referred to as the "Hudson River Group"; they thus proposed the concept of the Cincinnatian (Bartlett 1962; Merrill [1924] 1964; Meek and Worthen 1865a; Wilmarth 1925).

Herrlinger, Andrew

"Andrew Herrlinger, later an attorney in Cincinnati" is listed as a local fossil collector by Nickles (1936).

Herzer, Henry

It was Reverend Herzer who introduced E. O. Ulrich, then seven years old, to the wonders of fossil collecting (Croneis 1963; Ulrich 1891).

Hill, H. H.

Dr. Hill was associated with the Cincinnati Society of Natural History in the 1870s, including various terms as curator of archaeology, curator of conchology, and librarian (Anon. 1876, 1878). He also is listed as a local fossil collector by Nickles (1936).

Holbrook, R. H.

Professor R. H. Holbrook, of the National Normal University, Lebanon, Warren County, Ohio, lent the material upon which ***Stromatopora subcylindrica*** originally was based (U. P. James 1884a).

Hosea, L. M.

L. M. Hosea was co-proprietor and co-editor of the ***Cincinnati Quarterly Journal of Science,*** along with S. A. Miller, during its second year of publication, 1875, according to the covers of the journal.

Howe, A. J.

Curator of comparative anatomy in the Cincinnati Society of Natural History (Anon. 1876).

Hunter, W. H. H.

Dr. Hunter collected one of the specimens on which the species ***Conularia formosa*** was based (Miller and Dyer 1878a).

Huxley, T. H.

Thomas Henry Huxley was one of the foremost naturalists in Great Britain during the second half of the nineteenth century, and he was a vigorous proponent of the idea of organic evolution. Huxley visited Cincinnati on at least two occasions, but he only stayed overnight each time, and he did not give any speeches nor make any field trips (Kritsky, pers. comm.).

James, Joseph Francis (1857-1897)

(See chapter 2)

James, Uriah Pierson (1811-1889)

(See chapter 2)

Kemper, Willis	Lawyer; listed as a local collector by Shideler ([1952] 2002).
Lathrop, J. P.	Donated a collection of fossils to the Cincinnati Society of Natural History (Anon. 1882).
Lesquereux, Leo (1806-1889)	(Charles) Leo Lesquereux was born in Switzerland in 1806 but moved to the United States in 1848. He became, perhaps, the foremost paleobotanist of his day in the United States. He worked for a number of the state geological surveys, including the Illinois survey of A. H. Worthen *(q.v.),* and also worked for the great survey of the American West headed by F. V. Hayden *(q.v.).* Lesquereux authored two papers on what were then considered to be land plants in the rocks of the type-Cincinnatian. He died in 1889, and Edward Orton *(q.v.)* was one of his pallbearers (Bartlett 1962; Merrill [1924] 1964; Lesquereux 1874,1878, 2006; Tritt 2006).
Letton's Museum	Messrs. Letton and Willet founded a museum in Cincinnati in 1818—just about the same time that the Western Museum was initiated by Dr. Daniel Drake and his colleagues. In 1826 Ralph Letton was the proprietor, and the museum occupied two storeys of a building at the corner of Main and Fourth Streets. Exhibited there were birds, mammals, minerals, shells, fossils (including fifty mammoth bones), antiquities, and, as was common in those days, wax figures. (Drake and Mansfield 1827).
Lindahl, Josua (1844-1912)	Dr. (Johan Harald) Josua Lindahl was born and educated in Sweden. He was curator of the Illinois State Museum of Natural History and state geologist of Illinois, and then was director of the Cincinnati Society of Natural History, 1895-1906 (Anon. 1912; Lindahl 1906; Ulrich 1891).
Locke, John (1792-1856)	Dr. Locke was a chemist, educator, geologist, paleontologist, inventor of scientific instruments, and more; for example, he was one of the earliest photographers in Cincinnati (Gagel 1998). As an assistant geologist in the Mather Survey, the first geological survey of Ohio, he was the author of the 1838 report on the geology of southwestern Ohio (Locke 1838). He has been credited as the first local amateur to become a professional geologist, and he was the first person to recognize what is now called the Cincinnati Arch. He was one of the hosts when Charles Lyell, probably the foremost geologist on Earth, visited the Cincinnati area (Lyell 1845). The majority of Dr. Locke's paleontological contributions dealt with local trilobites. Biographical materials on Dr. Locke are voluminous and far flung (Bartky 2000; Becker 1938; Brandt and Davis 2007; Dexter 1979; Drake and Mansfield 1827; Hansen and Collins 1979; Hendrickson 1947; Merrill [1924] 1964; S. A. Miller 1882a; Shotwell 1902; Trollope 1832; Winchell 1894).

Lyell, Charles

The Englishman, Charles Lyell, was one of the founders of the science of geology as we know it today. In 1842 he accepted an invitation from the Western Academy of Natural Sciences to come to Cincinnati. His hosts were John Locke, Robert Buchanan, J. G. Anthony, and Joseph Clark, and they visited localities in the area, including Big Bone Lick, Kentucky, world famous for its remains of Ice Age mammals (Hendrickson 1947; Lyell 1845).

Lyon, Sidney S. (1808-1872)

Sidney Smith Lyon was born in Cincinnati. He was one of the assistant geologists in the geological survey of Kentucky by David Dale Owen *(q.v.)*, and he authored or co-authored a number of scientific papers of fossil echinoderms of Indiana, Kentucky, and Ohio (S. A. Miller 1882a).

Mather, William W. (1804-1859)

W. W. Mather was chief geologist of the first geological survey of Ohio (1836-1838). Assistant geologists included John Locke and Charles Whittlesey (Merrill [1924] 1964; S. A. Miller 1882a).

McCord, D. A.

Of Oxford, so listed as a local fossil collector by Nickles (1936).

Meek, F. B. (1817-1876)

Fielding Bradford Meek, although born in Madison, Indiana, was mostly associated with the Smithsonian Institution in Washington, D.C. He is well known for his involvement with the great geological surveys of the American West (Bartlett 1962), and he authored many paleontological contributions. Of most interest to readers of this volume is the fact that he was the author of the 1873 Ohio Geological Survey report on fossils of the type-Cincinnatian (Meek 1873), and a collection of his Ohio specimens went to Columbia University (Sherborn 1940). Moreover, Meek and Worthen (1865a) proposed the use of the term "Cincinnati Group" for the body of rocks in the Cincinnati region that hitherto had been referred to the "Hudson River Group"; they thus proposed the concept of the Cincinnatian. Biographical materials on F. B. Meek are extensive (Becker 1938; Brandt and Davis 2007; Caster 1981,1982; Croneis 1963; Merrill [1924] 1964; S. A. Miller 1882a; White 1877,1896,1902).

Mickleborough, John

(See chapter 2)

Miller, C. A.

Dr. Miller collected one of the specimens on which the species *Conularia formosa* was based (Miller and Dyer 1878a). The local trilobite, *Ceraurus milleranus,* was named after him (S. A. Miller and Gurley 1893). Dr. Miller also was the author of a short paper on present-day unionid clams (C. A. Miller 1874; Johnson 2002).

Miller, Samuel Almond (1837-1897)	(See chapter 2)
Milne-Edwards, Henri	Henri Milne-Edwards and Jules Haime described the Cincinnatian bryozoans now known as ***Parvohallopora rugosa*** and ***Dekayia aspera*** (Cuffey, Davis, and Utgaard 2002).
Misener, John	Listed as a collector of fossils at Richmond, Indiana, by Foerste (1917), who named ***Conchopeltis miseneri*** and ***Conularia miseneri*** after him.
Misener, S. R.	Of Richmond, Indiana, so listed as a local fossil collector by Nickles (1936).
Mohr, Paul	Mohr was associated with the Cincinnati Society of Natural History in the 1870s (S. A. Miller et al. 1879), and the cephalopod ***Orthoceras mohri*** was named after him (S. A. Miller 1875b). Mohr also was involved with Frederick Braun, another Cincinnati collector, in excavations for crinoids from Carboniferous rocks at Crawfordsville, Indiana (Van Sant and Lane 1964).
Moore, Richard B. (1815-1885)	Listed as a local fossil collector by Nickles (1936). He was an original member of the Cincinnati Society of Natural History, custodian 1873-1877, trustee 1876-1878, and president 1877-1878 (Anon. 1876, 1878; Cotton, Byrnes, and Heighway 1885).
Newberry, J. S. (1822-1892)	John Strong Newberry was born in Connecticut, but moved to Ohio at the age of two; he received his medical degree in the Cleveland area in 1848. His connection to the type-Cincinnatian lies in the fact that he headed the Second Geological Survey of Ohio (1869-1878); he employed F. B. Meek ***(q.v.),*** and the Ohio Survey published one of the important contributions to the paleontology of the type-Cincinnatian (Meek 1873). Newberry's 1874 paper, "On the So-called Land Plants from the Lower Silurian of Ohio," was republished the same year, but without the figures, in the ***Cincinnati Quarterly Journal of Science,*** which was, of course, edited by S. A. Miller (Meek 1873; Merrill [1924] 1964; Newberry 1874).
Newton, A. J.	Dr. Newton, of Richmond, Indiana, collected one of the specimens of ***Enoploura*** described by Wetherby (1879a).
Nicholson, H. Alleyn (1844-1899)	Although he did study Cincinnatian bryozoans in the 1870s and 1880s, Nicholson, a professor at the University of Aberdeen, Scotland, was not a member

of the Cincinnati School. It was Nicholson who introduced the study of thin-sections to the study of bryozoans (Cuffey, Davis, and Utgaard 2002). The name *Ceramopora nicholsoni* was proposed for a species of bryozoan by U. P. James (1875).

