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Mammoth Cave National Park

Paleontological Resource Inventory
(Public Version)



A paleoenvironmental reconstruction of the invertebrate and vertebrate assemblage of the Joppa Member of the Ste. Genevieve Formation (Viséan, Middle Mississippian, ~335 million years ago), based on fossils identified from Mammoth Cave National Park, Kentucky.
NPS / JULIUS CSOTONYI

Mammoth Cave National Park: Paleontological resource inventory (public version)

Science Report NPS/SR—2025/243

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Abstract

Mammoth Cave National Park (MACA) in south-central Kentucky protects one of the most famous and extensive cave systems in the world. Fossils, both in the bedrock of the cave system and as much more recent remains that date to the cave era, have been reported since at least the first half of the 19th century, but have rarely been a focus of investigation. In 2019, following a report of shark fossils in the wall of a cave passage, a team of MACA staff and volunteers, members of the National Park Service (NPS) Paleontology Program, and paleontological specialists from outside the NPS began a paleontological resource inventory at the park. This inventory was established to document the scope, significance, temporal and geospatial distribution, and management issues associated with these non-renewable resources at the park.

The Mammoth Cave System and other caves at MACA formed in bedrock that dates to the Middle to Late Mississippian, approximately 335 to 325 million years ago. At this time, the future area of MACA was submerged beneath a continental sea. The seafloor was carpeted with corals, crinoids, and other marine invertebrates. A diverse array of cephalopods, cartilaginous fishes, ray-finned fishes, and other animals swam above them. Occasionally the sea receded and was replaced by coastal lands that supported abundant plants. The resulting terrestrial beds, deposited as late as the early Pennsylvanian (approximately 320 million years ago), are not soluble like the marine beds and now cap the caves and ridges. Both marine and terrestrial beds preserve abundant fossils.

Hundreds of millions of years later, passages began to form in the ancient Mississippian marine carbonate rocks, and when these became connected to the surface, organisms from the outside began to enter or fall into the developing cave system, sometimes to be preserved as fossils. Fossils from the Quaternary (2.58 million years ago to the present) represent organisms that inhabited the area during the shifting climate of the Ice Age, including extinct animals such as mastodons, saber-toothed cats, and short-faced bears.

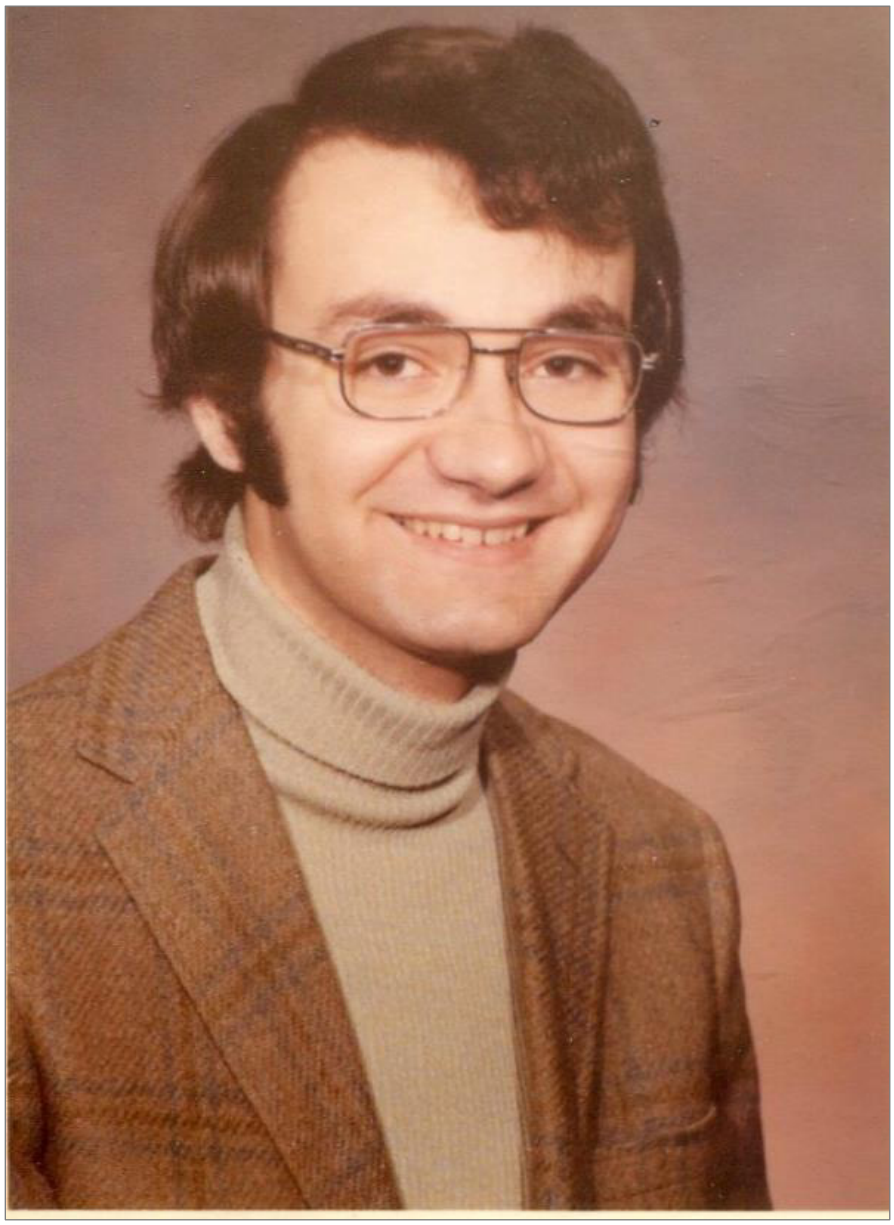
After several years of site visits, photography and photogrammetry, specimen collection and preparation, literature and archival research, expert consultation, and other study, documentation, and description, MACA can stake a claim to being one of the most paleontologically significant units in the NPS. This report summarizes the findings of the inventory team and will help future investigators understand and manage the park's paleontological resources.

Acknowledgments

The Mammoth Cave Paleontological Resource Inventory has benefited from the past and present contributions of many individuals. We first want to recognize the members of the research team who prepared chapters in this report: Art and Peg Palmer, Kelli Tolleson, Rick Olson, Michael Donovan, William Ausich, John-Paul Hodnett, Dave Elliott, and Jack Wood. The previous paleontological research undertaken by E.R. Pohl, Claude Hubbard, Mona Colburn, Rick Toomey, Ron Wilson, Tambra Eifert, Russell Graham, and Blaine Schubert helped to establish the foundation of this report. A long list of dedicated volunteers and partners, including representatives from the Cave Research Foundation have helped to uncover portions of the paleontological story at Mammoth Cave. The NPS staff at Mammoth Cave National Park enthusiastically supported this inventory and actively participated in many facets during the past five years, and we want to extend particular thanks to Barclay Trimble, Molly Schroer, Timothy Pinion, Rick Olson, Kelli Tolleson, Rich Boldon, Chelsea Ballard, Terry Langford, and Kathy Proffitt. We also want to acknowledge the support from staff in the NPS Geologic Resources Division, including Stephanie Gaswirth, Hal Pranger, Julia Brunner, Jason Kenworthy, Jim Wood, Pat Seiser, and Georgia Schneider. Stephen Thomas, program manager for the Cumberland Piedmont Inventory & Monitoring Network, provided invaluable aid as peer review coordinator for this report. Finally, we extend our appreciation to artists Julius Csotonyi and Benji Paysnoe, who produced original art bringing to life the Mississippian fauna preserved at Mammoth Cave.

Dedication

We dedicate this volume on the paleontology of Mammoth Cave National Park to Ron Wilson and the cavers of the Cave Research Foundation (CRF). Paleontologist Ron Wilson, former CRF President and NPS Chief Curator, guided CRF's attention to paleontological resources. He led CRF trips to record and recover paleontological resources. He also taught cavers how to look for paleontological resources and to make sure their finds were documented. The CRF cavers took up this mantle and recorded many types of paleontological resources (invertebrates, vertebrates, plants, and trace fossils). They have also supported numerous researchers as they studied paleontology deep in the caves of the park since 1957.



Paleontologist Ron Wilson of the University of Louisville. PHOTO COURTESY OF RON WILSON

Chapter 1. Introduction and Summary: The Paleontological Heritage of Mammoth Cave National Park

By Vincent L. Santucci[1], Justin S. Tweet[2], and Rickard S. Toomey III[3]

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Mammoth Cave has been a place of human interest for thousands of years, beginning with the exploration and use of the cave system by pre-Columbian indigenous people. More recent historic accounts attribute the first visitors to Mammoth Cave of European descent to be members of the Houchin family around 1797. A myriad of curious individuals, cave explorers, scientists, and other visitors have helped to document the rich natural and cultural resources associated with the largest known cave on Earth, which is part of the largest known cave and karst system on the planet. In an effort to preserve and protect this globally significant cave and surrounding landscape, Mammoth Cave National Park (MACA) was established on July 1, 1941, on the eve of the United States entry into World War II. The park became a World Heritage Site on October 27, 1981, and a UNESCO Man and the Biosphere Program International Biosphere Reserve on September 26, 1990. Today the boundaries of Mammoth Cave National Park incorporate 52,830 acres (21,350 ha) at the surface, including portions of the Green River and Nolin River flowing through the park, along with the world-renowned cave system beneath the surface (Figure 1).

Although there are hints of earlier fossil discoveries (see Chapters 2 and 5), the first published account of fossils from Mammoth Cave is attributed to naturalist Constantine Samuel Rafinesque in his publication titled "The Caves of Kentucky" (Rafinesque 1832). The Pleistocene / Holocene record for vertebrate fossils from MACA has been the focus of more recent study (Wilson 1981; Toomey et al. 1995, 1998; Colburn 2005). Publications focused more comprehensively on all fossils from MACA, including fossils from within the Paleozoic strata in which the cave developed and the more recent Pleistocene / Holocene record of fossils include Santucci and others (2001) and Hunt and others (2009).

In 2019, news of the discovery of some fossil shark teeth preserved in the cave passages at MACA by park staff was shared, along with photos, with the NPS Senior Paleontologist. JP Hodnett, a paleontologists who specializes in Paleozoic sharks, was contacted and arrangements were made for him to schedule a visit to Mammoth Cave National Park in October 2019. The important fossil discoveries associated with JP's visit to MACA, especially the diverse fish fauna preserved in the Mississippian strata exposed throughout the park's cave passages, has led to the decision to undertake a parkwide paleontological resource inventory at MACA.

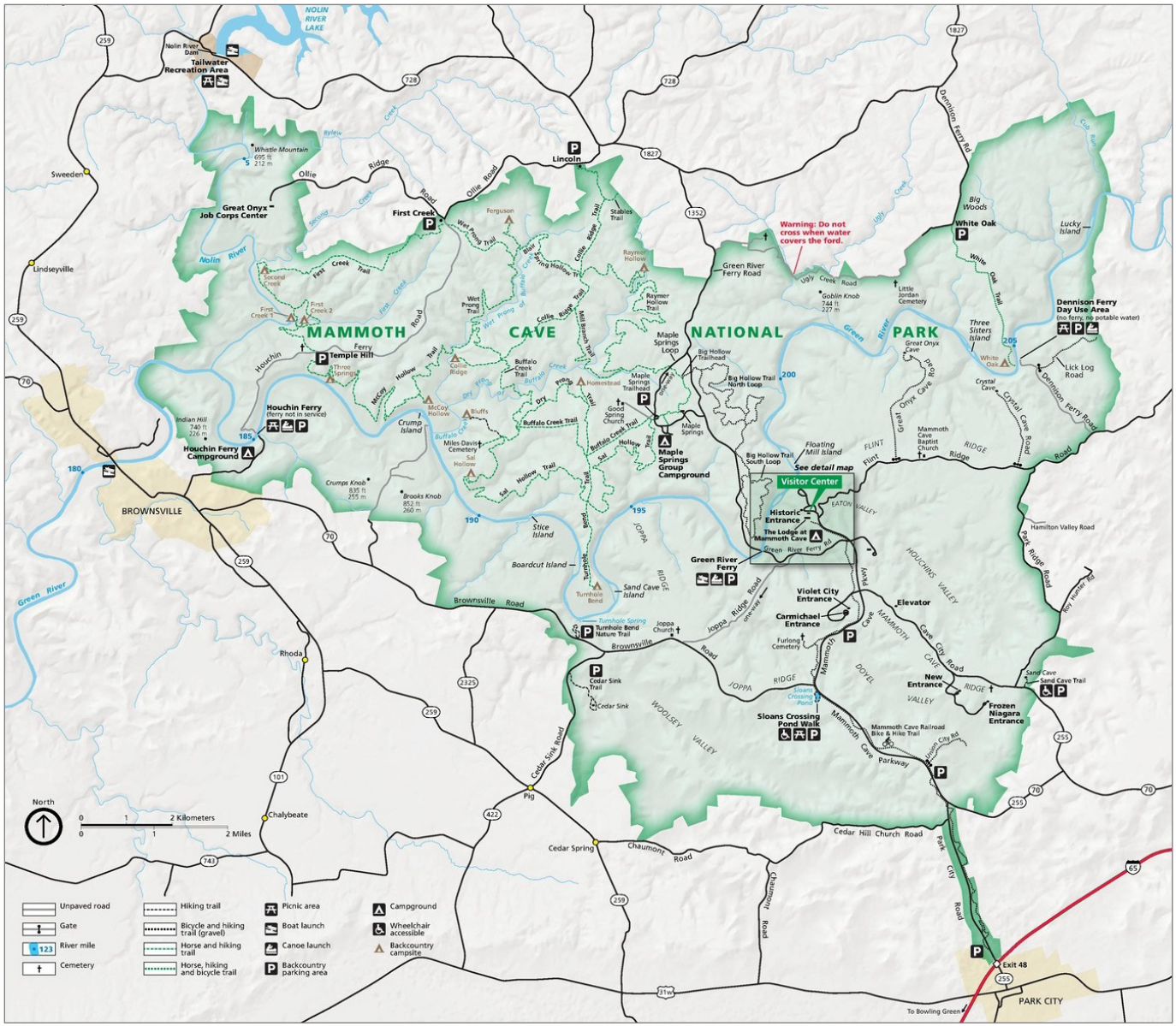


Figure 1. Map of Mammoth Cave National Park. NPS

The principal goals and objectives for the Mammoth Cave National Park Paleontological Resource Inventory are to identify the scope, significance, distribution, and management issues associated with the fossils from the park. Through this effort we have compiled baseline paleontological resource information for park managers and staff to better understand the non-renewable resources under their stewardship, and in turn help to inform park planning and decision-making which may relate to park fossils. This publication is written for park managers, in the language and content most useful for considering the many aspects of management, protection, interpretation and scientific study of National Park Service fossils.

The development of the Mammoth Cave Paleontological Resource Inventory is timely and consistent with the mandates put forth in the Paleontological Resource Preservation Act of 2009 (PRPA) and associated Department of Interior regulations. Specifically, Section 6302 of PRPA (16 USC 470aaa-1) mandates for the NPS and other Department of Interior bureaus that "The Secretary shall manage and protect paleontological resources using scientific principles and expertise. The Secretary shall develop appropriate plans for inventory, monitoring, and the scientific and educational use of paleontological resources." The work undertaken in conjunction with the Mammoth Cave National Park Paleontological Resource Inventory exemplifies this legal standard and scientific principle.