Nickles, John M. (1859-1945)

(See chapter 2)

Normal School

(See Cincinnati Normal School)

Oeh, George

George Oeh had a collection of fossils that included many fine Cincinnati crinoids, and *Heterocrinus (locrinus) oehanus* was named after him (Ulrich 1882).

O'Neall, J. Kelly

O'Neall was a fossil collector from Lebanon, Ohio; the trilobite, *Acidaspis onealli,* was named after him (S. A. Miller 1875a). The species of bryozoan now called *Parvohallopora onealli* was named by U. P. James, who spelt O'Neall's middle name "Kelley" (U. P. James 1875).

d'Orbigny, Alcide

The French paleontologist, Alcide d'Orbigny, described the Cincinnatian bryozoans *Monticulipora mammulata, Parvohallopora ramosa,* and *Heterotrypa frondosa* (Cuffey, Davis, and Utgaard 2002; d'Orbigny 1850).

Orton, Edward (1829-1899)

Edward Orton was born in Delaware County, New York, and his initial education was in that state. He also went to seminary, including a stint at the Lane Theological Seminary in Cincinnati, and he was ordained as a Presbyterian minister. Somewhat later, he became professor of natural science at Antioch College, and then its president. In 1873, he was appointed president of a new institution, the Ohio Agricultural and Mechanical College, and also professor of geology there; under his leadership, the college prospered and was renamed to become The Ohio State University. In 1869, Orton was one of two principal assistants to John Strong Newberry and the Second Geological Survey of Ohio. In 1882, he succeeded Newberry as state geologist of Ohio, and, as such, he gave employment to Ulrich and to Foerste. Orton became a nationally recognized scientific figure, and, in 1897, he was elected president of the Geological Society of America (Croneis 1963; Hansen and Collins 1979; Merrill [1924] 1964).

Orton, Edward, Jr.

Edward Orton, Jr., was appointed state geologist of Ohio upon the death of his father in 1899 and served in that position until his resignation in 1906 (Hansen and Collins 1979).

Owen, David Dale (1807-1860)	David Dale Owen, although not a member of the Cincinnati School, did much work in the region, and, indeed, in much of the American Midwest. He had connections with the Western Academy of Natural Sciences, and the Cincinnatian bryozoan, ***Fistulipora oweni,*** was named after him (Becker 1938; Croneis 1963; Hendrickson 1947; U. P. James 1879c, 1884a; Merrill [1924] 1964; S. A. Miller 1882a).
Patterson, W. J.	William J. Patterson was listed as a local fossil collector by Wetherby (1879a) and by Nickles (1936). The Cincinnatian crinoid, ***Glyptocrinus pattersoni,*** was named after him (S. A. Miller 1882b).
Plummer, John T.	Dr. Plummer was the author of an early paper on the geology of the area about Richmond, Indiana, in which fossils are discussed and illustrated (Plummer 1843).
Probasco, Henry (1820-1902)	Henry Probasco was in the hardware business in Cincinnati. He was an original member of the Cincinnati Society of Natural History, and his collection of fossils came to the University of Cincinnati. It was he who commissioned the Tyler Davidson Fountain, which gives the name to Fountain Square in downtown Cincinnati. In around 1875 Probasco apparently proposed the establishment of a "Cincinnati Museum of Science and Art" along the lines of the British Museum (Anon. 1875,1878; Caster 1951,1982; Cincinnati Society of Natural History; Writers' Program of the Work Projects Administration in the State of Ohio 1943).
Rafinesque, C. S. (1783-1840)	Constantine Samuel Rafinesque-Schmaltz is best known to fossil collectors because of the common Cincinnatian brachiopod, ***Rafinesquina*** Hall and Clarke, 1892. Rafinesque was born in Turkey, in what was then Constantinople, but he traveled widely, including the United States, where he eventually settled. Rafinesque taught for a time at Transylvania College in Lexington, Kentucky, and he gave public lectures at the Cincinnati museum of Joseph Dorfeuille ((/.v.). He seems to have been primarily a botanist, but his interests were very far reaching, and he named many genera and species in a multitude of different taxonomic groups. He was a prolific author, but many of his works were in obscure publications or even self-published, and many are quite rare. This may be part of the reason that his scientific work is not highly regarded today. There is extensive biographical material on Rafinesque available (Caster 1982; Johnson 2002; Merrill [1924] 1964; S. A. Miller 1882a; Rafinesque 1836).
Reinhardt, E.	E. Reinhardt collected the type-specimen of the crinoid species ***Glyptocrinus angularis*** S. A. Miller and Dyer, 1878a.

Richardson, J. M.

J. M. Richardson, of Wilmington, Clinton County, Ohio, found the original specimens of the crinoid species *Glyptocrinus richardsoni* Wetherby, 1880.

Riddell, John L.

Dr. Riddell, a famous botanist, was part of the faculty of the Medical Department of Cincinnati College, a short-lived medical college founded by Daniel Drake (Writers' Program of the Work Projects Administration in the State of Ohio 1943). About the same time, Dr. Riddell was a curator of the Western Academy of Natural Sciences, beginning in April of 1835 (Hendrickson 1947).

Roeminger, Carl

Carl Ludwig Roeminger was born in Germany and earned a medical degree (but with a geological thesis!) at Tubingen. At the time of the 1848 revolutions, he moved to Cincinnati, which, at that time, had a large German-speaking population, and he practiced medicine there for some twenty-five years. He studied what are now known to be fossil bryozoans—as spare time from his medical duties would allow. It was he who named *Rhombotrypa quadrata* (Roeminger, 1866). About that same time, he moved to Michigan, where he simultaneously conducted a medical practice, was a professor of geology at the University of Michigan, and was Michigan's state geologist. Roeminger's name appears both with and without the umlaut over the "o" or the "e" after the "o" (Cuffey, Davis, and Utgaard 2002; Merrill [1924] 1964).

Schlemmer, Charh (died 1933)

A plumber by trade, Charles Schlemmer was an associate of E. O. Ulrich and Charles Schuchert in their early collecting days. Schlemmer's interest in fossils is said to have been awakened largely by Charles Faber, as was that of Ashermann, Twitchell, Vaupel, and others (Shideler [1952] 2002).

Schuchert, Charle (1858-1942)

(See chapter 2)

Scott, William Berryman (1858-1947)

Scott, who became an eminent vertebrate paleontologist, was born in Cincinnati on Feb. 12,1858. In around 1861 his family departed Cincinnati for good and moved to Chicago, and then to Princeton, New Jersey. Scott's birthplace probably had little or nothing to do with his paleontologic career (Croneis 1963; Simpson 1984).

Scoville, S. S.

Dr. Scoville collected near Lebanon, Ohio; *Orthis scovillei* was named after him (S. A. Miller 1882c).

Shaler, Nathaniel Southgate (1841-1906)

Shaler was born and reared in northern Kentucky. He studied under Louis Agassiz and spent the bulk of his career at Harvard University. Shaler must have been an extraordinary individual; for example, from 1874 to 1880, he taught at Harvard, was state geologist of Kentucky, and was president of a mining company in Montana, all at the same time. In the upper echelon of his profession, he served as president of the Geological Society of America in 1895 and was a member of the National Academy of Sciences, but he also was a contributor to the *Atlantic Monthly* and to *Scrihner's* magazine and wrote five romantic dramas in blank verse. Although Shaler did author a paper that involved brachiopods of the Cincinnati region, he was not really a member of the Cincinnati School (Becker 1938; Caster 1951,1982; Croneis 1963; Hobbs 1907; Livingstone 1987; Shaler 1876; Shideler [1952] 2002).

Shideler, W. H. (1886-1958)

William Henry Shideler was born in West Middletown, Ohio, and graduated in 1907 from Miami University, Oxford, Ohio. Immediately upon receipt of his doctorate at Cornell University in 1910, he returned to his alma mater, where he spent the rest of his life on the faculty. He was recognized as an exceptional teacher, and, even though his publication record was not extensive (Shideler 1914,1916,1918,1939), his knowledge of the local rocks and fossils was extraordinary, and his influence on cohorts of students and colleagues was profound. Although not really a member of the Cincinnati School, he did know some of them personally and even spent time in the field with at least Ulrich and Faber (Becker 1938; Caster 1951,1961a, 1985; Croneis 1963; Shideler [1952] 2002).

Stevens, W. J.

W. J. Stevens, of Lebanon, Ohio, collected the type-specimen of the starfish species *Palaeaster simplex* S. A. Miller and Dyer, 1878a.

Trollope, Frances

The mother of British novelist Anthony Trollope. During her stay in Cincinnati, she had some association with the Western Museum and with Joseph Dorfeuille. Her reference to a "Dr. Lock" apparently was to John Locke (Trollope 1832).

Twenhofel, William Henry (1875-1957)

Twenhofel was born near Covington, Kentucky, just across the Ohio River from Cincinnati, and reared in the area. He taught in Kentucky public schools for six years and earned a bachelor's degree from the National Normal University in Lebanon, Ohio, in 1904. His geological training was at Yale University, where Schuchert taught. *The* bulk of Twenhofel's career was spent at the University of Wisconsin. He served as president of the Paleontological Society in 1931, but he is best remembered as one of the founders of the field of sedimentology (Becker 1938; Croneis 1963; Dott 2000).

Twitchell, George B. (died 1933)

George Twitchell was a physician and amateur fossil collector whose interest in fossils is said to have been awakened largely by Charles Faber, as was that of Ashermann, Schlemmer, Vaupel, and others. He was elected to membership in the Cincinnati Society of Natural History in 1885. His large collection of type-Cincinnatian bryozoans, including thin-sections, was bequeathed to the University of Cincinnati. He served as curator of microscopy at the society and authored several scientific papers, although not on fossils (Anon. 1885a; Caster 1982; Shideler [1952] 2002; Twitchell 1885,1887,1934).

Ulrich, E. O. (1857-1944)

(See chapter 2)

Vallandigham, George L.

George Vallandigham, of Cincinnati, was an active collector after whom ***Cyrtoceras vallandighami*** S. A. Miller, 1874 was named. He also collected one of the specimens on which the genus of carpoid echinoderms, ***Enoploura,*** was based (Wetherby 1879a). This is certainly the George L. Vallandingham listed as a local fossil collector by Nickles (1936).

Van Cleve, J. W.

Described the first-named type-Cincinnatian bryozoan, ***Constellaria constellata,*** which was published formally by Dana (1846, 1849), Van Cleve having died (Cuffey, Davis, and Utgaard 2002).

Vaupel, Ernst H. (died 1942)

Ernst Vaupel was a childhood friend of Charles Schuchert and of John M. Nickles. In 1885 Vaupel, along with Schuchert and Charles Faber, was proposed for membership in the Cincinnati Society of Natural History. A shirt maker by profession, Vaupel accumulated a large collection of local fossils and donated it to Yale University, where Schuchert taught; he then amassed a second collection and gave it to the University of Cincinnati (Anon. 1885a; Caster 1981,1982; Nickles 1936; Shideler [1952] 2002; Wetherby 1881).

Warder, John Aston (1812-1883)

John Warder is recorded as having given some fossils to the Western Academy of Natural Sciences on May 1, 1838, and he authored a paper on trilobites (although not type-Cincinnatian) published the same year. He was president of the Cincinnati Society of Natural History from its founding in 1870 until April 1875 (Moore, Heighway, and Howe 1883; Hendrickson 1947).

Weichold, Charles

One of the original members of the Dry Dredgers in 1942 (Felton, pers. comm.). Kenneth Caster used to refer to certain ring-shaped bryozoan colonies in the type-Cincinnatian as "Weichold Rings" or "Weichold Doughnuts," after Charles Weichold.

Welch, L. B.	Dr. Welch practiced medicine in Wilmington, Clinton County, Ohio. The original specimens of *Glyptocrinus richardsoni* Wetherby, 1880, were in Welch's collection (Wetherby 1880, 246; Foerste 1893a, 1893b).
Wessels, Charles	Charles Wessels found the specimen of *Lepidocoleus jamesi* described by Faber, when he named the genus *Lepidocoleus* (Faber 1886,17).
The Western Academy of Natural Sciences (1835-1871)	The Western Academy of Natural Sciences was founded by Dr. Daniel Drake in 1835. In 1840 the Natural Science Section of the Cincinnati Society for the Promotion of Useful Knowledge, of which John Gould Anthony was secretary, merged with the academy. In 1871 the remaining members of the Western Academy of Natural Sciences donated all the assets of the academy, including money, books, and their collection, to the Cincinnati Society of Natural History, which had been founded the previous year (Anon. 1878,5; Hendrickson 1947).
The Western Museum (1820-1867)	A society was formed in 1819 or shortly before by a group, including Daniel Drake ***(q.v.),*** to establish a museum in Cincinnati. The Western Museum opened on June 10,1820, with Dr. Robert Best as the principal curator. John James Audubon was an early employee. In 1823 the Western Museum Society transferred ownership to Joseph Dorfeuille ***(q.v.).*** In 1839 he sold the museum and most of its exhibits and collections to a local group and took the rest with him to New York and opened a new establishment. In 1867 the exhibits and collections in Cincinnati were put up for public auction; their whereabouts are unknown today. (Contrary to the typographic error in Caster [1982, 23], it was not the collections of the Western Museum, but, rather, those of the Western Academy of Natural Sciences that were taken over by the Cincinnati Society of Natural History in 1871.) (Anon. 1878, 5; Drake and Mansfield 1827,44-46; Hart-Davis 2004, 39; Johnson 2002; Kellogg 1945; [Silliman] 1819; Tucker 1965,1967).
Wetherby, Albert Gallatin (1833-1902)	(See chapter 2)
Whitfield, R. P.	R. P. Whitfield served as a paleontologist with a number of the federal and state geological surveys in the second half of the nineteenth century, commonly associated with James Hall. With respect to the type-Cincinnatian, he was one of the assistants to the Ohio Geological Survey during the Newberry years and extending on into the Edward Orton years, and some of his work even was published in the *Journal of the Cincinnati Society of Natural History,* including descriptions of fossil pelecypods obtained from John Mickleborough (Hall and Whitfield 1875; Hansen and Collins 1979;

Merrill [1924] 1964; Whitfield 1878). The "R. P. Whitefield" in Nickles (1936) must be the same person.

Whittlesey, Charles

Although primarily associated with the Cleveland area, Colonel Whittlesey made an agricultural survey of Hamilton County, Ohio, in 1844. Prior to that, he had been in charge of the topographic work for W. W. Mather's 1836-1838 geological survey of Ohio. Later he was party to an apparently vicious dispute as to whether Newberry or Whittlesey should have become state geologist of Ohio in 1869; Newberry was so appointed (Hansen and Collins 1979; Merrill [1924] 1964).

Willet

(See Letton's Museum)

Wilson, Wm. W.

Judge William Wilson, of Lebanon, Warren County, Ohio, found the type-specimen of *Prioniodus dychei* U. P. James, 1884, and the three specimens on which *Polygnathus wilsoni* U. P. James, 1884 was based. He, Dyche, and James were friends (U. P. James 1884c, 147-148).

Worthen, A. H.

Amos Henry Worthen was born in Vermont in 1813, but, beginning in 1834, taught school in Cumminsville, Ohio, now part of Cincinnati. He moved to Warsaw, Illinois, in 1836, and devoted himself to business ventures for a living and rocks and fossils in his spare time. In 1855-1857 Worthen was assistant in James Hall's geological survey of Iowa and, in 1858, was appointed the state geologist of Illinois. In the latter post, he hired Meek and Ulrich to document the Paleozoic fossils of that state. Meek and Worthen (1865a) proposed the use of the term "Cincinnati Group" for the body of rocks in the Cincinnati region that hitherto had been referred to the "Hudson River Group"; they thus proposed the concept of the Cincinnatian (Croneis 1963; Meek and Worthen 1865; Merrill [1924] 1964; Wilmarth 1925).

GLOSSARY

How to pronounce scientific terms can be a real bugaboo. In the following glossary, and elsewhere in this volume, we have included occasional advice on how to pronounce terms. As you know, lexicographers have developed a scheme of symbols to indicate how they feel particular letters, syllables, and words should be pronounced. We have tried to keep the use of such symbols to a minimum. We hope that, in so doing, we still have managed to help you pronounce words in a way useful to you.