The Mammoth Cave National Park Paleontological Resource Inventory represents the collaboration of a team of paleontologists, NPS staff, and a number of partners. Subject matter experts with previous research and experience involving Mammoth Cave geology and fossils were involved in various aspects of this inventory including drafting or peer review of the manuscripts presented in this undertaking. The MACA Paleontology Resource Inventory includes chapters on the following topics: the history of paleontology at the park (Chapter 2); the geology and stratigraphy of Mammoth Cave (Chapter 3); Paleozoic paleobotany (Chapter 4); Paleozoic invertebrates (exclusive of echinoderms) and trace fossils (Chapter 5); Paleozoic echinoderms (Chapter 6); Paleozoic vertebrates (Chapter 7); Pleistocene and Holocene paleontology (Chapter 8); and paleontological resource management (Chapter 9).

The collective work is represented by this publication, by new fossil specimens cataloged in the park's museum collection, and through new interpretive media focused on Mammoth Cave National Park. This work represents the compilation of historical and current research and fossil collections associated with paleontology of Mammoth Cave National Park. In addition, fossils documented from outside the administrative boundaries of the park, from the greater Mammoth Cave region, have also been considered as part of this inventory.

The study of the paleontological resources at Mammoth Cave is brief, spanning more than 190 years since the first definitive report of fossils in 1832. The team contributing to this publication is dedicated to the paleontology of Mammoth Cave National Park and all recognize that we have just scratched the surface in terms of the potential for future fossil discovery. This report is intended to provide a baseline of paleontological resource information to inform the management and stewardship of these resources at Mammoth Cave National Park. We collectively admire and benefit

from the work of those paleontologists who have come before us and hope that our work will inspire and support the work by those paleontologists and park managers who will come in the future.

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Chapter 2. History of Paleontology at Mammoth Cave National Park

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Introduction

Mammoth Cave has been a magnet for world-renowned geologists and scientists since its popularization as a tourist attraction began in 1816. Many visited as regular tourists and later published first-hand accounts of their travel experiences, while others made intended scientific studies of the region's caves. Some of these first-hand accounts included observations of fossils.

Ambiguous Early 1800s Reports and a Mislabeled *Megalonyx*

People may have taken notice of fossils in the vicinity of Mammoth Cave as early as 1808, when Samuel Latham Mitchill included a report of a "Petrified echinus from Kentucky," continuing, "They are said to be frequent in the Great Cavern, near the Green River." (Fay 1961). It is unclear whether this was actually within the bounds of the current Mammoth Cave National Park (MACA) (Chapter 5).

Of the region's caves, the naturalist Constantine Samuel Rafinesque (Figure 2) claimed he was "the first to examine them geologically and zoologically, from 1818 to 1826," and indeed is responsible for the earliest published paleontological observation in Mammoth Cave, in his "The Caves of Kentucky" (Rafinesque 1832): "They [mineral encrustations] cover the few fossils of the strata, yet I observed some Madrepores, a fine *Mastrema*, and a *Turbinolite*."

According to NPS paleontologist Justin Tweet, "madrepore" presumably refers to the modern *Madrepora*, a heavily branching scleractinian colonial coral; in the context of Mammoth Cave, he might have been looking at a branching coral or bryozoan instead. "*Mastrema*" is a name Rafinesque coined that is not otherwise in use, and may be some kind of branching colonial fossil that was not as bushy as a "madrepore." "*Turbinolite*" may be a garbled reference to the modern solitary coral *Turbinolia*, so he may have been describing a horn coral of some kind (Justin Tweet, NPS, pers. comm., 2022).

Another report worth mentioning includes a group of specimens belonging to *Megalonyx* accompanied by a label reading, "White Cave, Kentucky," a location now within the National Park. Yet, despite this seemingly clear statement, there has been much confusion over the years about the origin of these bones, now deposited in the Academy of Natural Sciences (now part of Drexel University) in Philadelphia (ANSP Specimens 12487–12490 and 12492–12499).



Figure 2. Naturalist Constantine Samuel Rafinesque claimed to be the first to study fossils in Mammoth Cave. Rafinesque Hall in the Historic section is named in his honor. Plate 76 in U.S. National Museum (1901). PUBLIC DOMAIN

The bones in question were from the collection of John D. Clifford. They then passed into the possession of a Mr. Dorfeuille (proprietor of the Cincinnati Museum), were sold to and described by Richard Harlan in 1829, were subsequently purchased by John Price Wetherill Esq., and finally given to the ANSP, in 1831 (Spamer et al. 1995).

The incorrect label may be attributed to either Mr. Clifford or Mr. Dorfeuille, because Richard Harlan seems to have doubted the White Cave origin. In Harlan (1831), he appeared to acknowledge that White Cave may not be the correct location. After stating, “the fossil bones…. were labelled, ‘White Cave,’ Kentucky; being one of those saltpetre caves so numerous in the limestone formation, in the states of Kentucky, Tennessee, and Virginia,” he then mentions in a footnote his correspondence with his “intelligent friend Dr. Black” that “saltpetre, so common in other caves, has not been detected in this,” implying this is not the described cave (Harlan 1831).

The history of the specimens then took a strange turn. In the 1832 publication mentioned above, Rafinesque made the following statement:

> *White Cave, near the Mammoth Cave…. It was not there, as stated erroneously by Harlan, that the Aulaxodon was found, but in the Mummy Cave near it; a saltpetre cave, where 3 mummies were also discovered.*

"*Aulaxodon*" is a genus name Rafinesque intended to introduce for the sloth, but this name has never been used in a serious context anywhere else and can be ignored. Nearly two centuries later, his role in the story of the sloth seems part "red herring," part non sequitur. His statement raises a new question as to the origin. Is Rafinesque referring to Short Cave, another saltpetre cave located just outside the current boundary of Mammoth Cave National Park? Harold Meloy believes so (Meloy 1968), as Short Cave produced several "mummified" (desiccated by the cave environment) human bodies during its use as a saltpetre cave. Given other developments that place the specimen's origin firmly outside of Kentucky, it is unknown why Rafinesque would have thought as such, or what he was getting at in the first place.

Rafinesque (1832) described all the saltpetre caves of the Mammoth Cave region in a single paragraph where he mentioned,

> *Saltpetre Caves…. The largest of all is the Mammoth Cave…. It is in these that bones of antediluvial quadrupeds have been found…. While digging for saltpetre…. A few collected by Mr. John D. Clifford and others.*

His short list began with,

> *1. The Megatherium, or an animal very near it. 2. My Aulaxodon speleum, since called Megalonyx laqueatus, by Harlan.*

These words prompted Harlan to respond with, "Rafinesque's claim that *Aulaxodon speleum* is a misappropriation, and the allegation that the bones were obtained elsewhere is a deceit" (Harlan 1832).

Despite Harlan's assurance, the bones were obtained elsewhere. Confirmation of the correct discovery location is attributed to Gerard Troost, who in 1835 visited the Big Bone Cave, Tennessee, and ascertained that the *Megalonyx* bones in question were from there. Locals and a man named Squire Fisk informed him that in addition to purchasing saltpetre from Big Bone Cave, John Clifford also received a barrel full of bones from the same cave (Troost 1835).

In 1835, Harlan published a concession, after being convinced by Troost:

> *The observations of Dr Troost on the locality of these fossils, render it quite probable that all the bones of this animal, hitherto described as coming from White Cave, Kentucky, are in reality relics from Big Bone Cave, Tennessee.*

Despite the confusion cast on this specimen, current consensus is that this *Megalonyx* specimen was indeed discovered in White County, Tennessee, at the Big Bone Cave during saltpetre mining around

1811. The original yet incorrect label information, that *Megalonyx* was discovered in White Cave, Kentucky, continues to be reproduced in publications to this day.

The trials and tribulations of this *Megalonyx* specimen exemplify the difficulties associated with early 19th century documentation. Other historical records of paleontological discoveries are more clear-cut.

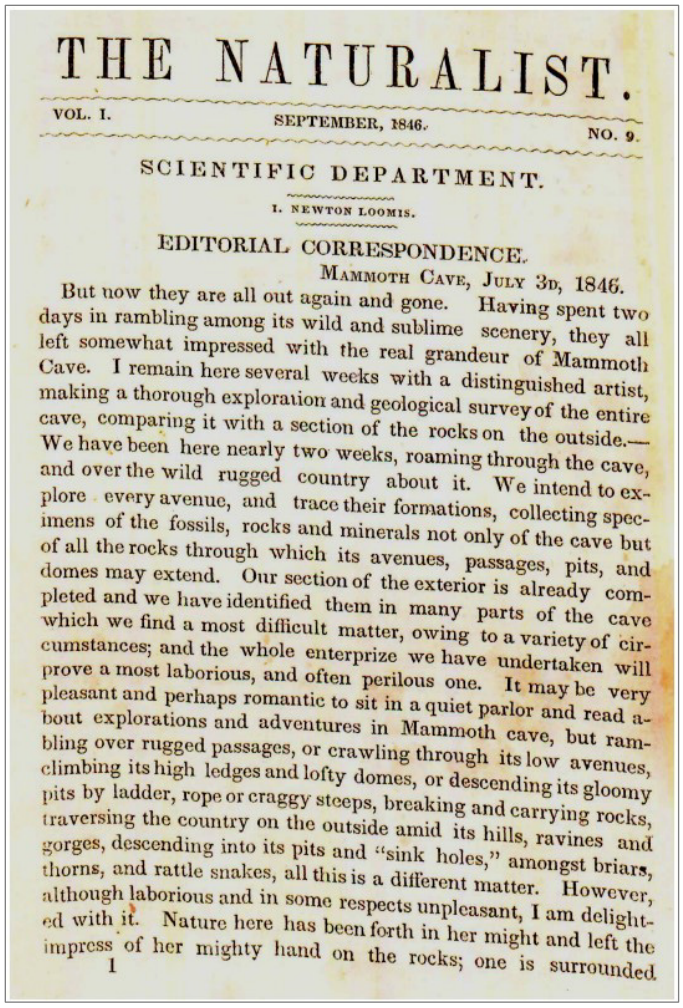
Physician and published gothic novelist Robert Montgomery Bird wrote about his 1835 visit to Mammoth Cave in his book, "Peter Pilgrim: Or A Rambler's Recollections." Bird observed a beaver-like tooth in a woodrat nest in Solitary Cave, which is a passage in Mammoth Cave (Bird 1838: 140). Although not part of a specific geologic study, this goes to show that cave paleontology, in the form of bones from the cave deposits, were reported very early on.

The First Field Camp, and the End of the Century: 1840s–1900

In 1846, the now dissolved Franklin College of Nashville, Tennessee sent Professor Isaac Newton Loomis to lead a student geology field camp. He published about the experience in the college's short-lived journal, "The Naturalist" (Figure 3). Leading a party of 120 students in seven companies, they walked for over a week to reach Mammoth Cave, and at least a few faculty stayed for four weeks total. He noted they collected fossils en route, and also within what are now the borders of the National Park, but he frustratingly failed to detail what kind of fossils they collected and from specifically where.

> *Continuing on the same road, we soon came to a fine exposure in the upper portion of the Blue shaly Limestone, corresponding with that found in the Harpeth Hills. Then the satchels were brought into requisition in carrying away some beautiful fossils. (Loomis 1846 No.8)*
>
> *We intend to explore every avenue, and trace their formations, collecting specimens of the fossils, rocks and minerals not only of the cave but of all the rocks through which its avenues, passages, pits, and domes may extend. Our section of the exterior is already completed and we have identified them in many parts of the cave which we find a most difficult matter… (Loomis 1846 No.9)*

Despite the publication's shortcomings, this appears to be the earliest systematic geologic study of Mammoth Cave, not counting Rafinesque's earlier and limited personal observations.



THE NATURALIST.

VOL. I. SEPTEMBER, 1846. NO. 9.

SCIENTIFIC DEPARTMENT.

I. NEWTON LOOMIS.

EDITORIAL CORRESPONDENCE.

MAMMOTH CAVE, JULY 3D, 1846.

But now they are all out again and gone. Having spent two days in rambling among its wild and sublime scenery, they all left somewhat impressed with the real grandeur of Mammoth Cave. I remain here several weeks with a distinguished artist, making a thorough exploration and geological survey of the entire cave, comparing it with a section of the rocks on the outside.— We have been here nearly two weeks, roaming through the cave, and over the wild rugged country about it. We intend to explore every avenue, and trace their formations, collecting specimens of the fossils, rocks and minerals not only of the cave but of all the rocks through which its avenues, passages, pits, and domes may extend. Our section of the exterior is already completed and we have identified them in many parts of the cave which we find a most difficult matter, owing to a variety of circumstances; and the whole enterprize we have undertaken will prove a most laborious, and often perilous one. It may be very pleasant and perhaps romantic to sit in a quiet parlor and read about explorations and adventures in Mammoth cave, but rambling over rugged passages, or crawling through its low avenues, climbing its high ledges and lofty domes, or descending its gloomy pits by ladder, rope or craggy steeps, breaking and carrying rocks, traversing the country on the outside amid its hills, ravines and gorges, descending into its pits and "sink holes," amongst briars, thorns, and rattle snakes, all this is a different matter. However, although laborious and in some respects unpleasant, I am delighted with it. Nature here has been forth in her might and left the impress of her mighty hand on the rocks; one is surrounded

1

Figure 3. "The Naturalist," a journal from Franklin College of Nashville, contains a description of the first known geology field camp at Mammoth Cave.
PHOTO COURTESY OF TENNESSEE STATE LIBRARY AND PUBLIC ARCHIVES, NASHVILLE

In a letter titled "On the Mammoth Cave of Kentucky" to a "Professor Guyot," from November 8, 1850 (later published as Silliman 1851), geologist Benjamin Silliman Jr. briefly noted the presence of bedrock fossils in the walls of Mammoth Cave. Although he does not say in which passage he noticed them, he references what seem to be corals and crinoids, and then elaborates on the vastness of geologic time.

> *There were the delicate silicious forms of Cyathophylla [coral] and Encrinites [crinoid], protruding from the softer limestone which had yielded to the dissolving power of the water; these carried me back to that vast and desolate ocean in which they flourished and were entombed as the crystalline matrix was slowly cast around them, mute chroniclers of a distant epoch.*

Milne-Edwards and Haime (1851) claimed that a horn coral from Kentucky was a new taxon, *Zaphrentis cliffordana*, but locality information is not entirely clear even though Mammoth Cave is mentioned. For further discussion, see Chapter 5.

A Geological Survey of Kentucky was published in 1856 (Owen 1856), with some mention of the limestones near Mammoth Cave, "A few fossil brachiossæ [brachiopods?] and polypiferæ [corals] occur in the limestone of this part of Green river, but they are by no means abundant."

John Francis Campbell, a Scottish author, collected at least one fossil from within Mammoth Cave in 1864 and published a sketch of it the following year (Figure 4): "In the summer of 1864 a holiday trip to North America was so arranged as to test glacial theories…." During a larger search for evidence of glaciation, "the Mammoth Cave in Kentucky was visited for its own sake" (Campbell 1865).

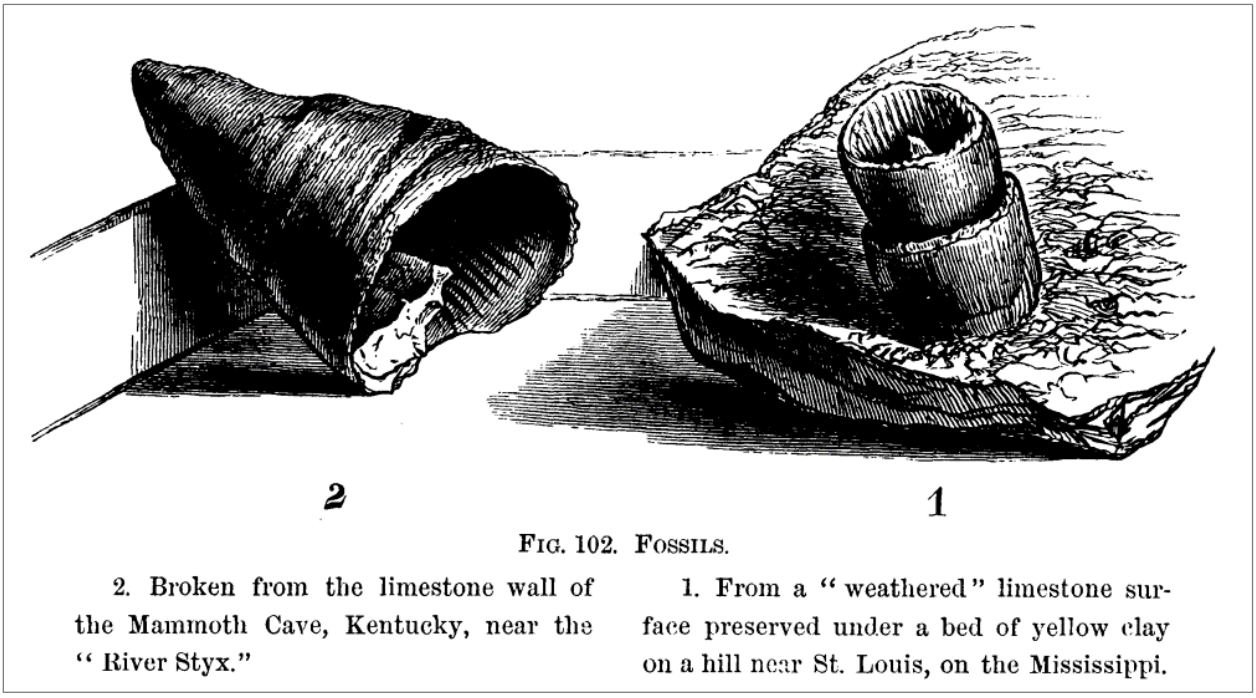


FIG. 102. FOSSILS.

2. Broken from the limestone wall of the Mammoth Cave, Kentucky, near the "River Styx."

1. From a "weathered" limestone surface preserved under a bed of yellow clay on a hill near St. Louis, on the Mississippi.

Figure 4. A horn coral collected from within Mammoth Cave by John Francis Campbell (Figure 102 in Campbell 1865). J.F. CAMPBELL

In 1866, Cincinnati photographer Charles Waldack took the first cave photos in North America during his visit to Mammoth Cave and called the collection "Magnesium Light Views in Mammoth Cave." Several of these photographs were published by Forwood in "An Historical and Descriptive Narrative of the Mammoth Cave of Kentucky" (Forwood 1870). All of the photos he produced were stereopairs, to simulate three dimensions, and several of his subjects included surface scenes, such as the "Curious Sand-stone Rock" "…Excavated near the cave about 15 years since, and now to be seen in the Hotel yard" (Figure 5) This sandstone boulder contains an impression of a scale bark tree, and

has been a mainstay attraction for visitors since its discovery (Figure 6). It is now to be seen in the Visitor Center Exhibit Hall.



Figure 5. A stereopair of photographs taken by Charles Waldack in 1866 of an impression of a scale bark tree fossil. The caption on the reverse reads, “Curious Sand-stone Rock. Excavated near the cave about 15 years since, and now to be seen in the Hotel yard.”
PHOTO COURTESY OF WESTERN KENTUCKY UNIVERSITY LIBRARY SPECIAL COLLECTIONS

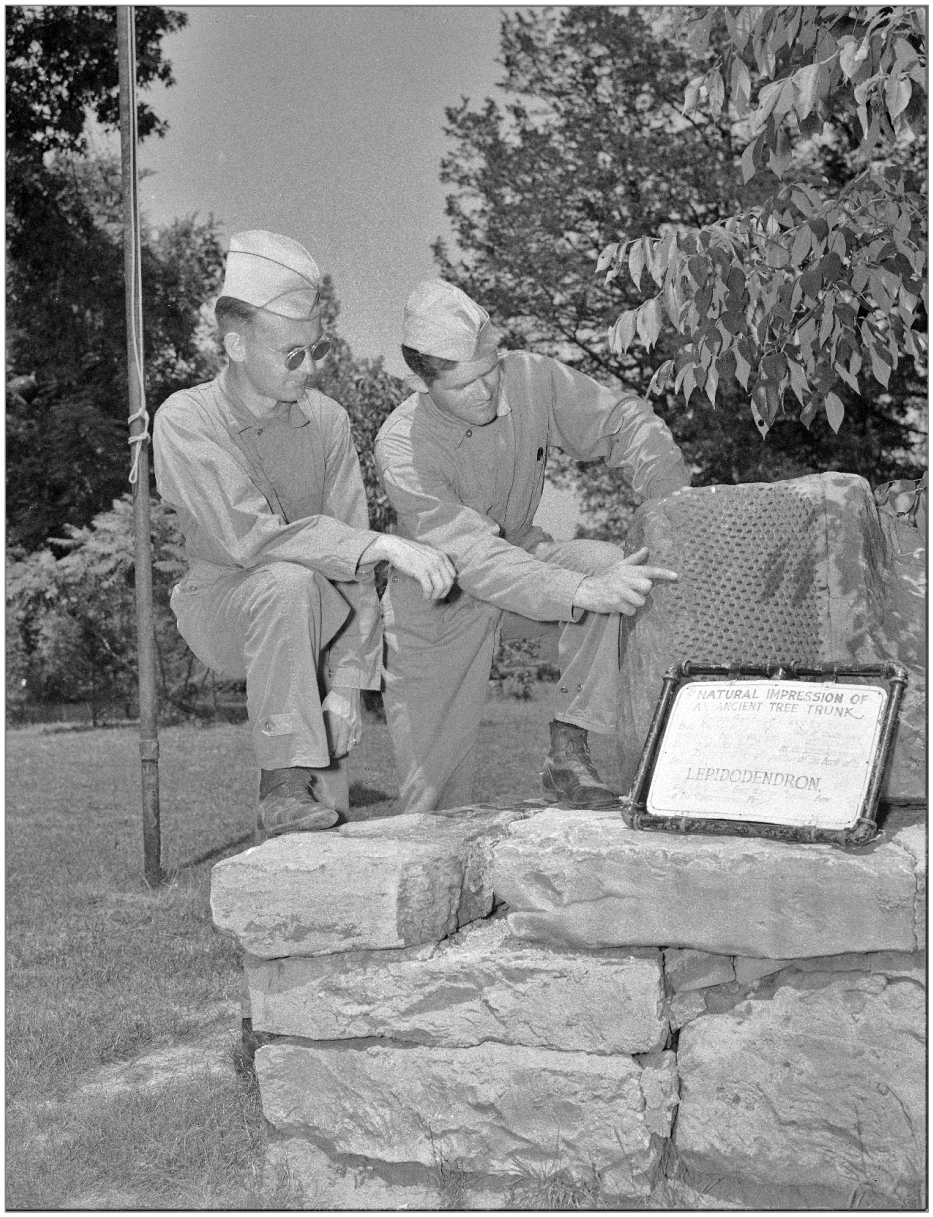


Figure 6. The sandstone rock with scale tree fossil impression from Figure 4 is seen here being examined by visiting servicemen. It is now on display in the MACA Visitor Center. Caption on signage reads, “Natural impression of an ancient tree trunk. Eons ago forest trees of different types than those of to-day flourished in this district. One of those here represented toppling over was covered with sand making the mold(?) which has been preserved as the sand became rock. The imprint is that of a portion of the bark of a tree called Lepidodendron, a lycopod, and lived during Cypress time of the Mississippian period.” Photo taken June 1941, accessible from Open Parks Network at http://purl.clemson.edu/84DA12111837CDCBB47BE94152FBC056. NPS

The Kentucky Cave Wars Climax: 1900s–1920s

To reach the next works focused on paleontology or geology we must move forward considerably in time. “Contribution to Indiana Palæontology” by G. K. Greene named the horn coral *Lithodrumus veryi* from 6 km (4 mi) southeast of Mammoth Cave (Greene 1904) (see Chapter 5 for more

information). The locality may well be in MACA, as the geography and geology are consistent. The stratigraphy is uncertain but thought to be Renault (=Girkin) per Easton (1944), which moved the species to *Caninia*. The type specimen is apparently lost, per Easton; it should have been at the American Museum of Natural History (Easton 1944).

Author and self-taught geologist Horace Carter Hovey contributed fifteen editions of his guide to Mammoth Cave from the 1880s to the early 1900s (Clarke 1915). In his 1909 "Hovey's Hand-Book of the Mammoth Cave of Kentucky: A Practical Guide to the Regulation Routes," he described Gorin's Dome. "Its vertical walls sweep in an S-shaped curve and spring from the river level to the apex of the dome, with projecting bosses of coral and with cascades that awake the echoes as they fall" (Hovey 1909).

In his updated 1912 edition, "Mammoth Cave of Kentucky: With an Account of Colossal Cavern" (Hovey and Call 1912), he elaborated on the corals in Gorin's Dome.

> *Vertical walls rising one hundred and fifty-nine feet [48.5 m] to the very top of the dome, with here and there bosses which on careful closer examination prove to be masses of coral, and these throw long shadows toward the top that move and wave in long black lines as the lamps flicker and swing…*

The same 1912 publication included fossils in Colossal Cavern, now known to be part of the Mammoth Cave system and within the National Park. "We also found fossil corals, known as '*Zaphrentis*,' [horn coral] having value in determining the geological horizon of the limestone" (Hovey and Call 1912). At a location near the Sandstone Mountain, "On the wall near by we saw an exquisite branching variety of the coral known as *Tubipora* [modern soft coral; perhaps fossil *Syringopora* or *Schoenophyllum*], sixteen inches [40 cm] long by six [15 cm] wide" (Hovey and Call 1912).

In 1925, geologist Willis T. Lee (Figure 7) visited Mammoth Cave and several other caves in the area, including George Morrison's New Entrance to Mammoth Cave, White Cave, Colossal Cavern, Salts Cave, Crystal Cave, Great Onyx Cave, and Proctor's Cave, all now within MACA; and Diamond Caverns, Horse Cave (now Hidden River Cave), and Mammoth Onyx Cave. Soon thereafter he produced a report called "A Visit to the Mammoth Cave Region of Kentucky." His month-long visit and subsequent report had been requested by a joint commission involving Congress, the Secretary of the Interior, and the U.S. Geological Survey, to examine the potential of a new national park. His visit was mostly to take photographs (40+) and generally "sight-see" as a potential national park visitor; therefore, his only paleontological reconnaissance was paraphrased from Hovey (Lee 1925):

> *In many places fossil shells which have been replaced by silica stand out in bas-relief on the walls where the limestone has been dissolved away. Several groups of the coral Zaphrentes were noted, and also of the branching coral Tubipora.*



Figure 7. Willis T. Lee with daughter Elizabeth Lee outside George Morrison's New Entrance to Mammoth Cave, 1925. USGS, WILLIS T. LEE COLLECTION

In the early 1900s tourism era, often called the "Kentucky Cave Wars," dozens of privately owned show caves popped up in the vicinity of Mammoth Cave, hoping to siphon off some of the tourist dollars flooding into the region due to improved roads and widespread adoption of the automobile. Exploration yielded many small caves, used for tourism, or for mining souvenir minerals and formations. One such short-lived show cave run by Andy Lee Collins (brother to ill-fated cave explorer Floyd Collins who died while exploring Sand Cave) and Otis Turner was called Collins' Onyx Cave, Dixie Onyx Cave, and many additional names. In a 1928 promotional brochure, Collins advertised pictures of mastodon bones (Figure 8) alleged to have been found in the cave, and even quoted a tourist as saying, "The bones of the mammal are, to say the least a very novel sight"

(Thompson and Thompson 2003). Further investigation of this cave and another nearby resulted in a 1934 paper by Webb and Funkhouser, wherein they identified additional bones belonging to *Megalonyx* and *Mastodon* (=*Mammut*) (Webb and Funkhouser 1934). These mostly collapsed caves were not located in the park, which was under development at the time, but are close enough to be worth mentioning.



Figure 8. Andy Lee Collins (left foreground) and Otis Turner (right foreground) with mastodon forelimb bones later displayed at Andy Collins's Onyx Cave. Photo taken by early 1928 for Collins' cave business, used without accreditation in 1920s and 1930s works, e.g., Figure 2 in Webb and Funkhouser (1934). PUBLIC DOMAIN

George Morrison (Figure 9), "King of the Cave Wars," was an important figure in the history of the Mammoth Cave region for his development of tourist trails and artificial entrances in far-flung parts of the cave which are still toured today. Although he made no specific paleontological study of the cave, he did mention the presence of fossils in his Guidebook, "New Entrance to Mammoth Cave," published sometime after 1924, most likely 1929.