Unfortunately, not all scientific terms are included in dictionaries, not even in the premier dictionary of the English language, ***The Oxford English Dictionary*** (Simpson and Weiner 1989). The names of genera and species are very rarely included, except in some specialized works. One that we have found helpful is ***The Biologist's Handbook of Pronunciations*** (Jaeger 1960), and there other similar works. Alas! Space here does not permit us to list all such works, but the friendly professional librarians at the library of your choice can be of tremendous help here.

symbols

abbreviation	meaning
adj.	adjective
cf.	compare (Latin, "*confer*")—used to direct reader to terms related to the entry
ĭ	the standard "short i" of dictionaries, like the "i" in "tip"
n.	noun
ō	the standard "long o" of dictionaries, like the "o" in "toe"
pl.	plural
q.v.	which see (Latin, "*quod vide*")
see	there is another, preferred term for the same concept as the entry
sing.	singular
syn.	synonym

A

absolute age (n.) geologic age in years, usually determined by radiometric dating.

acritarch (n.) microfossil of organic composition representing unknown but possibly algal, single-celled organism, particularly abundant in Paleozoic marine rocks.

adapertural (adj.) in cephalopods, the direction toward the opening of the shell (and, hence, away from the apex of the shell); some workers prefer to use the synonymous term "adoral" ***(cf.:*** adapical).

adapical (adj.) in cephalopods, the direction toward the apex of the shell (and, hence, away from the opening of the shell) ***(cf.:*** adapertural).

adductor muscle (n.) one of the muscles of a brachiopod or a pelecypod whereby the animal closes its shell ***(cf:*** diductor muscle; adjustor muscle).

adjustor muscle (n.) one of the muscles of a brachiopod whereby the animal moves its shell with respect to the pedicle ***(cf:*** adductor muscle; diductor muscle).

adoral (adj.) adapertural *(q.v.)*.

aegism (n.) "Associations for protection, either through camouflage of surrounding vegetation, residence upon or within another animal, or even transport within the protective umbrella or aegis of a larger partner are very common in the animal kingdom." "... this term collects under its banner all those associations which are not principally concerned with food acquisition. .." (Morton 1989,10) ***(cf:*** commensalism; mutualism; parasitism).

age (n.) geologic time unit, equivalent to stage in the time-stratigraphic classification; the hierarchy of geologic time units, from largest to smallest is: eon, era, period, epoch, and age (cf.: eon, epoch, era, period).

aglaspids (n.) arthropods with a head shield and segmented body, possibly related to horseshoe crabs and eurypterids ("sea scorpions"), restricted to Cambrian and Ordovician.

anterior (adj., n.) on or toward the front of the animal. (Note that what is functionally anterior in a given animal may not correspond to the anatomical anterior. For example, in humans, the head is anatomically anterior, but, as you walk around, your head is at the top of your body and, hence, is functionally "dorsal"; ***cf:*** distal; dorsal; lateral; medial; posterior; proximal; ventral.)

Aplacophora (n.) a class of phylum Mollusca; present-day aplacophorans that lack hard parts (from the Greek "a" + "plax, plakos" + "phoreus," meaning "no plate bearer").

aragonitic (adj.) composed of the mineral aragonite ***(cf:*** calcareous, calcific).

autoecology (n.) ecology of a single species of organisms in a given time and place ***(cf.:*** synecology).

B

ball and pillow structure (n.) sedimentary structure characterized by ball- or pillow-shaped masses of sandstone or limestone, often embedded in matrix of a different lithology.

benthic, benthonic (adj.) living in, on, or associated with the bottom of a body of water ***(cf:*** nektonic; planktonic).

benthos (n.) collective term for benthic organisms.

bilaterally symmetrical (adj.) said of an animal in which the left and right sides of the animal are mirror images of one another; humans are bilaterally symmetrical ***(cf:*** plane of symmetry, symmetry).

binomen (see: species name).

bioclaustration (n.) the process whereby a soft-bodied organism that infests another organism or colony is embedded by the skeletal growth of that other organism or colony. The word was coined for instances in which a particular parasitic organism, suggested to be a hydroid or a colonial ascidiacian tunicate, was engulfed by the bryozoan colony on which it was growing; the result is a pattern of holes called ***Catellocaula vallata*** Palmer and Wilson, 1988.

biofacies (n.) characteristics of a sedimentary rock based on fossil content ***(cf.:*** facies, lithofacies).

bioherm (n.) a feature that is elevated above the sea floor and was produced by organisms (Davis 2004, 283); a fine, upstanding example is a coral reef, ***(cf.:*** biostrome).

bioimmuration (n.) usually an external mold of a soft-bodied organism that was overgrown by a calcareous organism, followed by decay of the soft-bodied organism.

biostratigraphic unit (n.) a body of rock characterized by fossils of a particular species or group of species; at a given locality, this is represented by the thickness of strata so characterized, (cf: biozone, lithostratigraphic unit, time-stratigraphic unit).

biostratigraphy (n.) study of distribution of fossils in sedimentary rocks.

biostrome (n.) sheet-like, non-mounded, accumulation of densely packed or intergrown calcareous organisms such as corals or bryozoans.

biotal succession (n.) the Principle of Biotal Succession was developed by the English geologist William Smith in the years shortly prior to 1800. He realized that, as one goes upward in the rock record, one suite of fossils is succeeded by another, which is, in turn, succeeded by a third, and so on, in a particular order. This principle is the basis for biostratigraphy and, hence, for relative dating of rocks by the use of fossils ***(cf:*** ecologic succession; fossil succession).

biozone (n.) a biostratigraphic unit characterized by fossils of a particular species or group of species; sometimes called a "fossil zone". Commonly the word "zone" is used for this concept, but, because that word is used in more than one sense in geology, it is preferable not to use the term "zone", except with a modifier to indicate which kind of zone is intended, (cf: epibole).

bivalved (adj.) said of a shell that consists of two similarly sized pieces, each of which is called a valve; brachiopods and pelecypods are bivalved ***(cf:*** univalved; pseudobivalved).

bivalve (n.) alternative name for a pelecypod.

body fossil (n.) one that involves the remains of an organism or replica of those remains ***(cf:*** trace fossil; ichnofossil; ***Lebensspur).***

C

calcareous (adj.) composed of calcium carbonate, whether the mineral calcite or the mineral aragonite, or both ***(cf:*** aragonitic; calcific),

calcite (n.) a calcium carbonate mineral

calcific (adj.) composed of the mineral calcite ***(cf:*** aragonitic, calcareous).

cast (n.) a replica of an organism made from a mold of that organism ***cf:*** mold).

Chaetognatha (n.) a small phylum of marine invertebrates living mostly as plankton, commonly called "arrow worms"; fossils are known from the Pennsylvanian, and possibly the Cambrian (Valentine 2004).

chitin (n.) a complex organic material produced by arthropods, for example, by insects; the comparable material produced by molluscs is termed conchiolin, although some people use the term "chitin" to refer not only to chitin, in the strict sense, but to conchiolin and other such organic materials.

chitinozoans (n.) a group of marine planktonic microfossils with generally flask-shaped organic walls; of uncertain affinities, but presumably animals (Jansonius and Jenkins 1978).

Chordata (n.) animal phylum characterized by the notochord, includes the vertebrates.

Cincinnati Arch (n.) a broad upwarping of strata extending from Kentucky through Ohio.

Cincinnatian (n.) geologic age term for the Late Ordovician Epoch in North America.

Cincinnatian Series (n.) time-stratigraphic term for the Upper Ordovician in North America.

class (n.) the level in the Linnaean hierarchy below phylum and above order.

classification (see: taxonomy).

coelom (n.) body cavity in certain kinds of animals formed by or within mesodermal tissue; also called a eucoelom. A coelom is lined with a tissue called the peritoneum.

commensalism (n.) a relationship in which an animal lives attached to or as a tenant of another, and ordinarily shares its food, but does not consume its host (distinguished from a parasite, which feeds on the body of its host) ***cf:*** aegism; mutualism; parasitism; predation; host; symbiosis).

competition, competitive interaction (n.) interaction(s) between two or more species in which all species are inhibited or harmed, usually because they seek the same resource, such as food, which is in limited supply.

compression (n.) a kind of preservation in which the fossil specimen is flattened; a fossil produced by such a process.

conchiolin (n.) a complex organic material produced by molluscs; the outermost layer of the molluscan shell consists of conchiolin, as do the opercula of some snails; the comparable material produced by arthropods is termed chitin.

consumer (n.) animal in the food chain above the level of primary production; it feeds on other organisms or organic matter.

convergent evolution (n.) organic evolution in which changes in two or more evolutionary lineages result in organisms that look alike. For example, porpoises, which are mammals, look like fish.

coprophagous (adj.) feeding upon dung.

coprolite (n.) a specimen of fossil excrement (from the Greek "kopros" + "lithos," meaning "dung" + "rock").

correlation (n.) process of determining the correspondence of strata in different sections or locations.

coquina (n.) a kind of sedimentary rock that consists almost exclusively of shells, shell-fragments, or both (from the Spanish for "little shell"; pronounced: ko-keen-uh).

cotypes (n.) in taxonomy, when two or more type-specimens are designated for a species, and all of them are considered to be equally representative of the species, they are called cotypes. Sometimes, in former years, the term "syntype" was used ***cf.:*** holotype; paratype).

cyclicity (n.) in stratigraphy, the regular repetition of a pattern or ordering in sedimentary strata.