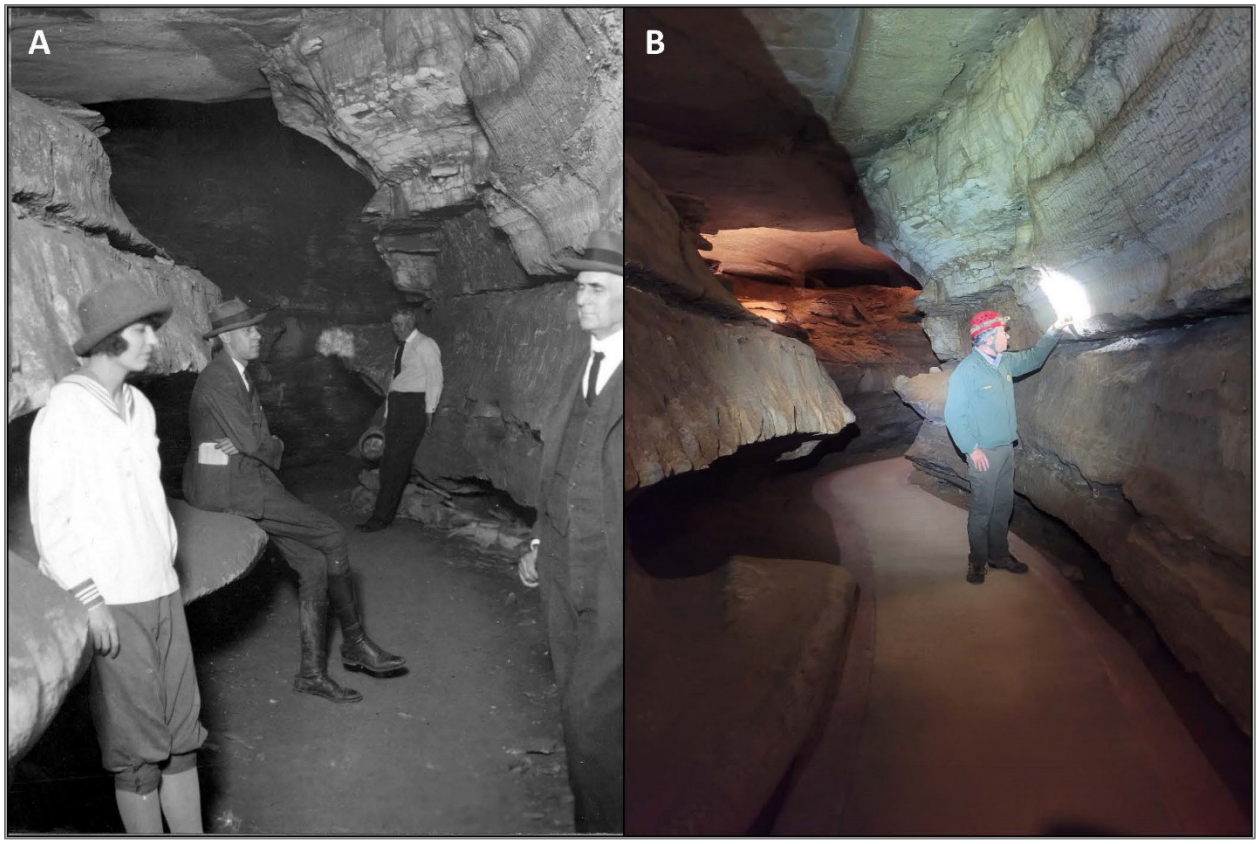


Figure 9. A side passage off Grand Central Station. **A.** George Morrison (second from the right), two unknown members of the National Park Commission, and Elizabeth Lee (far left), during the visit of Willis T. Lee and daughter Elizabeth to the New Entrance in 1925. USGS, WILLIS T. LEE COLLECTION. **B.** Ninety-six years later, this same passage yielded several shark teeth as part of this inventory project. NPS

You have now entered the Jaw Bone Dome, so called for the jaw bone that is shown imbedded firmly in the floor of the dome. This specimen, with the teeth attached, caused considerable speculation as to the kind of animal and how it was possible for it to reach that spot, etc. Many Naturalists have viewed the relic—none have offered a positive theory. Passing on we enter the Crescent or Fossil Dome. This is a beautiful crescent-shaped Dome and abounds in fossil, so either name is appropriate. (Morrison 1929: 30).

You now pass through the region known as the Ruins of Martinique. Here you are shown the bones of a pre-historic animal. (Morrison 1929: 45).

The first to attract your attention is the White Ceiling, colored Gypsum, … Coon Tracks and Skeleton… (Morrison 1929: 46).

The path continues between the limestone walls in an ever winding, ever changing crevice to Fox Avenue, so named due to the finding of the remains of three foxes at the extreme end of the terminal of this avenue. Evidently these animals found their way into the cavern from

> *some other point and following this avenue to the end which is completely sealed, they were unable to find an exit. The three being found in close proximity brings up the question—a fox track will remain for ages as plain in the cavern as the day made, and the question is, does the scent remain also? (Morrison 1929: 46–47).*

The "Jaw Bone" has not been relocated, while the fossils in "Fossil Dome" refer to abundant invertebrate fossils, mostly colonial corals, weathering from the limestone walls at shoulder height.

The "pre-historic animal" bones have not been relocated.

For the section describing a trip through Morrison Ave, the "Coon Tracks and Skeleton" have not been relocated, but the "foxes" described next were later identified as raccoon.

Much later, Mona Colburn of the Illinois State Museum located the remains of two raccoons in Fox Avenue, but had this to say in conclusion (Colburn 2005):

> *…no one, today, would judge the two sets of remains to be close to the "extreme end" of Fox Avenue. If these two skulls represent Morrison's original specimens, then, clearly they have been redeposited. Perhaps the bones were transported by water because it is evident that Fox Avenue has had flowing water since the deposition of the bones. Thus, there still exists a slight chance that the third of Morrison's "fox" skeletons and additional skeletal elements are yet to be discovered.*

Paleontology and Park Preparation: Late 1920s–1930s

Willard Rouse Jillson (Figure 10) was a hugely influential figure in local geologic study. In 1920, one year after becoming State Geologist of Kentucky, he visited Mammoth Cave and left his name engraved in at least two places inside the Historic section of the cave. Perhaps he was so impressed by his visit that it spurred him to action. Under his tutelage, the Kentucky Geological Survey (KGS) undertook a public education campaign to enliven the earth sciences for the general public. In a 1928 article called "Geology in the Service of a New National Park" he even claimed "Maps, documents, and booklets prepared by the Kentucky Geological Survey became the basis of an authoritative demand for the creation of a national park at Mammoth Cave."

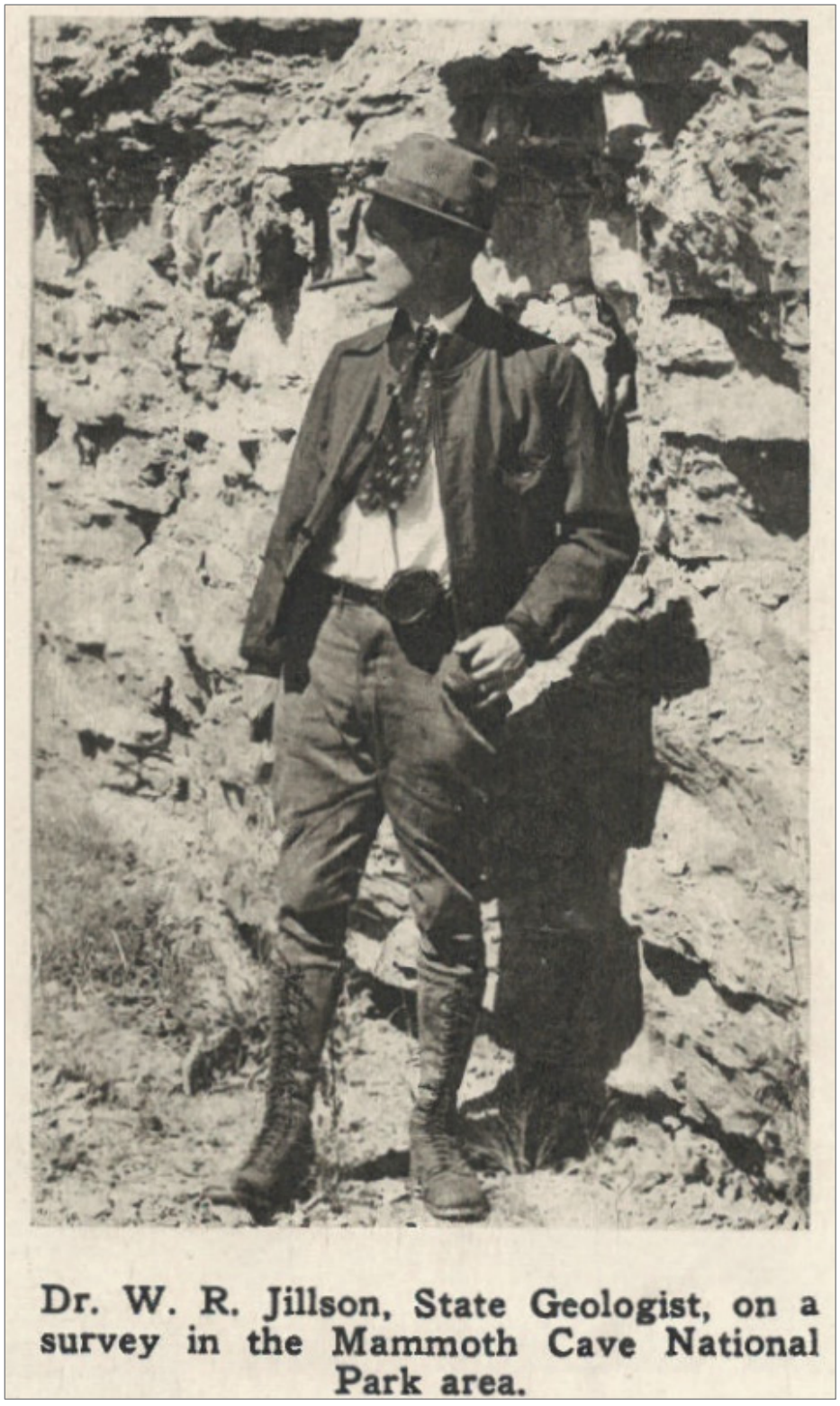


Figure 10. Willard Rouse Jillson, on a survey in MACA (Jillson 1928). PUBLIC DOMAIN

Despite his enthusiasm for Mammoth Cave and for paleontology, his publications rarely combined the two. However, in 1927, Assistant Geologist James M. Weller (serving under Jillson) published a

remarkable book titled “The Geology of Edmonson County” (Weller 1927). Much of Mammoth Cave is in this county and so of course the cave and others were discussed. However, fossils in caves were not mentioned, and on page 102 he stated, “The Ste. Genevieve Limestone of Edmonson County has yielded no extensive fauna.” If only he had looked at solutional walls of cave passages in the St. Genevieve, then he would have found abundant fossils! Though Weller did not look for fossils in caves, there are impressive lists of mostly invertebrate fossils from the Renault-Paint Creek Formation (today the Girkin Formation) in Bylew Creek, which is partially in the park, and also at Great Onyx Cave, which is fully within the park. Weller reported that the Golconda Limestone (Haney today) was rather unfossiliferous and that no collections were made in Edmonson County but did report fossils in this stratum from other locations. Fossils in the Glen Dean Limestone figure prominently in the book with one location given as “…at Brownsville, road back of jail.” This is almost certainly not in the park but very close, and besides the more typical invertebrates included the trilobite *Phillipsia* and shark relative *Psephodus*. Fossils in residual blocks of the Cypress Sandstone (Big Clifty today) are mentioned in a railroad cut west of Glasgow Junction (Park City today). This is of note because the Big Clifty is generally bereft of fossils. The noted brachiopods and pelecypods occurred in a shale layer (Weller 1927).

In 1931, as State Geologist, Jillson compiled a volume titled “Paleontology of Kentucky.” Within this volume, J. R. Weller’s chapter included Mississippian fossils across the state (Jillson 1931). Mammoth Cave is not specifically referenced in this state-scale publication, but this book is comprehensive and significant nonetheless. Decades later, in 1958, Jillson published “The Geology of Barren County, Kentucky,” and summarized many of the paleontological finds from the previous several decades, many of which are near Mammoth Cave and thus described in the following pages as individual publications (Jillson 1958).

The fossils of a passage called Croghan Hall have been known, and the subject of interest, since at least 1931, when Young Hunt, who guided at Mammoth Cave for 43 years (1921–1964), circled two of them on the wall (Joe Douglas, Volunteer State University, pers. comm., 2020) (Figure 11). Goniatite cephalopod fossils in the ceiling of Croghan Hall have been identified as part of this inventory project (Chapter 5).

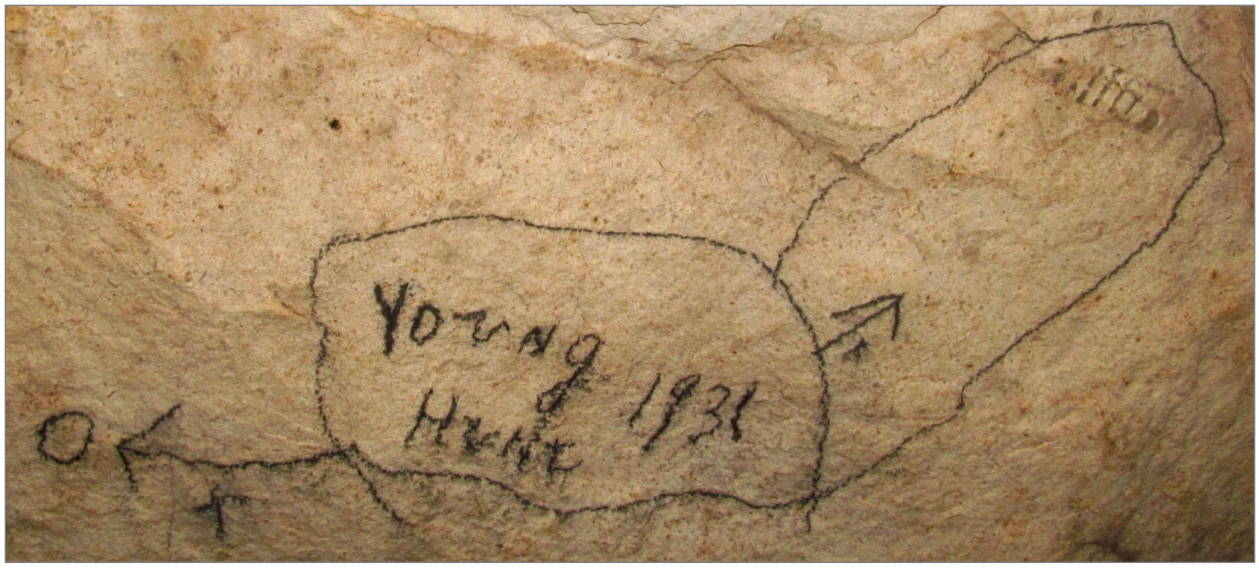


Figure 11. Photo of cave wall in Croghan Hall passage of Mammoth Cave showing historic graffiti by Guide Young Hunt. An undetermined fossil (left) and a partial nautiloid cephalopod fossil (right) are circled with arrows pointing to them.
PHOTO COURTESY OF JOE DOUGLAS AND MARION SMITH, 2022

The 1930s brought much preparation for National Park status at Mammoth Cave, including hiring a park naturalist, one who coincidentally would later become a noted vertebrate paleontologist. After receiving his M.A. in Zoology (1934) from the University of Kansas, Claude Hibbard (Figure 12) became a Wildlife Technician for the National Park Service. As park naturalist for the proposed Mammoth Cave National Park, he surveyed the surface flora, fauna, and miscellaneous points of interest in natural history, including reports of fossils, which he kept in a log of his activities from June 1, 1934, to August 22, 1935 (Hibbard 1935). Most observations were vague mentions, others turned out to be pseudofossils, and some localities were eventually excluded from the national park boundary.



Figure 12. Naturalist and paleontologist Claude Hibbard.
PHOTO COURTESY OF MEADE COUNTY HISTORICAL SOCIETY

June 12, 1934: *Went to the office to look at fossil from Stockholm quarry, reported as fish vertebrae, was* Archimedes.

June 20, 1934: *Went to Stockholm. Checked formation and got fossil fish spine.*

June 26, 1934: *Worked in office. In afternoon checked on find, which was fossil plant from Cypress Sandstone, made by Tom Grove.* [No other context for locality]

December 5, 1934: *The Stockholm quarry was vacated in hopes of find some remains of vert fossils. The base of the quarry carries a layer rich in fossils invertebrate and a*

few vert. fossils but they were destroyed by quarry crew not realizing their presence & value. Fossil fish remains… The quarry at Mill Creek branch was carefully gone over in search of vert. fossils (fish remains) only invertebrate were found.

January 16, 1935: *Just cave, with the exception of invertebrate fossils which are plentiful in Boones Avenue and would be of interest to anyone studying geology.*

March 27, 1935: *The forenoon was spent with Mr. Martin, camp supt. of C.C.C. camp #1, at his office checking invertebrate fossils and other rocks that C.C.C. boys had picked up.*

April 22, 1935: *I then went to Rosin Hollow to check on what is known as Rosin. I had previously reported this but many seemed to believe that it was left by an early plant making turpentine in that area. I dug into the deposit and removed all fragments until I came to a layer of amber at the base of sandstone. There is fossil amber scattered through 14" of formation with two layers from 3" to 4" in thickness. It was not worked to see if fossil plant or insects were present in it due to the fact that I had to return on foot; though this is a point of outstanding geological interest in the maximum area.*

June 19, 1935: *[Cave #028 in MACA] is too small and not suitable for bats. It is evident that this cave was either used by Indians to live in or as a burial place. Plant chips were found on the floor, fragments of mussel shells, also bird, mammal, frog and reptile bones were observed, also a femur (probably man). The cave gets its name from the bones. The bones, many of small birds and mammals, were probably carried in by pack rats. Nests were found in the back part of the cave. The front of the nest being open and the two rats were curled up, one in each nest, but ran up the side of the Cave as we approached. Probably bones of new extinct forms in the park may be found in this cave since a deer tooth was observed in the cave. The bones were left in place and reported to Mr. Holland.*

The report of amber is interesting because no fossil amber is known from the region. It may indeed be turpentine slag as he suggested, and further investigation is unlikely because the location is on private land outside the current national park boundary.

NPS Paleontologist Justin Tweet came across an entry in the University of Kansas collections showing that Hibbard collected a bison tooth from within Mammoth Cave National Park (KUVP 255 Division of Vertebrate Paleontology, Biodiversity Institute & Natural History Museum, University of Kansas, Lawrence, Kansas) (J. Tweet, pers. comm., 2022). He later visited KU and had the specimen photographed (Figure 13). From its color and density, Tweet believes it to be fossil rather than modern. This find is otherwise unpublished.



Figure 13. KUVP 255, a *Bison* sp. tooth collected by Claude Hibbard at Mammoth Cave in 1934. NATALIA LOPEZ CARRANZA, RUDOLPH SERBET, AND JUSTIN TWEET

Dr. Erwin Robert Pohl (Figure 14) was another extremely important person in local geologic study. Originally from Loudonville, New York, after studying at Georgetown University in Washington, D.C., he came to Kentucky and was soon assigned as Park Geologist to the budding national park. Throughout the 1930s until his death in 1973 he was involved with many cave-country ventures. He served on the Kentucky National Park Commission and even became an adjunct professor at Western Kentucky University.

In 1929 he married Ruth Thomas, daughter of Dr. Harry Thomas, owner of three show cave rivals of Mammoth (Mammoth Onyx Cave, Hidden River Cave, and Crystal Cave). Upon Dr. Thomas' death in 1948, Dr. Pohl managed the Thomas estate, which included the Floyd Collins Crystal Cave (now within the MACA boundary). He oversaw and permitted the exploration of lower Crystal Cave by his nephew Bill Austin, which arguably led to the origination of the Cave Research Foundation—the group currently responsible for exploration and survey of Mammoth Cave (Brucker and Watson 1976).

In pursuit of creating a geologic map of Mammoth Cave National Park (which was completed and exists as an internal park document), Pohl recorded his fieldwork in several Weekly Activity Reports from July 15 to November 9, 1935 (Pohl 1935). Only some of these reports survive, and not all

contain fossil information. It was during this fieldwork that Dr. Pohl amassed the bulk of MACA's fossil collection (previous to the recent inventory), currently held on-site in curatorial.



Figure 14. Dr. Erwin Robert Pohl.
PHOTO COURTESY OF WILLIAM T. AUSTIN FAMILY AND HIDDEN RIVER CAVE

In the report from July 20, 1935 he suspected a 1.2 m (4 ft)-thick layer of "siltstone may prove to be the equivalent of the Bethel Sandstone of western Kentucky and Southern Illinois." He recommended "Collections of fossil associations must be carefully made on either side of this bed to establish the possibility of its separating the Gasper section into its component beds, the Renault below and the Paint Creek above." It is unclear whether he did indeed collect fossils at this locality, as many MACA specimens collected by Pohl are missing locality information. He also discussed the value of brachiopod fossils in tracing a marker bed he speculated might be the lower part of the Gasper (=Girkin Formation).

From September 21, 1935:

> *Fine collections of fossils were obtained from the sandstone of the transition zone between the Cypress [=Big Clifty Formation] and the Golconda [=Haney Formation]. ...It is further by far the most prolific faunals ever recorded from either the Cypress or Golconda and the determination of its composition will shed much light on the paleontology of this portion of Chester time. ...Good specimens have been obtained at various locations. Good*

> *paleontologic collections from the residual chert of the Golconda were secured near Union City.*

Again, it is not clear which of his collections pertain to this interval, although informed speculation can be made from collection dates. It also does not appear that he later published this information in any significant detail; perhaps it was superseded by later finds.

From September 28, 1935:

> *During the field work several good specimens of Lepidodendron imprints were obtained from the Cypress sandstone. Note of one in particular should be made. This was secured in a block of sand-stone of approximately one cubic foot in size in which the leaves are to be seen extending in natural position from the leaf scars of the truck. …Collections were also secured from Gasper and Golconda horizons at various localities.*

There are two much smaller specimens in MACA curatorial that could have been chipped off this "one cubic foot" block, but locality information is missing. Otherwise, the location of the "one cubic foot" block is unknown.

In a report dated Niv. (=November) 9, 1935, he noted the presence of large fragments of St. Louis Formation *Lithostrotion canadensis* coral (now *Acrocyathus floriformis*) near Turnhole Bend in a Green River terrace above the present-day high-water stage. He speculated that they must have washed downriver from the nearest known occurrence of the St. Louis Formation, 32 km (20 mi) upstream.

Some early research on Mammoth Cave fossil shark remains occurred during the 1930s. Specimens from locations and persons unknown were sent to geologist and cave scientist Dr. J Harlen Bretz at the University of Chicago. One reply from Bretz to Mr. W.W. Thompson, General Manager of Mammoth Cave, dated November 29, 1937, explained that the fossil in question was a fragment of a dorsal fin spine of a large shark, but further identification was impossible. Another letter (Figure 15) from February 11, 1938, referred to a fin spine and he stated, "The name to which he did not answer during his lifetime is *Ctenacanthus*." Referring to other samples he stated that "The glossiness of the tooth is a record of the original dentine which covered it." (Bretz 1937–8).

The University of Chicago

Department of Geology

W.W. Thompson G.I.

February 11, 1938

Mr. W. W. Thompson,
General Manager,
Mammoth Cave,
Mammoth Cave, Ky.

Dear Mr. Thompson:

The shark to which the spine belonged lived in an inland sea spreading over what is now the Mississippi Valley and the Appalachian Mountains something like 300 million years ago. The geological period during which he lived is known as the Mississippian. In this sea, which endured for possibly 30 million years, there was deposited a vast amount of mud, much of which was lime mud. In the course of shark events the shark died and his body was broken up and decomposed and the hard parts - the teeth and the spine - were scattered by the waves. Thus the entire body cannot be expected as a fossil. Indeed, sharks have no bones and the only possible hope would be an impression of the cartilaginous skeleton. This is rarely found for any fossil sharks. Your shark was probably 10 to 12 feet long. The spine indicates that he was probably of an average size, not especially large for this particular kind. The name to which he did not answer during his life is Ctenacanthus.

Following the Mississippian period of geologic time came the Pennsylvanian, during which the sandstones, shales and coal measures of Kentucky and the Appalachian region were deposited on top of the lime mud in which the shark spine was already embedded. Then millions of years later this whole interior sea became drained and on the land thus formed streams eroded away all of the Pennsylvanian strata from your particular region and a good portion of the Mississippian strata. Mammoth cave is in one of the lower formations of the Mississippian system of rocks. All the rest has long since been carried off as detritus in the millions of years since the uplift.

One of the latest (geologically) events in your region has been the cutting of Green River Valley and the consequent draining into it through springs of ground water from Kentucky rain fall. This ground water working along cracks has dissolved out a certain amount of the lime mud, which is now limestone, and made the exceedingly complicated system of chambers of Mammoth and associated caves. The cave, therefore, is millions of years younger than the shark. The shark is as old as the rock in which the spine was embedded.

The glossiness of the tooth is a record of the original dentine which covered it. It is of course now a petrifaction

Figure 15. Page one of a letter from Dr. J Harlen Bretz to Mr. W. W. Thompson at Mammoth Cave regarding shark fossils, 1938. NPS / MAMMOTH CAVE NATIONAL PARK ARCHIVES

A New Discovery as a New National Park Emerges: Late 1930s–1940s

National Park status (1941) ushered in an era of prolific scientific study, including the investigation of geology and paleontology that continues to this day.

In October of 1938, Guides Carl Hanson, Pete Hanson, Claude Hunt, and Leo Hunt descended in Mammoth Cave to Roaring River, then scrambled up several crawlways to emerge in a pristine gypsum encrusted section of Mammoth Cave dubbed the New Discovery. Despite many locations in the past also being temporarily called New Discovery, this time the name stuck and the name still applies today. Frederick Vosburgh of the National Geographic Society (Figure 16) wrote about his July 1939 visit to the New Discovery section of Mammoth Cave (Vosburgh 1940).

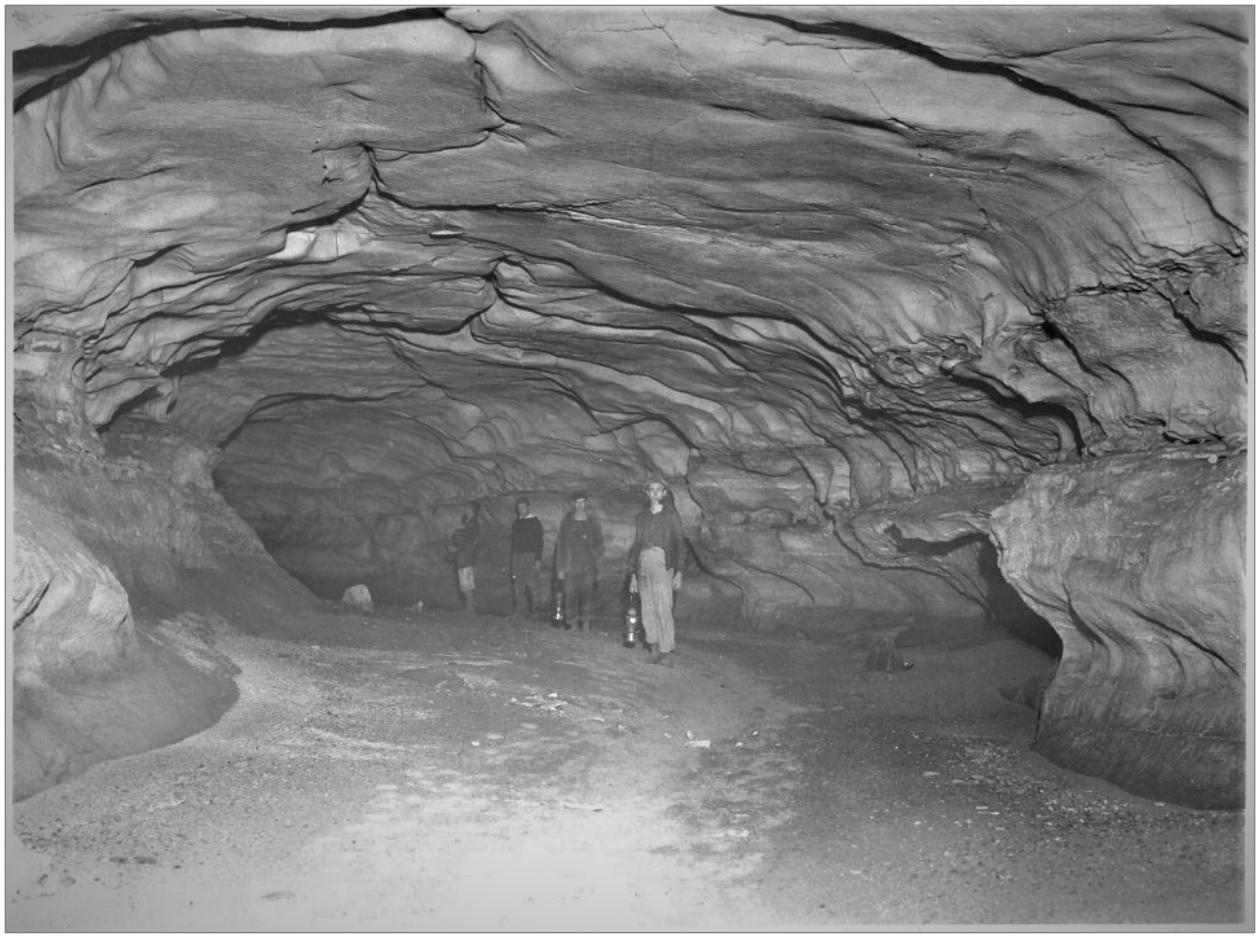


Figure 16. Frederick Vosburgh and others in the Fossil Avenue section of New Discovery. Original caption: “This section of the newly-discovered cave is known as Fossil Avenue. It is a graphic illustration of the force exerted by the underground stream which cut its way through the limestone walls. Fossils embedded in the walls and ceiling gave the avenue its tentative name. From left to right, Frederic [sic] Vosburgh of the National Geographic, Washington; R. Taylor Hoskins, acting superintendent of Mammoth Cave National Park; and guides Leo Hunt and Pete Hanson.”
NPS / MAMMOTH CAVE NATIONAL PARK ARCHIVES / RAY SCOTT

His trip focused on the glorious gypsum formations and the story of discovery by the guides, but he did include a section on animal bones found in the cave. He noticed

> *"…millions of bats' bones in this avenue," "…scratches found on the wall of Fossil Avenue…made by a raccoon," "…several bones…identified by Dr. C. Gilmore of the Smithsonian Institution as those of a raccoon," "A single bone…representing the ulna of a large bear." (Vosburgh 1940)*

Vosburgh also described a new 28-m (92-ft) drill hole (Figure 17): "With a sense of almost luxurious safety we sat on the rocks below while down the shaft came sandwiches, coffee, films, and fuel for our lamps."

A biological reconnaissance of the New Discovery section of Mammoth Cave was conducted in January 1941 by Mr. Kenneth Dearolf, Educational Director of the Public Library Museum in Dayton, Ohio. In Fossil Avenue, he collected bones which were sent to the "National Museum" (Smithsonian) for identification. Among the animals represented were Allegheny woodrats, little brown bats (Figure 18), American martens, Eastern pine martens, raccoons, and bobcats. Scratches from raccoons on the walls of Fossil Avenue were noted along with possible mouse scratches near the rimstone dam. Mississippian fossils (Figure 19) observed in the walls of Fossil Avenue included corals, crinoids, and brachiopods (Dearolf 1941). Jegla (1963) confirmed that the bat bones in Fossil Avenue were indeed *Myotis lucifugus* (little brown bat). Fossil Avenue continues to yield paleontological discoveries, including shark fossils (Chapter 7).