D

death assemblage (n.) fossils in a stratum that represent remains of organisms that died at some time before final burial, and usually accumulated from various original locations ***[cf.:*** life assemblage).

dentition (n.) collective name given to the teeth and sockets along the hingeline of an articulate brachiopod or pelecypod; the teeth and sockets serve to prevent the valves from being twisted apart by, for example, a predator; note that the term "dentition," in this sense, has nothing to do with the "dentition" of a jawed vertebrate such as yourself ***(cf.:*** socket; tooth).

deposit feeding (n., adj.) ingestion of food materials located on or within the sediment ***(cf:*** suspension feeding; filter feeder).

diagenesis (n.) chemical, physical, or biological changes occurring in sediments and rocks subsequent to initial formation at relatively low temperatures and pressures ***(cf:*** metamorphism).

diagnosis (n.) a special kind of description that tells how individuals of a given taxon differ from all other members of taxa at the same level in the Linnaean hierarchy. For example, the diagnosis of a species tells how to differentiate it from all other species in the same genus.

dimorphism (n.) the existence in a taxon of two phenotypic forms; the term is used especially in reference to sexual dimorphism ***(cf:*** polymorphism).

dinoflagellates (n.) a group of marine phytoplankton organisms, each of which has organic walls, two flagella, and chloroplasts.

distal (adj.) away from the center of the animal; for example, your finger tips are distal, whereas your shoulder is proximal ***(cf:*** anterior; dorsal; lateral; medial; posterior; proximal; ventral).

diversity (n.) the number of taxa of a particular level that occur in a given time and place; the term, unmodified, generally refers to the number of species, with the meanings of "generic diversity," "familial diversity," and so on, denoting diversity at particular higher taxonomic levels.

dolomite (n.) 1. a mineral composed of calcium magnesium carbonate; 2. a sedimentary rock that consists of the mineral dolomite, sometimes called rock dolomite or dolostone ***(cf:*** aragonite, calcite).

dorsal (adj.) on or toward the top of the animal; the noun form of the concept is "dorsum." (Note that what is functionally dorsal in a given animal may not correspond to the anatomical dorsal. For example, in humans, the head is anatomically anterior, but, as you walk around, your head is at the top of your body and, hence, is functionally "dorsal"; ***cf:*** anterior; distal; lateral; medial; posterior; proximal; ventral.)

durophagous (adj.) said of predators that crush the shells of their prey.

E

ecology (n.) 1. the study of the environment; 2. the environmental needs of organisms of a given taxon or group of taxa (***cf:*** autecology; synecology).

ecosystem (n.) all the organisms in a given time and place, along with the chemical and physical aspects of the environment in which they live in that time and place.

Edenian (n.) term for the lowermost stage of the Cincinnatian Series, also the earliest age of Cincinnatian Epoch,

endosymbiont (n.) organism living within the body of another living organism.

eon (n.) largest geologic time unit, as in Phanerozoic Eon, which comprises the Paleozoic, Mesozoic, and Cenozoic Eras; the hierarchy of geologic time units, from largest to smallest is: eon, era, period, epoch, and age (cf.: age, epoch, era, period).

epibole (11.) a stratigraphic interval characterized by abundance of a particular kind of fossil; sometimes called an acme zone (cf.: biozone).

epibyssate (adj.) said of pelecypods in which the byssus is attached to objects that are beneath the actual sediment-water interface of the sea floor.

epicole (n.) a fossilized animal found attached to the exterior of another fossilized animal, and it is not clear whether the latter was alive when the former was attached (***cf:*** epizoon; epifauna).

epicontinental seas (n.) mostly shallow water marine bodies of water extending over continental crust (syn., epeiric seas).

epifauna (n.) animals living on a substratum such as the sea floor (***cf:*** infauna; epizoon; epicole).

epireliefs (n.) trace fossils on the upper surface of a stratum, occurring as depressions or raised structures.

epizoon (pl., epizoa; n.) an animal that spends its life on or attached to the exterior of another living animal (Davis et al. 1999, 33; pronounced: ep-pi-zo-un). In former years, the word would have been written "epizoon"; the two dots over the second "o" is called a diaeresis, and it indicates that the second "o" is in a different syllable from the first "o." Some people incorrectly use the words "epizoan" and "epizoans" as the singular and plural, respectively (***cf:*** epicole; epifauna).

epoch (n.) a subdivision of a geologic period, equivalent to series in the time-stratigraphic classification; the hierarchy of geologic time units, from largest to smallest is: eon, era, period, epoch, and age (cf: age, eon, era, period).

era (n.) a geologic time unit, as in the Paleozoic Era, which includes, among others, the Ordovician Period; the hierarchy of geologic time units, from largest to smallest is: eon, era, period, epoch, and age (cf.: age, epoch, eon, period).

eustatic (adj.) global, referring to changes of sea level.

event horizon or event bed (n.) a sedimentary layer formed by a short-term depositional process or disturbance, such as a layer of volcanic-ash, or a storm bed.

exoskeleton (n.) shell or carapace that encloses the body of an animal.

external mold (n.) a mold of the exterior of an object *(cf:* internal mold; steinkern).

F

facies (n.) any characteristics of rocks used for recognition of lateral or vertical variations, and usually reflecting the processes forming the rock *(cf:* biofacies; lithofacies).

facultative (adj.) refers to an instance of an organism that is a party to an association that may be convenient, but is not required for the survival of the organism; if, on the other hand, a given parasite is unable to exist outside of its particular association with its host, the association is an obligate one ***(q.v.).***

family (n.) the level in the Linnaean hierarchy below order and above genus.

filter feeder (n.) an organism that gets its sustenance by removing micro-organisms or other small particles of organic matter from the water. Examples include brachiopods, bryozoans, corals, and crinoids *(cf:* deposit feeding; suspension feeding).

food chain, food web (n.) a series of organisms connected by feeding relationships such as predators and prey, or grazers and vegetation, reflecting the transfer of energy from primary producers through consumers.

formation (n.) a rock-unit having distinctive lithologic features and mappable on a regional scale of geologic mapping (generally, 1:24,000 scale) *(cf:* group; member).

forms (n., pl.) a general term used for groups of morphologically distinct organisms that have not been sufficiently studied to warrant their being called "subspecies" or "varieties," both of which terms may have formal taxonomic implications.

fossil record (n.) the evidence of ancient life as preserved in the rocks of the Earth's crust.

fossil succession (n.) a series of fossil assemblages occurring in a vertical stratigraphic sequence,

fossil zone see biozone).

fucoid (n.) an archaic name for certain kinds of *Lebensspuren* (= trace fossils); it stems from the fact that it once was thought that they were the remains of ancient seaweeds related to the well-known group of present-day seaweeds, *Fucus.*

generic name (n.) the name of the genus to which an organism belongs; it is the first word of the species name ***[cf.:*** species name; specific name; trivial name).

genus (pl., genera; n.) the level in the Linnaean hierarchy below family and above species.

grainstone (n.) a limestone characterized by fragments in grain-to-grain contact, and less than 1 percent of interstitial mud ***(cf.:*** packstone).

group (n.) a rock-stratigraphic unit composed of two or more formations.

growth-lines (n.) concentric ridges, grooves, or striations on a shell that mark the successive positions of former margins of the shell or valve.

guild (n.) a group of species individuals of which use food resources in a similar manner.

hardground (n.) a sedimentary bed surface that was cemented or lithified before final burial; it commonly is encrusted or bored by organisms.

holotype (n.) in taxonomy, a single type-specimen designated as representative of a species ***(cf:*** cotype; paratype).

homeomorph (n.) the result of convergent evolution in which two or more evolutionary lineages have evolved so that the organisms at the ends of these lineages look alike.

host (n.) "an animal or plant having a parasite or commensal habitually living in or upon it" (Simpson and Weiner 1989,1336).

hyporeliefs (n.) trace fossils on the lower surface of a stratum, occurring as depressions or raised structures.

Iapetus Sea (n.) ancient ocean that occupied the approximate position of the present-day Atlantic during early Paleozoic time.

ichnofacies (n.) a sedimentary rock characterized by particular trace fossils.

ichnofossil (n.) a trace fossil ***(q.v.);*** pronounced: Ik-no-fossil,

ichnology (n.) the study of trace fossils.

impression (n.) outline or imprint in sediment or sedimentary rock of an organism or part of an organism.

incertae sedis (n.) of unknown biological affinities (Latin, "incertus", "doubtful, unsettled, uncertain", + "sedes, sedis", "place").

incolent (n.) an animal that lives in or occupies the shell of another animal after that other animal has died; for example, a trilobite that has found shelter in an empty cephalopod shell on the sea floor. (According to the Oxford English Dictionary [Simpson and Weiner 1989], "incolent" is an obsolete and rare word that dates from 1597, when it meant simply "an inhabitant," from the Latin "incolo, incolere," meaning "to inhabit.") ***(cf.:*** inquiline).

infauna (n.) the organisms that live beneath the sediment-water interface; the adjectival form is "infaunal" ***(cf:*** epifauna).

inquiline (n.) an animal that lives in the nest or abode of another ***(cf:*** incolent).

internal mold (n.) a mold of the interior of an object; the internal mold of a shell sometimes is called a steinkern *(q.v.)* *(cf.:* external mold),

isochronous (adj.) equivalent in age.