Figure 17. Guide Young Hunt and Cave Manager Marty Charlet lower supplies down the 28 m (92 ft) drill hole for scientists, explorers, and photographers in New Discovery, summer 1939.
COURTESY OF RICH KLINE / RAY SCOTT

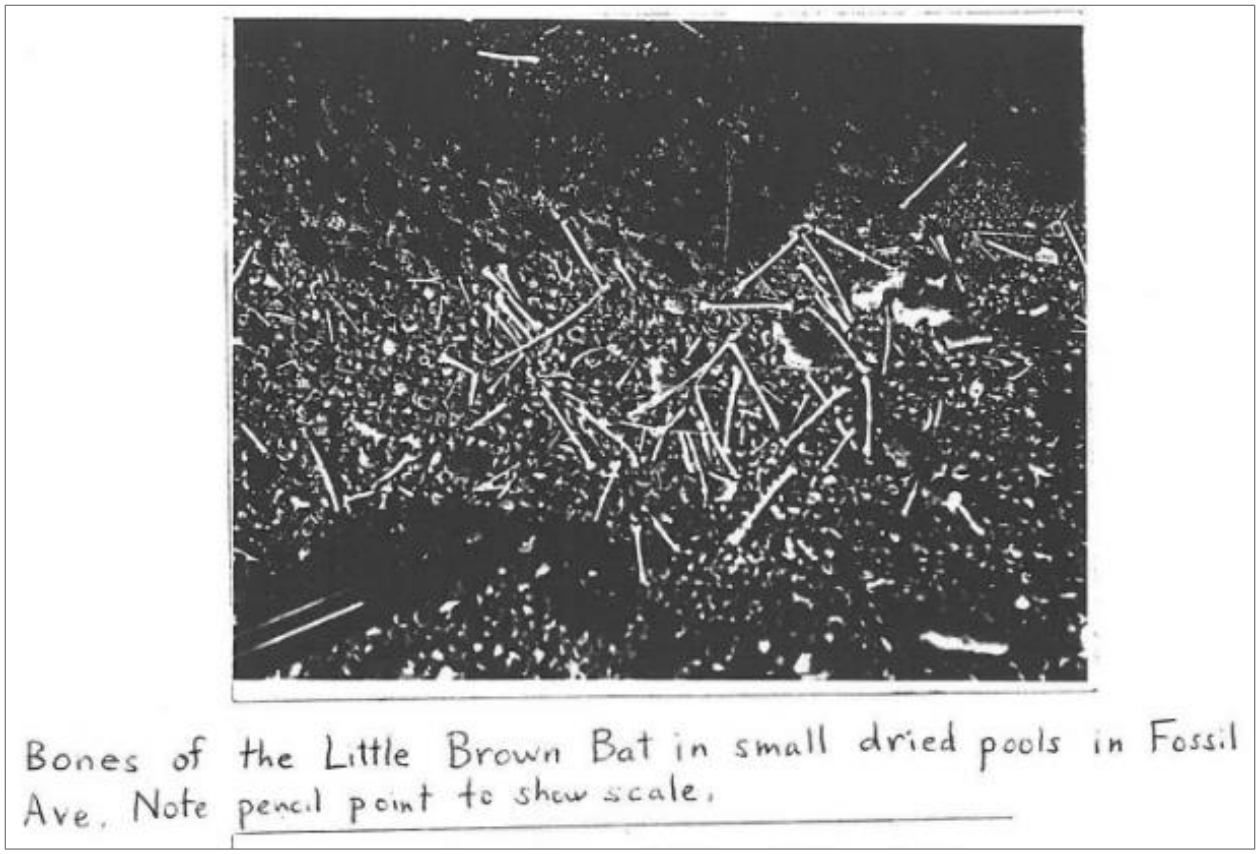
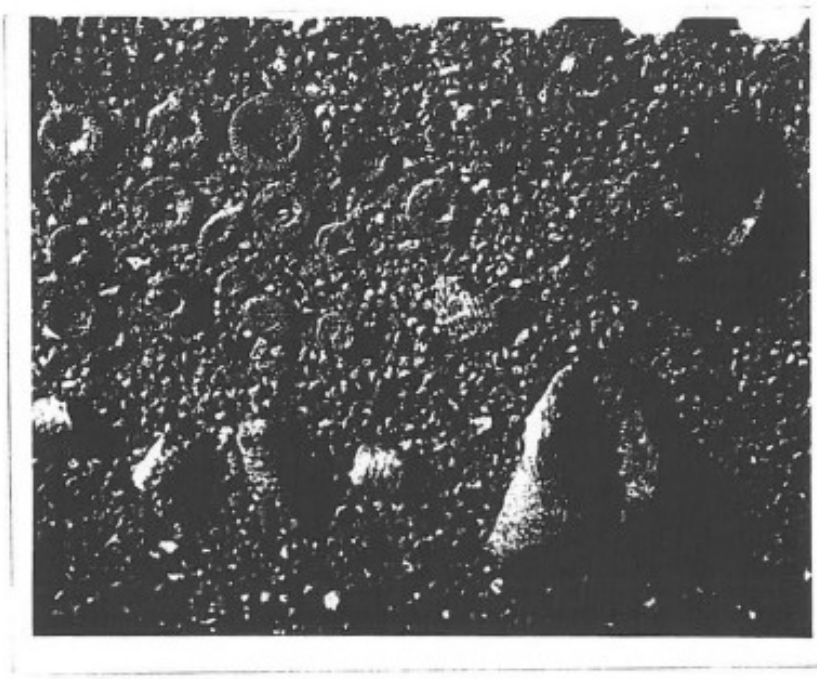
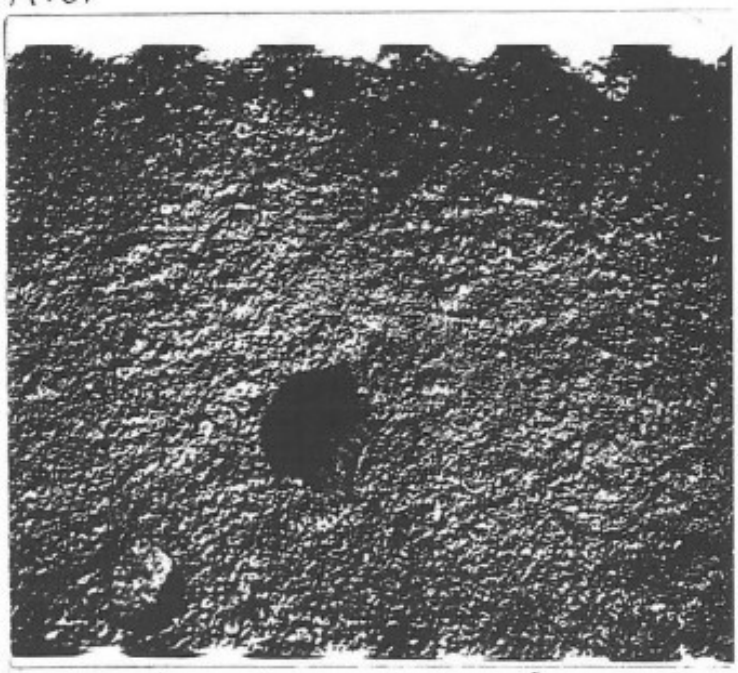


Figure 18. Bat bones in Fossil Ave (Dearolf 1941).
NPS / MAMMOTH CAVE NATIONAL PARK ARCHIVES



Fragments of fossil corals, Brachiopods & crinoids in the sand of Fossil Ave.



Fossil Cup Coral eroded part way from ceiling in Fossil Ave.

Figure 19. Invertebrate fossils observed in Dearolf (1941).
NPS / MAMMOTH CAVE NATIONAL PARK ARCHIVES

More Interest by Outside Entities: 1950s

In April 1954, the Geological Society of Kentucky held their spring meeting at MACA. As part of a field excursion to geologic sites of the region, they identified some fossils (McGrain 1954).

> *...the writers viewed 7 feet [2 m] of coarse-grained fossiliferous limestone, containing both Productus inflatus [brachiopod] and a large unidentified crinoid stem on the south bank of Green River at Houchins Ferry in the western part of Mammoth Cave National Park.*

They included two additional localities outside of the national park, containing the same rock layers, wherein they identified the following: coral *Campophyllum gasperense* from the upper Renault Limestone (=Girkin); crinoid *Talarocrinus* from the middle Renault (=Girkin); crinoid *Platycrinus penicillus* from the Ste. Genevieve; and corals *Lithostrotion proliferum* (=*Acrocyathus proliferum*), *L. canadense* (=*Acrocyathus floriformis*), and *Syringopora* from the St. Louis Limestone (McGrain 1954).

In a memorandum (Figure 20) dated February 2, 1959, from Frank E. Buffmire, Acting Chief, Branch of Museums, to the unnamed Regional Director, Region One, a unique echinoid (Figure 21) is described as "the finest specimen of *Melonites* ever discovered." A few paragraphs later he elaborates, "…to establish the superlative value of the specimen and verify the opinion of the National Museum specialists that this is the best-preserved *Melonites* specimen ever found." A second letter dated April 21, 1959, from Perry E. Brown, Superintendent, Mammoth Cave, to the unnamed Regional Director, Region One, states he is "agreeable to donating it to the National Museum." These letters do not contain any information as to where in Mammoth Cave National Park the specimen was discovered, but they do say further publications would follow on account of its perfect preservation. At the time of publication, the specimen is on display (specimen number USNM PAL 380837, echinoid *Melonechinus indianensis* from Mississippian rocks of Edmonson Co., Kentucky, "NAT.PARK SERV. LOC 6320"). However, to date, no additional publications have been located. See Chapter 6 for more information on this specimen.

February 2, 1959

Memorandum

To: Regional Director, Region One

From: Acting Chief, Branch of Museums

Subject: Fossil Specimen, Mammoth Cave

We have been informed by the U.S. National Museum that among the fossils submitted for identification prior to inclusion in the Mammoth Cave exhibits was a probable new species of echinoid of the Genus Melonites.

This particular specimen has created unusual interest inasmuch as it appears to be the finest specimen of Melonites ever discovered. The National Museum therefore has inquired whether the specimen may be retained in its collections. There are several considerations the Superintendent may wish to take into account before reaching a decision.

The inclusion of a type specimen in the proposed exhibit is not mandatory, since the purpose of the display is to illustrate the geological story with a group of representative fossils from Mississipian time.

The National Museum has been very cooperative with us in the past, and in this instance has offered to provide some fine quality exhibit crinoids to add to those in the Mammoth Cave collection which have been incompletely preserved.

It may be that additional specimens are available at Mammoth Cave, in which case one or more could be deposited with the National Museum. It may be also that there exist in the collections of the University of Kentucky similar specimens of which a surplus individual could be provided the National Museum. For exhibit purposes we would like to establish the superlative value of the specimen and verify the opinion of the National Museum specialists that this is the best-preserved Melonites specimen ever found. They indicate that even if the specimen is not a new species it will be described and published on because of its nearly perfect condition.

Figure 20. First page of a memorandum from Frank E. Buffmire, Acting Chief, Branch of Museums, to unnamed Regional Director regarding a unique echinoid fossil found at Mammoth Cave.
NPS / MAMMOTH CAVE NATIONAL PARK ARCHIVES

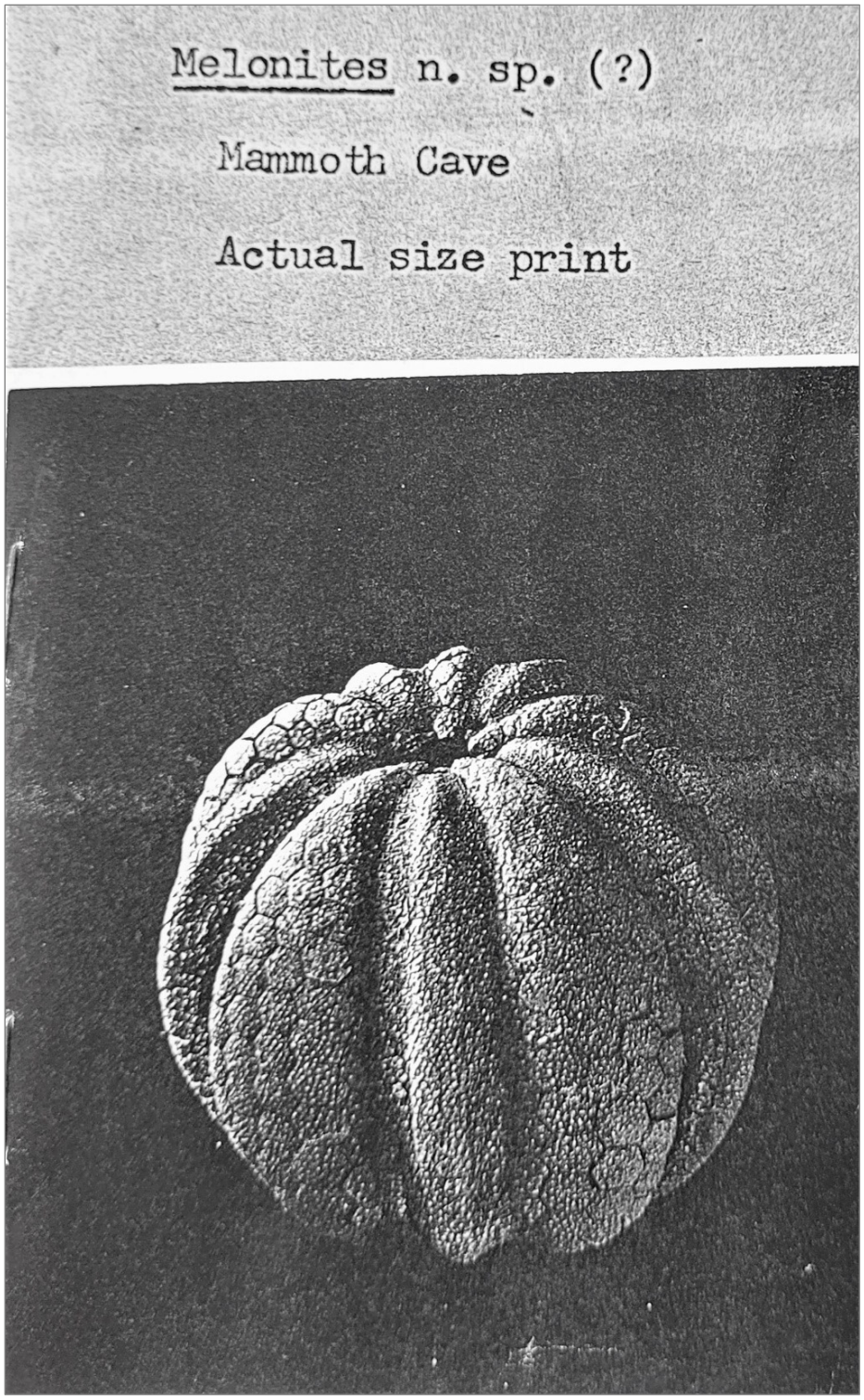


Figure 21. Picture of a *Melonites* echinoid fossil included with the memorandum in Figure 20.
NPS / MAMMOTH CAVE NATIONAL PARK ARCHIVES

An extensive study of sediments in Mammoth Cave was carried out in the mid-1950s by William E. Davies and E. C. T. Chao of the U.S. Geological Survey. The emphasis of this project was on grain

sizes, distribution, and mineralogy, but they also investigated ancient bat guano in a passage called Chief City. Radiocarbon dating put the age at greater than 38,000 years, which was the limit of analysis at the time (Davies and Chao 1959). Colburn (2005) also attempted to date this guano but again it came out as greater than the analysis limit (54,000 years) after calibration. Jegla and Hall (1962) further investigated this guano and found bones from three genera of mammals: *Peromyscus* (mouse), *Myotis* (bat), and *Tadarida* (free-tailed bat). This latter genus is of great significance because free-tailed bats do not range this far north today, and so these bats were probably living here during the last interglacial period, known as the Sangamon (130,000–71,000 years ago). They reported that the area of guano accumulation was more than 0.4 km (0.25 mi) long and so this was most certainly a large colony.