K

K-bentonite (n.) a potassium-rich clay mineral formed by chemical alteration of volcanic ash deposited in salt water,

kingdom (n.) the level in the Linnaean hierarchy above phylum.

L

lag deposit (n.) sedimentary accumulation remaining after erosion of finer-grained size fractions or types of sediment.

lateral (adj.) on or toward the side of the animal *(cf:* anterior; distal; dorsal; medial; posterior; proximal; ventral).

Lebensspur (pl., *Lebensspuren;* n.) a trace fossil (= ichnofossil). *("Lebensspur"* is a German word that literally means "trace of life"; the German word "Spur" is related to the archaic English word "spoor.")

life assemblage (n.) fossils in a stratum that represent remains of organisms that were living at the time of final burial, usually at or near the site of burial *(cf:* death assemblage).

lithofacies (n.) characteristics of a sedimentary rock based on rock-type content *(cf:* biofacies, facies).

lithology (n.) the nature of a particular kind of rock, including such properties as minerallic composition and the size of the particles or crystals of which the rock consists; the word sometimes is used for the description and systematic classification of rocks, a science more properly designated "petrography."

lithostratigraphic unit (n.) a rock-unit characterized by a particular rock-type or suite of rock-types *(cf:* biostratigraphic unit; time-stratigraphic unit).

longitudinal (adj.) with respect to bryozoans, referring to a section cut parallel to the length of zooecial tubes (Bassler 1953, G11, G18) *(cf:* tangential; transverse).

lophophore (n.) a ciliated, food-gathering structure found in brachiopods, ectoprocts, and some other animals; although these structures are similar in appearance and function in various groups of animals, they may not have a common evolutionary origin.

M

mantle (n.) the tissue of a brachiopod or mollusc that secretes the material that comprises the shell; it is part of the mantle-complex, and it generally encloses or lies on both sides of the mantle-cavity.

marker bed (n.) a stratum with unique rock-type, fossil content, or other feature making it useful for correlation or recognition of strata.

mass extinction (n.) global disappearance of many groups of organisms over a relatively short time interval.

Maysvillian (n.) term for the middle stage of the Gincinnatian Series, also the middle age of Cincinnatian Epoch.

medial (adj.) on or toward the middle of the animal, that is, toward the plane of symmetry of the animal. Some people, to avoid potential confusion with the statistical term "median," use the term "mesial" (*cf.:* anterior; distal; dorsal; lateral; posterior; proximal; ventral).

megacycle (n.) repeated set of sedimentary strata of about one to two meters in thickness.

member (n.) lithostratigraphic subdivision of a formation.

mesodermal (adj.) pertaining to the middle layer of tissue in the body plan of triploblastic animals (those having three embryonic tissue layers: ectoderm, mesoderm, and endoderm).

metamorphism (n.) processes of chemical or physical alteration of rocks under the influence of heat, pressure, or both (*cf:* diagenesis).

metazoans (n.) alternative term for "animals."

Milankovitch cycle (n.) repeated pattern of events or strata on a frequency similar to periodicity of one or more variations of the Earth's orbit, such as obliquity or eccentricity. Named after the Yugoslav mathematician Milutin Milankovitch (1879-1958).

mineralization (= replacement) (n.) an alternative for "replacement" (*q.v.*).

mold (n.) an impression or other negative replica of the internal or external parts of an organism formed by sediment enclosing the organism (specifically, an external mold) or enclosed in a cavity within the organism (specifically, an internal mold or steinkern) (*cf:* cast).

mutualism (n.) an association between organisms of two species in which each receives some benefit from the association (*cf:* aegism; commensalism; parasitism; symbiosis).

N

nektonic (adj.) swimming within a body of water (*cf:* benthic; planktonic).

nomenclature (n.) the science of naming the groups into which organisms are classified (*cf:* taxonomy).

nomen dubium (pl., *nomina dubia;* n.) in taxonomy, a name of a taxon that is so poorly understood as to be of doubtful status. The phrase literally means "dubious name."

nomen nudum (n.) in taxonomy, a name of a taxon that was mentioned, but for which no description, designation of a type, illustration, and so on, was given. The phrase literally means "naked name." A *nomen nudum* is not the valid name of a genus or species; however, it may be of historical interest.

O

obligate (adj.) refers to an instance of an organism that is a party to an association that is required for the survival of the organism; thus, if a given parasite is unable to exist outside of its particular association with its host, the association is an obligate one (*cf:* facultative).

obrution deposits (n.) sedimentary layers formed by rapid deposition, usually of fine-grained particles so as to smother any organisms.

ontogeny (n.) everything that happens to an organism from the beginning of its life to death. Included within "ontogeny" are embryology, development, growth, maturation, and so on (***cf.:*** taphonomy).

order (n.) the level in the Linnaean hierarchy below class and above family.

Ordovician Biodiversification Event (n.) appearance of numerous major groups of skeletonized marine invertebrate organisms during the Ordovician Period (syn., Ordovician Radiation).

Ordovician Period (n.) geologic time unit following the Cambrian Period and preceding the Silurian Period.

outcrops (n.) surface exposures of bedrock formed by natural processes.

p

packstone (n.) a limestone characterized by fragments in grain-to-grain contact, with interstitial calcareous mud (***cf:*** grainstone).

paleobathymetry (n.) depth of an ancient body of water.

paleontology (n.) the study of ancient life based on evidence provided by fossils (from the Greek "palaios," meaning "ancient," + "on, ontos," meaning "being," "thing," or "that which has existence," + "logos," meaning "discourse," and, by extension, "study of"); the word also commonly is spelled "palaeontology."

paleoslope (n.) a change in elevation of an ancient topographical surface such as the sea floor.

Paleozoic Era (n.) oldest major division of the Phanerozoic Eon (from the Greek "palaios," meaning "ancient," + "zoon," meaning "animal").

parasitism (n.) a kind of predation in which one animal lives within, attached to, or as a tenant of another of a different species and feeds on the host, which generally is adversely affected, but rarely killed (***cf:*** aegism, commensalism; predation; host; symbiosis).

paratype (n.) in taxonomy, when two or more type-specimens are designated for a species, and one of them, the holotype, is identified as being most representative of the species, the others are paratypes (***cf.:*** cotype; holotype).

pelagic (adj.) living within the water column, either by swimming, drifting, or floating.

period (n.) a geologic time unit, as in the Ordovician Period, during which time the rocks in the Cincinnati area were deposited; equivalent to system in the time-stratigraphic classification; the hierarchy of geologic time units, from largest to smallest is: eon, era, period, epoch, and age (cf.: age, epoch, eon, era).

Phanerozoic Eon (n.) major subdivision of geologic time marked by occurrence of abundant fossils of metazoans.

phylum (pl., phyla; n.) the level in the Linnaean hierarchy below kingdom and above class.

plane of symmetry (n.) the plane of symmetry commonly is called the "midline" of the animal (see: bilaterally symmetrical),

planispiral (adj.) said of a shell coiled in a single plane.

planktonic (adj.) suspended within or floating upon a body of water, with transportation exclusively or primarily by currents and other movements of the water itself ***cf.:*** benthic; nektonic).

polymorphism (n.) the existence in one species of individuals of more than one size, shape, or nature; in bryozoans, for example, there may be several different polymorphs in a given colony, each of which, presumably, performed a different function ***(cf.:*** dimorphism).

posterior (adj., n.) on or toward the rear of the animal. (Note that what is functionally posterior in a given animal may not correspond to the anatomical posterior. For example, in humans, the back is anatomically dorsal, but, as you walk around, your back is at the rear of your body and, hence, is functionally "posterior"; *cf.:* anterior; distal; dorsal; lateral; medial; proximal; ventral.)

predation (n.) a relationship in which one animal consumes another organism; the consumer is called a predator, and that consumed is called the prey *(cf.:* aegism; commensalism; mutualism; parasitism; symbiosis).

primary producers (n.) organisms at the base of a food chain that form organic compounds such as carbohydrates from simple components such as carbon dioxide and water by the process of photosynthesis.

priority (n.) in taxonomy, the convention that, when there is an older name and a younger name that both have been used to designate the same taxon, the older name becomes the official name of the taxon.

proximal (adj.) on or toward the center of the animal; for example, your finger tips are distal, whereas your shoulder is proximal *(cf.:* anterior; distal; dorsal; lateral; medial; posterior; ventral).

pseudobivalved (adj.) said of a shell that is sharply folded along the dorsal axis so as to give the appearance of being bivalved, although calcification is continuous across the axis; thus, there is no true hinge; rostroconch molluscs are pseudobivalved *(cf.:* bivalved; univalved).

R

radiometric dating (n.) determination of geologic age through measurement of the decay of radioactive isotopes contained in certain minerals; common methods are uranium-lead, potassium-argon, and carbon-14 analysis.

recrystallization (n.) the process whereby the original substance of a shell, for instance, is reconstituted or converted to crystals or to crystals of a different nature; for example, some mollusc shells consist of the mineral aragonite, which, under certain taphonomic conditions, may, over time, convert to the mineral calcite. Aragonite and calcite have the same chemical composition ($CaCO_3$), but have a different three-dimensional crystal structure.

relative age (n.) time of occurrence of an event in geologic time relative to another, in the sense of older or younger *(cf.:* absolute age).

replacement (= mineralization) (n.) a taphonomic process in which the actual substance of an organism is removed bit-by-bit, and mineral matter is left in its place; a fossil produced by such a process.

Richmondian (n.) the youngest stage of the Cincinnatian Series; also the youngest age of the Cincinnatian Epoch,

rock-stratigraphic unit (see lithostratigraphic unit).

S

scientific name (see: species name).

sea floor spreading (n.) process by which new oceanic crust is formed by upwelling of molten material along a fissure or rift.

seismite (n.) rock layer formed or altered by earthquake shock.

serial sectioning (n.) cutting a fossil, for example, a brachiopod, into a number of thin, equally spaced slices of known orientation. From these slices, it is possible to reconstruct the interior of the shell; in effect, one is doing a paleontological CAT scan. In specimens in which the interior of the shell is filled with rock matrix, this may be the only practical way to see what is inside the shell.

series (n.) a time-stratigraphic subdivision of a system, such as Cincinnatian Series or Upper Ordovician Series ***(cf.:*** stage; system).

sequence boundary (n.) stratigraphic horizon marking the beginning or termination of strata deposited during an interval of sea level rise or fall, usually indicating a cessation of sedimentation or interval of erosion ***(cf:*** unconformity).

sequence stratigraphy (n.) the study of sequences of sedimentary rocks bounded by surfaces of non-deposition or erosion, usually related to major changes in sea level.

shell pavement (n.) dense accumulation of shells of molluscs or brachiopods.

siliciclastics (n.) sediments consisting of particles of clay, mud, silt, sand, or coarser material composed of silica-rich materials.

socket (n.) one of the depressions along the hingeline of an articulate brachiopod or pelecypod into which fits into a tooth of the opposite valve; the teeth and sockets, collectively termed the dentition, serve to prevent the valves from being twisted apart by, for example, a predator ***(cf:*** dentition; tooth).

species (pl., species; n.) the level in the Linnaean hierarchy below genus; a species is the basic kind of organism recognized by scientists.

species name (n.) the formal name of a species, consisting of both the generic name and the specific (or trivial) name; commonly called a binomen, because it consists of two names; commonly called the scientific name of the species ***(cf:*** generic name; specific name).

specific epithet (see: specific name).

specific name (n.) the second word of a species name; commonly called the trivial name; sometimes called the "trivial epithet" ***(cf:*** generic name; species name).

stage (n.) a time-stratigraphic subdivision of a series, such as the Edenian Stage; often used for intercontinental or regional correlation. There is an equivalence between a given stage and the time span during which that body of rock was deposited; for example, the rocks of the Edenian Stage were laid down during the Edenian Age ***(cf:*** series; system).

steinkern (n.) petrified sediment infilling of a shell or body cavity, an internal mold (from the German "Stein," meaning "stone," + "Kern," meaning "kernel"); although a German noun, it commonly appears neither capitalized nor in italics (***cf.:*** cast; mold).

storm cycles (n.) a layer of sedimentary rock produced during a single storm, commonly it consists of an interval representing intense disturbance of the sea floor followed by an interval representing waning of storm activity.

stratigraphy (n.) the study of layered or stratified rocks (***cf:*** biostratigraphy),

stromatolites (n.) finely laminated sedimentary accumulations resulting from trapping and binding of sedimentary particles by cyanobacteria; usually sheet-like, dome-shaped or columnar in form; sometimes called "algal stromatolites," because cyanobacteria once were thought to be algae.

stromatoporoids (n.) dome-shaped, columnar, or branching calcareous skeletons, usually with finely laminated microstructure, formed by calcareous sponges, occurring in Ordovician through Cretaceous rocks.

subspecies (n.) a level in the Linnaean hierarchy just below species; sometimes called variety.

substratum (n.) a surface on which an organism might be attached; it might be the surface of a stratum, rock, shell, or other hard object. (Not to be confused with "substrate," which has a precise biological meaning and should not be used in this context.)

succession (n.) in ecology, the replacement of one assemblage of organisms by another, often in which the activities of the initial assemblage of organisms altered the environment in such a way that a different assemblage of organisms can occupy the environment; commonly called "ecologic succession" (***cf:*** biotal succession; fossil succession).

suspension feeding (n., adj.) (***cf:*** deposit feeding; filter feeder).

symbiont (n.) each of the organisms involved in a symbiotic relationship.

symbiosis (n.) a close association between organisms of two species; commonly a symbiotic relationship is beneficial to both organisms involved, but parasitism also can be considered a symbiotic relationship (***cf:*** commensalism; mutualism; parasitism).

symmetrical, symmetry (see: bilaterally symmetrical; plane of symmetry).

synecology (n.) ecology of several or many species of organisms together in a given time and place (***cf:*** autoecology).

syntypes (see: cotypes).

system (n.) a major time-stratigraphic subdivision, the rock record of a period of geologic time, such as the Ordovician System (***cf:*** series; stage),

systematics (see: taxonomy).

T

Taconic Orogeny (n.) episode of intense crustal deformation that occurred during the Late Ordovician when the plate of oceanic crust beneath the Iapetus Sea was subducted beneath the continental Laurentian plate; named for the 'laconic Mountain region of eastern New York where this deformation first was recognized.

tangential (adj.) with respect to bryozoans, referring to a section cut parallel to the surface of the zoarium and close enough to the surface of the colony to show the mature features of the zooecia in cross-section; such a tangential section is perpendicular to a longitudinal section (Bassler 1953, G15, G18) ***cf.:*** longitudinal; transverse).

taphonomy (n.) 1. everything that happens to an organism after it dies; 2. the study of those phenomena that tend to destroy the remains and traces of a living thing as well as of those that tend to preserve those remains and traces (from the Greek "taphos," meaning "grave" or "tomb," + "nomos," meaning "law").

taxobases (sing., taxobasis; n.) characteristics on which the taxonomic position of a group of organisms is based (pronounced: tax-uh-base-ease).

taxon (pl., taxa; n.) a formal biological group to which an organism is assigned; humans, for example, belong in a taxon at the family-level of the Linnaean hierarchy called Hominidae.

taxonomy (n.) the science of assigning organisms to their proper biological groups (alternative names are classification and systematics).

tempestites (n.) sedimentary rocks formed by storm processes, often exhibiting features such as particle-size sorting, fossil breakage, abrasion, and orientation resulting from violent water movement.

time-averaged (adj.) pertaining to sedimentary deposits or fossil assemblages that represent accumulation over a relatively long time interval, often consisting of mixtures of fossils from successive generations.

time-stratigraphic unit (n.) a body of rock formed during a particular interval of geologic time, such as a system or series ***(cf:*** biostratigraphic unit; lithostratigraphic unit).

tooth (n.) one of the projections along the hingeline of an articulate brachiopod or pelecypod that fits into a socket in the opposite valve; the teeth and sockets, collectively termed the dentition, serve to prevent the valves from being twisted apart by, for example, a predator ***(cf:*** dentition; socket).

trace fossil (n.) a fossil that shows that an animal or plant existed, but which lacks actual remains or replicas of remains; it was made by or is the result of genuine activity of the living organism, rather than involuntary movement, such as a shell's being dragged across the sea floor by currents or wave action; included here are footprints, trails, burrows, borings, tooth marks, and so on (= ichnofossil = ***Lebensspur)*** ***(cf:*** body fossil).

transverse (adj.) with respect to bryozoans, referring to a section cut at right angles to the direction of growth of the zoarium (Bassler 1953, G15, G18) ***(cf:*** longitudinal; tangential).

trivial name (see: specific name).

U

unconformity (n.) a surface separating layers or other bodies of rock that represents either a cessation of deposition or an interval of erosion.

univalved (adj.) said of a shell that consists of a single valve ***(cf.:*** bivalved; pseudobivalved).

V

variety (n.) in former times, equivalent to the taxonomic rank of subspecies, but no longer recognized within the zoological community (International Commission on Zoological Nomenclature 1999,19); nowadays commonly used specifically for kinds of plants bred deliberately by horticulturists.

ventral (adj.) on or toward the bottom of the animal; the noun form of the concept is "venter." (Note that what is functionally ventral in a given animal may not correspond to the anatomical ventral. For example, in humans, the belly is anatomically ventral, but, as you walk around, your belly is at the front ofyour body and, hence, is functionally "anterior"; *cf:* anterior; distal; dorsal; lateral; medial; posterior; proximal.)