Microfossils Abound: 1960s–1970s

The tooth-like oral elements of extinct creatures called conodonts can be used to correlate beds of rock across regions. Conodonts were small jawless eel-like creatures, but their tooth-like hard structures are very distinctive when viewed under a microscope. On behalf of the Illinois State Geological Survey, Rexroad and Jarrell (1961) used conodont fossils to correlate beds in the Beech Creek Limestone (upper Girkin), Big Clifty Sandstone, and Haney Limestone across southern Illinois, Indiana, and western Kentucky. Beech Creek (upper Girkin) Limestone was sampled along the roadcut down to Houchins Ferry in MACA for this purpose. The following year, Rexroad and Liebe (1962) used conodont fossils to look at the Paoli (lower Girkin) and equivalent formations in southern Illinois, Indiana, and western Kentucky. No sampling was done in the park, but rocks were sampled at a large quarry several miles away near Horse Cave. One interesting conodont found only at Downey's Bluff in Illinois along the Ohio River was *Gnathodus texanus*. This species is a useful index fossil, indicating a Middle Mississippian age between approximately 346.7 and 336.5 million years old (Ogg et al. 2016). It would be extremely helpful if some enterprising paleontologist could find *G. texanus* in the Paoli Limestone in Mammoth Cave! Ongoing paleontological work in Specimen Avenue has produced a variety of conodont fossils; *G. texanus* has not been identified to date.

In the 1960s, Dr. Pohl took a great interest in microfossils, particularly foraminifers, which are single-celled organisms with a protective shell or "test." There are thousands of species still alive today that inhabit mostly marine settings. Partially, Dr. Pohl's research was to help differentiate between different geologic formations (Pohl 1970), which was and can still be very difficult to do. He also took an interest in microfossils in the Fraileys Shale at the base of the Big Clifty Sandstone. In this shale, he and others found a superabundance of foraminifers representing 16 families and 37 genera, which is quite high diversity (Pohl et al. 1968). The sampling site for this study was 13 km (8 mi) north of MACA, in the town of Broadford, Kentucky (Browne and Pohl 1973). Also during this time frame Dr. Pohl and Robert Cushman (then-president of the Geological Society of Kentucky) collaborated on a field trip with stops in MACA for the 1964 Annual Spring Field Conference of the Geological Society of Kentucky. They reported a variety of invertebrate fossils from two road cuts in the park (Pohl and Cushman 1964).

Mammoths in Mammoth Cave?: 1970s–1980s

Retired paleontologist and Hart County native, Ron Wilson (Figure 22) contributed greatly to the study of Pleistocene fossils in Kentucky, specifically in caves. At one time or another he has been affiliated with the University of Louisville, the Department of the Interior, the Carnegie Museum of Natural History, and later, even served as Director and President of the Cave Research Foundation. Wilson was very active in the park in the late 1970s.

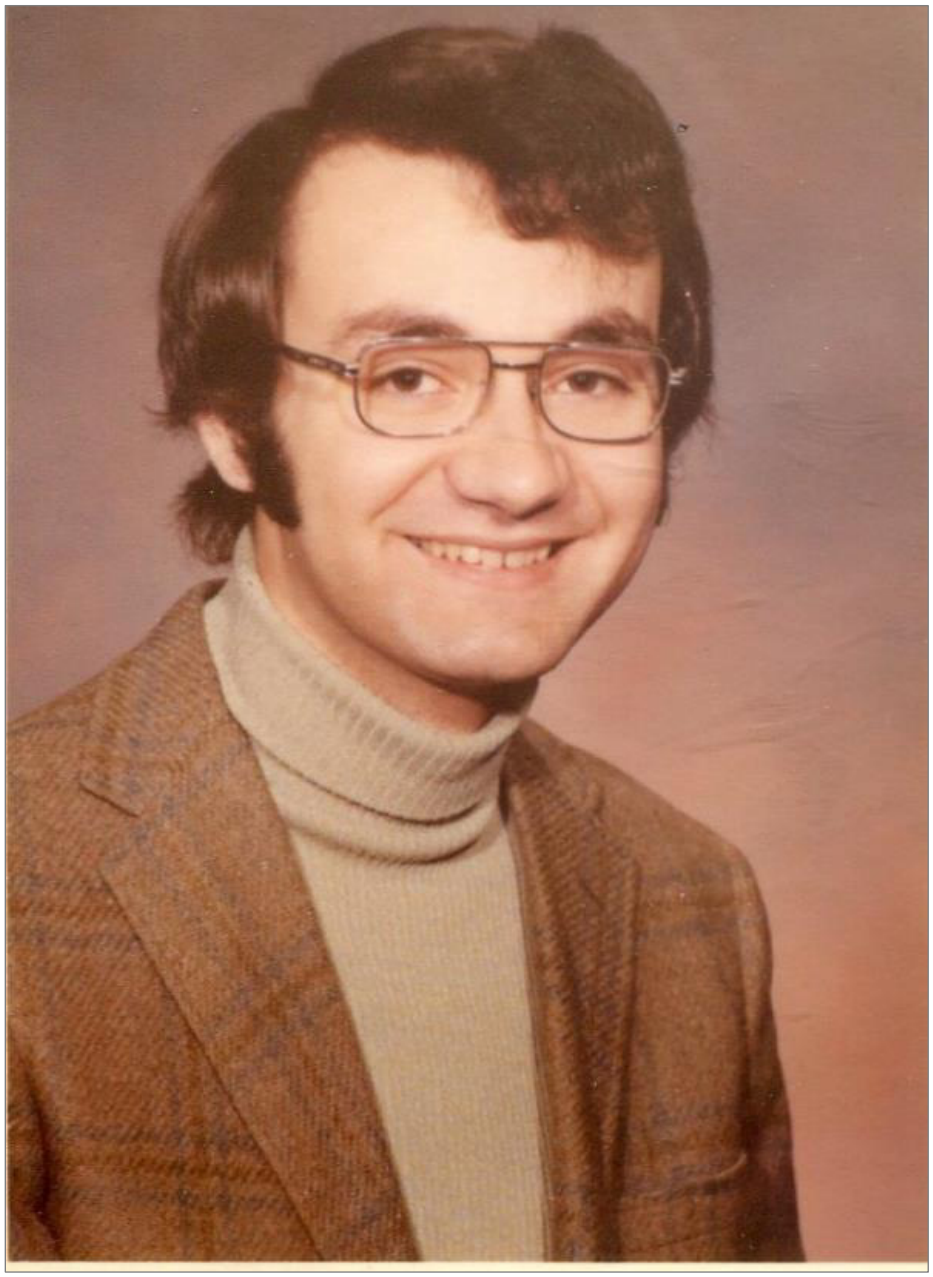


Figure 22. Paleontologist Ron Wilson of the University of Louisville. RON WILSON

As a member of the Cave Research Foundation (CRF), he developed cave resource inventory forms and used them to inventory many small caves both in and outside of Mammoth Cave National Park. While he was at Carnegie, a CRF survey crew shared survey notes that included a sketch of a large mandible they encountered deep in Proctor Cave (Figure 23). John E. Guilday of the Carnegie Museum identified the sketch as a mandible from a short-faced bear (*Arctodus simus*). Wilson obtained paleontological collecting permits and planned a trip to retrieve the *Arctodus* specimen, then used the permits to search for and collect other bone samples from park caves (R. Wilson, pers. comm., 2020).

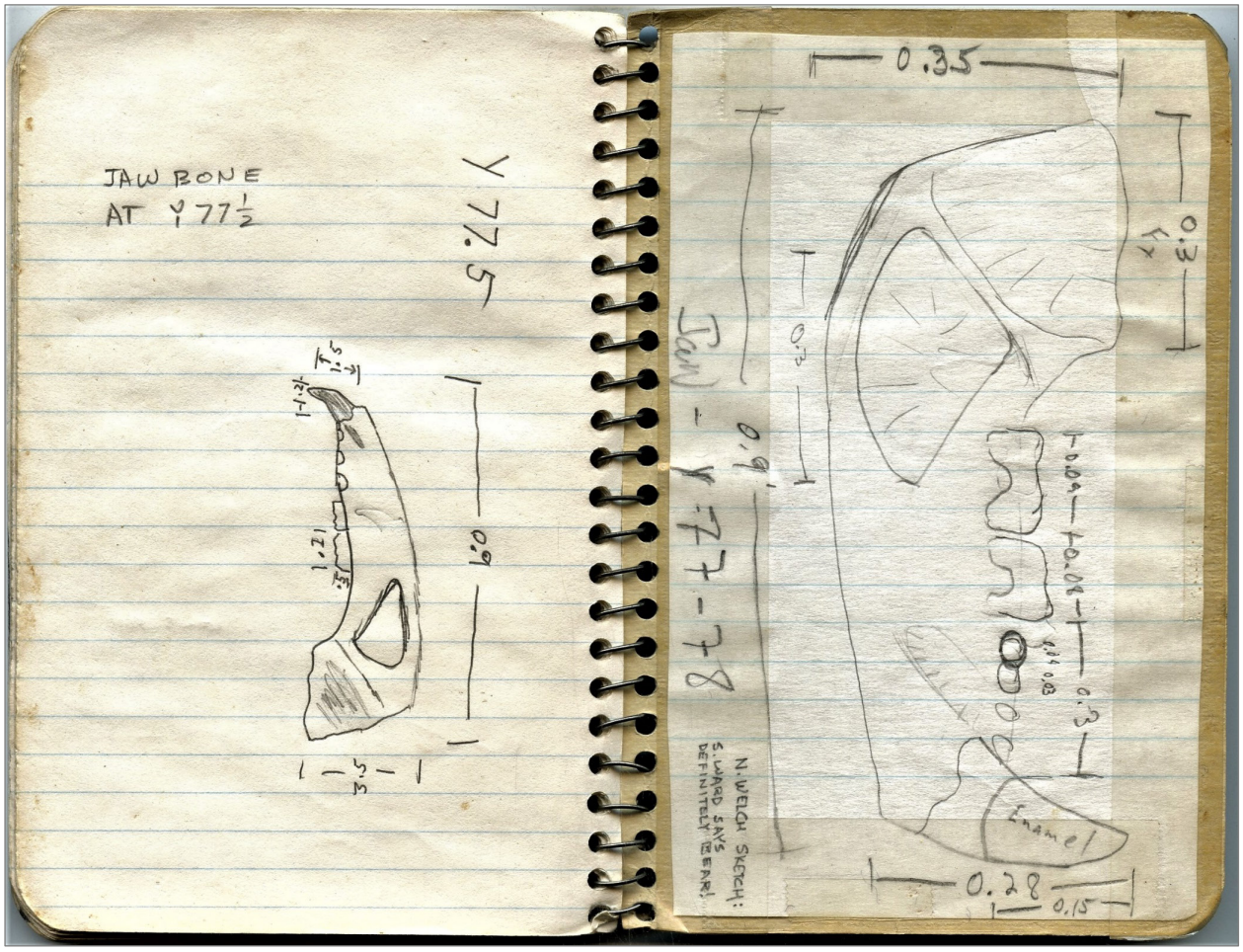


Figure 23. Sketch of *Arctodus* bear jaw fossil from a CRF survey trip report, dated 04/24/1976. Sketch by N. Welch, CRF. Field Survey Book 1224, April 24, 1976, Cave City, Kentucky.
COURTESY OF THE CAVE RESEARCH FOUNDATION

Many specimens from Great Onyx Cave, Proctor Cave, Bedquilt Cave, and Mammoth Cave were reposited at the Carnegie Museum of Natural History (Wilson 1980). In addition to the bones of the giant short-faced bear (*Arctodus simus*), tusk fragments from a proboscidean (either mammoth or American mastodon) and bones of a flat-headed peccary (*Platygonus compressus*) were found in

remote parts of the cave (Wilson 1981, 1985). This was the first time that extinct mammals had been reported from Mammoth Cave (Wilson 1979).

No discussion of geology and paleontology in the park would be complete without at least mentioning Art Palmer's geological guidebook to the park and region. The general section on fossils will be very helpful to readers who are new to this topic (Palmer 1981). This book is invaluable for the lithology and stratigraphy of each formation even though it does not contain a paleontological study of Mammoth Cave. Art Palmer and his wife Peg Palmer (Figure 24) conducted a stratigraphic study wherein thin sections revealed microfossils (Chapter 3). They continue to be an active part of ongoing research at MACA to this day.



Figure 24. Arthur Palmer and Margaret Palmer, State Univ. of New York, Oneonta (emeritus). PHOTOS COURTESY OF ART PALMER

As part of a master's thesis from University of Kentucky concerning the origin of a passage called "The Brucker Breakdown," a team led by Cory BlackEagle reported invertebrate fossils and ichnofossils from various horizons in the Ste. Genevieve within the cave. They identified rugose corals, a few tabulate corals, bryozoans, brachiopods, and crinoids (BlackEagle 1989).

Cherty Trace Fossils and Dead Bats Discourse: 1990s–2000s

Extensive and fascinating fossil burrows (Figures 25 and 26) preserved by chert infilling are located in the Lost River Chert Member of the St. Louis Formation, in the Logsdon River passage. A team led by Tambra Eifert from Southeast State Missouri University studied these burrows in the mid-1990s (Eifert 1996) and determined that such complex burrows had not been known before the Permian Period (299–252 million years ago). At a place called P. Strange Falls the burrows are unusually large, 3.8–8.0 cm (1.5–3.1 in) in diameter, and with chambers measuring up to 1.3 m (4.3 ft) in length. All of the burrows at the Logsdon River site have been partially replaced by hard, corrosion-resistant chert and are covered with a thin coating of pyrolusite (MnO_2). There are other places in the Mammoth Cave System with minor fossil burrows, but none are as extensive and enormous as those in Logsdon River. It is still unknown what organisms made these burrows, but maybe someday someone will find the fossilized remains of these creatures preserved in the chert.