Z

zone (see biozone).

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INDEX

Page numbers in italics indicate illustrations.

Like most indexes, this one is nowhere near as thorough as it might have been; the tremendous number of items that might have been included would have made the index completely unwieldy.

Certain words and concepts are not separately listed in the index, because they appear far too many times in the book. Examples include Cincinnatian, Ordovician, and Ohio River. Although places in the states of Indiana, Kentucky, and Ohio are included in the index, every appearance of the name of the whole state is not.

This volume is not intended as a comprehensive taxonomic work. Hence, we have not endeavored to put every genus, species, and so on, in its complete Linnaean Hierarchy in the index. Rather, we have used the names of upper-level taxa that appear in the text. However, we have departed from this policy in some cases, with the hope of greater clarity and usefulness for the reader.

Although so-called "common names"—things like "brittle star" and "spiny oyster"—probably should he sandwiched between quotation marks, we chose not to do this so *as not to clutter the index more than absolutely necessary.*

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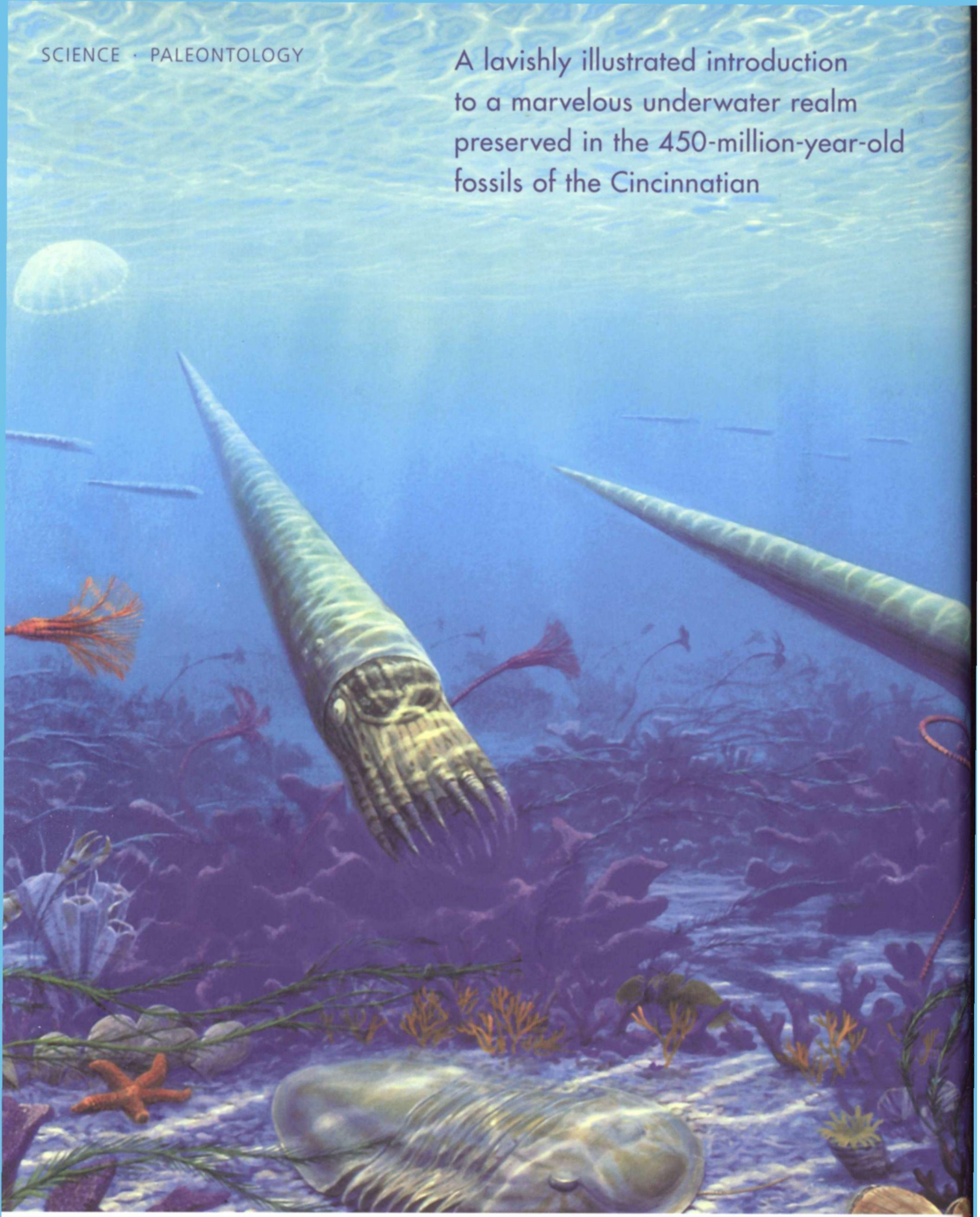

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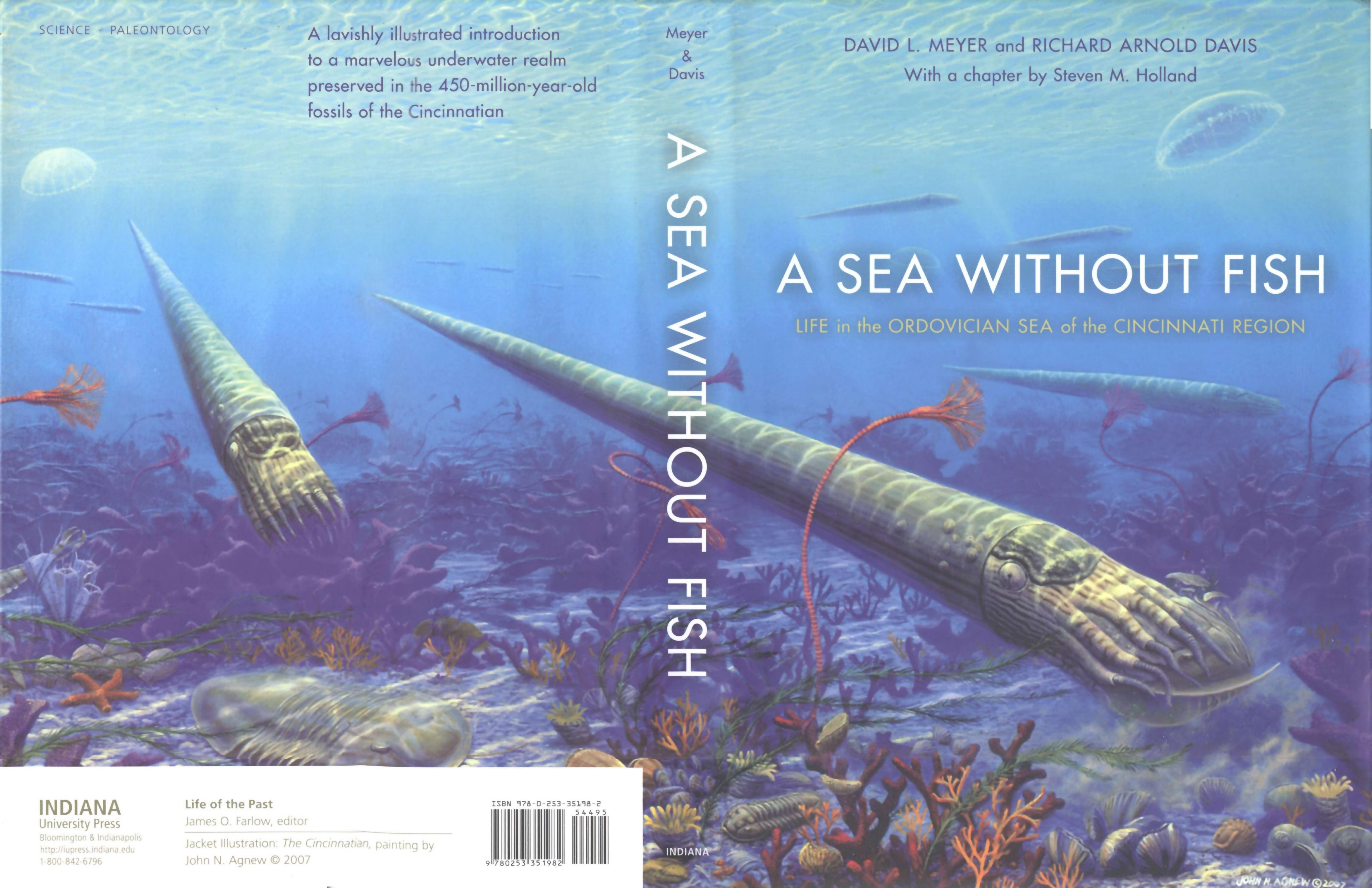

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A SEA WITHOUT FISH

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With a chapter by Steven M. Holland

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LIFE in the ORDOVICIAN SEA of the CINCINNATI REGION