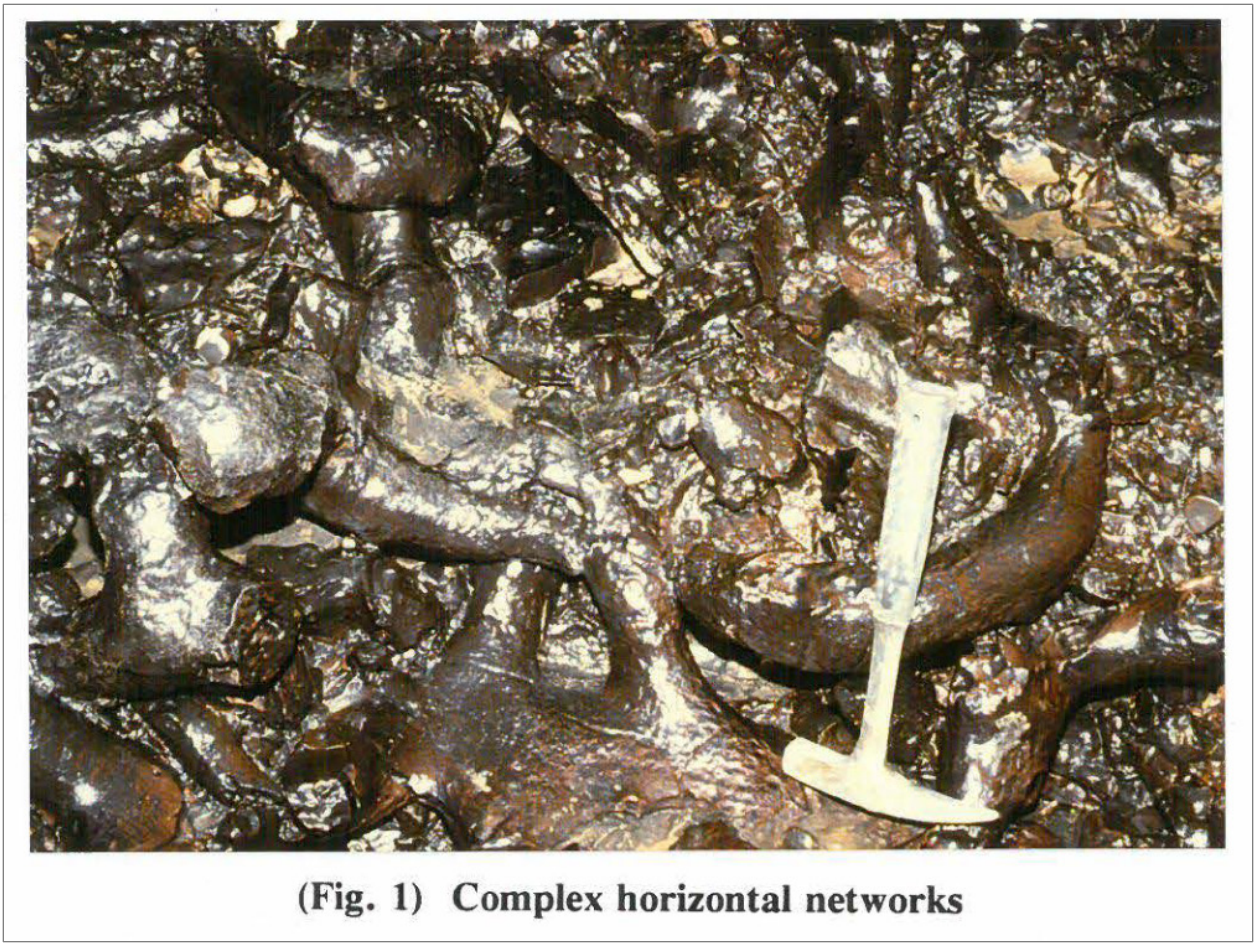


Figure 25. In situ chertified burrow structures in the Logsdon River of Mammoth Cave. Figure published as Fig. 1 in Tambra Eifert's Senior Thesis at Southeast State Missouri University, 1996.
REPRINTED COURTESY OF TAMBRA EIFERT / WASHBURN UNIVERSITY

The next major effort regarding vertebrate paleontology in the park started out small and quickly built up over the coming years. In Bat Cave within the park there are impressive deposits of bat bones in a crawlway. The crawl was dug out decades ago, exposing layers of bone so thick it looked like fragments of straw or grass sticking out between sediment layers. The prevailing opinion at the park was that thousands of bats were killed by major 20th century floods, but the bone bed seemed much older to the park's new ecologist, Rick Olson. Fortunately, in 1994 he met recent doctorate Rick Toomey at the National Speleological Society Convention in Brackettville, Texas. Toomey headed a session on biology and paleontology where he presented his work on Hall's Cave in Texas. Olson, impressed with Toomey's presentation, introduced himself after the session concluded and invited Toomey to investigate the bone deposit in Bat Cave. Colburn (2005) provides an excellent overview on the history of research on Bat Cave and the understandable confusion of the process of trying to sort this out. After two decades, Colburn et al. (2015) finally figured it all out: the bones were deposited during at least 11 flooding events over a period ranging from 10,800 to 2,200 years ago!



Figure 26. In situ chertified burrow structures in the Logsdon River of Mammoth Cave. Figure published as Fig. 4 in Tambra Eifert's Senior Thesis, 1996.
REPRINTED COURTESY OF TAMBRA EIFERT / WASHBURN UNIVERSITY

Throughout the 1990s things developed quickly. Yes, Bat Cave was very interesting but there were major problems in the Historic Section of Mammoth Cave. As late as the mid-1800s, Mammoth Cave had been a major bat hibernaculum. For many decades, however, the entrance had been largely blocked up to prevent cold surface air from making the cave uncomfortable for people in winter

months. Then, in 1989 the park decided to restore bat habitat in the cave: they removed the blockages and installed an open grid gate in the entrance passage. They did not know that the entrance passage, called Houchins Narrows, had been enlarged by roughly a factor of two during saltpetre extraction in the early 1800s. Therefore, cold winter air entered the cave like never before, and in January of 1994 forty tons of rock fell from the Rotunda ceiling, smashing some of the War of 1812 saltpetre mining artifacts. Condensation from the influx of cold air was falling like rain on other saltpetre works but management could not reduce airflow without a scientific basis. Rick Toomey and a science team stepped in to help determine what the cave environmental conditions were before the alterations to the cave entrance. Dead bats can talk, so to speak. By identifying bat bones to species level in places like Little Bat Avenue, it was possible to know what hibernating temperatures existed there in the past. Radiocarbon dating can place portions of the fauna in a framework of changing climate over time; one result is that we can identify bones dating to times with climatic conditions comparable to the present. The park used this information to install wind baffles at the Historic Entrance, restoring the original opening and air flow. All this was done via two cooperative agreements with the Illinois State Museum (ISM) where Toomey, Mona Colburn, and Blaine Schubert worked (Toomey et al. 1995, 1998).

Proctor Proboscidean Revealed and a New Kentucky Cat: Early 2000s

The question of whether the tusk fragments collected by Wilson in 1979 were mammoth or mastodon was a burning one for Guide Colleen O'Connor Olson (Figure 27). In the 1990s Olson tried repeatedly and eventually succeeded in getting a sample from the Carnegie Museum sent to a specialist who could determine which it was (Olson 2017). A team returned to Frost Avenue (in the Proctor section of Mammoth Cave) in July of 2001, and they collected more tusk fragments. Mona Colburn of the ISM cleaned up the pieces and sent one to specialist Dr. Dan Fisher at the University of Michigan, who determined the tusk fragment was from an American mastodon (*Mammut americanus*), much to the disappointment of many at Mammoth Cave (Colburn 2005).

This same team continued on to the Y survey passage in Proctor where the giant short-faced bear (*Arctodus simus*) jaw was found in 1979. They collected many bone fragments which Colburn prepared at the ISM. Many of the bones represented unremarkable species, such as horse, cow, raccoon, or rabbit, but one piece of a left fibula intrigued her. It turned out to belong to *Smilodon*, otherwise known as a saber-toothed cat. This was a new record, not just for the park but also for the state of Kentucky (Colburn 2005).



Figure 27. Guide Colleen O'Connor Olson examining the shale layer between the Big Clifty and Girkin Formations in MACA. NPS / RICK OLSON

Twin Tibiae, a Frozen Former Entrance, and a Paleontological Inventory in Two Parts: The 2000s Continued

Kentucky's first *Smilodon* was preceded by another remarkable fossil find, in the form of two black bear tibiae. In February of 1979 Ron Wilson and team visited Sophy's Avenue within Mammoth Cave. In addition to bits of smaller mammals they found a tibia from a black bear (*Ursus americanus*). That bones could be washed into the cave was not surprising because the north end of Sophy's Avenue terminates near Hunts Sink on the surface. Fast forward to the paleontological inventory project beginning in 2001 when a team went in to see if any more remains could be recovered. Not much was found except for another black bear tibia! These bones are rare enough that one might expect both tibiae to be from the same individual. Strangely enough, though, the bones were both left tibiae, indicating two individuals.

In January of 2000, Rick Toomey and Mona Colburn went to the Frozen Niagara entrance (an artificial entrance made by George Morrison) to do some paleontological work. They brought Rick Olson along for a memorable 50th birthday, as they discovered interesting bones beneath a flowstone layer that had been cut through decades before to make the tourist trail. This flowstone was later aged

at 125,000 to 126,000 years old via uranium series dating, which corresponds to the Sangamon interglacial period. Bones of species that no longer live there were found, including remains of beautiful armadillo (*Dasypus bellus*), pocket gopher (*Geomys* sp.), water rat (*Neofiber* sp.), and flat-headed peccary (*Platygonus* sp.) (Colburn et al. 2000). This assemblage of fossils represents a former natural cave opening where the sediments have since been capped by flowstone and metaphorically frozen in time.

It is difficult to overstate the importance of the 2005 paleontological inventory already referenced several times in this document. Officially titled "The Paleontological Inventory Project on vertebrate remains found in select passages and caves at Mammoth Cave National Park, Kentucky" (Colburn 2005), the study was conducted by Mona Colburn (Figure 28) of the Illinois State Museum, in collaboration with Rick Toomey and Rick Olson. In addition to previously stated specimens, an upper-level cave passage filled with fine sediment from backflooding yielded some unique fossil finds, including a proximal half of a right(?) femur of an extinct vampire bat (*Desmodus stocki*) and poorly preserved fragmentary bones of a hellbender (cf. *Cryptobranchus*). The current report could be regarded as the second part of the paleontological inventory that was begun in 2005.

Chris Widga and Mona Colburn investigated bat guano deposits as part of environmental compliance for future cave trail work in Mammoth Cave. Because test plots were put in for simultaneous archeological evaluation, this work was probably the first stratigraphically controlled Quaternary paleontological work in Mammoth Cave. They learned interesting things, for example that the free-tailed bats that roosted in Chief City appear to have been foraging in a forested landscape rather than an open one based on stable isotope data, which is unusual for this species. Gothic Avenue also has ancient guano, but it is not the same as that in Chief City. This deposit dates to what is called the Farmdalian interstadial, and based on calibrated radiocarbon data it is 29,000–27,200 years old (Widga and Colburn 2015).



Figure 28. Mona Colburn and Chuck DeCroix examine a raccoon skull in Fox Ave. Photograph also published as Figure 9-8 in “The Paleontological Inventory Project on vertebrate remains found in select passages and caves at Mammoth Cave National Park, Kentucky” (Colburn 2005). NPS / RICK OLSON

Conclusion, and a New Chapter

In 2019, National Park Service Senior Paleontologist Vincent Santucci reached out to Mammoth Cave National Park looking for photos of specimens to be included in a traveling exhibit about fossils in caves within national parks. Rick Olson and Rick Toomey responded with photographs of a particular fossil (Figure 29) in the wall of a passage called “Specimen Ave” that included shark teeth

and, they suspected, potential cartilage. It had been discovered in the 1990s by Guide Tres Seymour. Paleontologists Santucci and JP Hodnett were then concluding the paleontological resource inventory of Grand Canyon National Park and immediately recognized the importance of the specimen. JP traveled to Mammoth Cave to research the specimen and identified it as a partial cartilaginous jaw of a *Saivodus* shark. He also identified 10 species from 30 additional specimens during his first visit. He and Santucci then recommended the initiation of the Mammoth Cave National Park Paleontological Resource Inventory.



Figure 29. The shark tooth fossil in Specimen Ave within Mammoth Cave that jump-started this Paleontological Inventory Project in 2019. The tooth is about 3 cm (1 in) across. NPS / RICK OLSON

This Paleontological Resource Inventory Report was initiated in 2019 with the intention of furthering our understanding of the rich diversity of fossils in Mammoth Cave National Park by continuing prior studies and uncovering previously unknown resources. The following chapters illustrate a cooperative effort to further our scientific understanding in this field. Much of the fieldwork and ground truthing was performed by volunteers who continue to contribute to the park. This work hopes to advance the role of scientific inquiry and lay the foundation for improved management and stewardship of resources for future research and public education.

Acknowledgments

The authors thank Kathy Proffitt for inviting Guide Kelli Tolleson's involvement with this project, park management at all levels for deciding to take on this important inventory, as well as the ever-growing Paleo Team, which consists of the authors and organizers (Bill Ausich, Mike Donovan, JP Hodnett, Art Palmer, Peg Palmer, Rick Olson, Vincent Santucci, Kelli Tolleson, Rick Toomey, and Justin Tweet), and also numerous people who volunteered their time as spotters, photographers, general field assistants, researchers tracking down historical documents, reviewers of early draft editions, etc. We're certain this is not an all-inclusive list, and we apologize for any omissions.

First and foremost, Guide Rich Boldon for putting in more cave hours than most of us put together. Also, Basia Gawin, Chelsea Ballard, Taylor Harlow, Alex Verde, Miriam Matthias, Jonathan Rager, Mary Schubert, Alisha Wyatt, and Kailey Alessi for fieldwork; Laine Roberts, Anya Gupta, and Michael Goodman, for researching historical databases; and Joe Douglas and his research team Kristen Bobo and Marion Smith for all of the above reasons. Justin Tweet would like to acknowledge Natalia Lopez Carranza, Rudolph Serbet, and Megan Sims of the University of Kansas Biodiversity Institute & Natural History Museum for their assistance with photographing KU collections, including KUVP 255. Thanks also to Tambra Eifert (Washburn University), Ron Wilson, and Tennessee State Library and Public Archives for their assistance with images. Stanley Sides and David Spence (Mammoth Cave National Park) provided reviews.

We'd also like to dedicate this chapter to the memories of Guide/Caver/Author/Researcher Colleen O'Connor Olson, and Caver/Researcher Marion Smith.

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Chapter 3. Stratigraphy of Mammoth Cave National Park

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Introduction

Mammoth Cave National Park, located in west-central Kentucky (Figure 30), is known for its cave, considered world famous for the past two centuries, mainly because of its size and long history of exploration. Since 1972 it has been the world's longest known cave and now contains more than 685 km (426 mi)[1] of surveyed passages. The cave intersects strata that extend through most of the Mississippian System and provides a convenient display of the rock units typical of this part of the continent. Although this report focuses on the strata exposed in the cave, it also includes a summary of the poorly soluble rocks that cap the ridges over the cave.

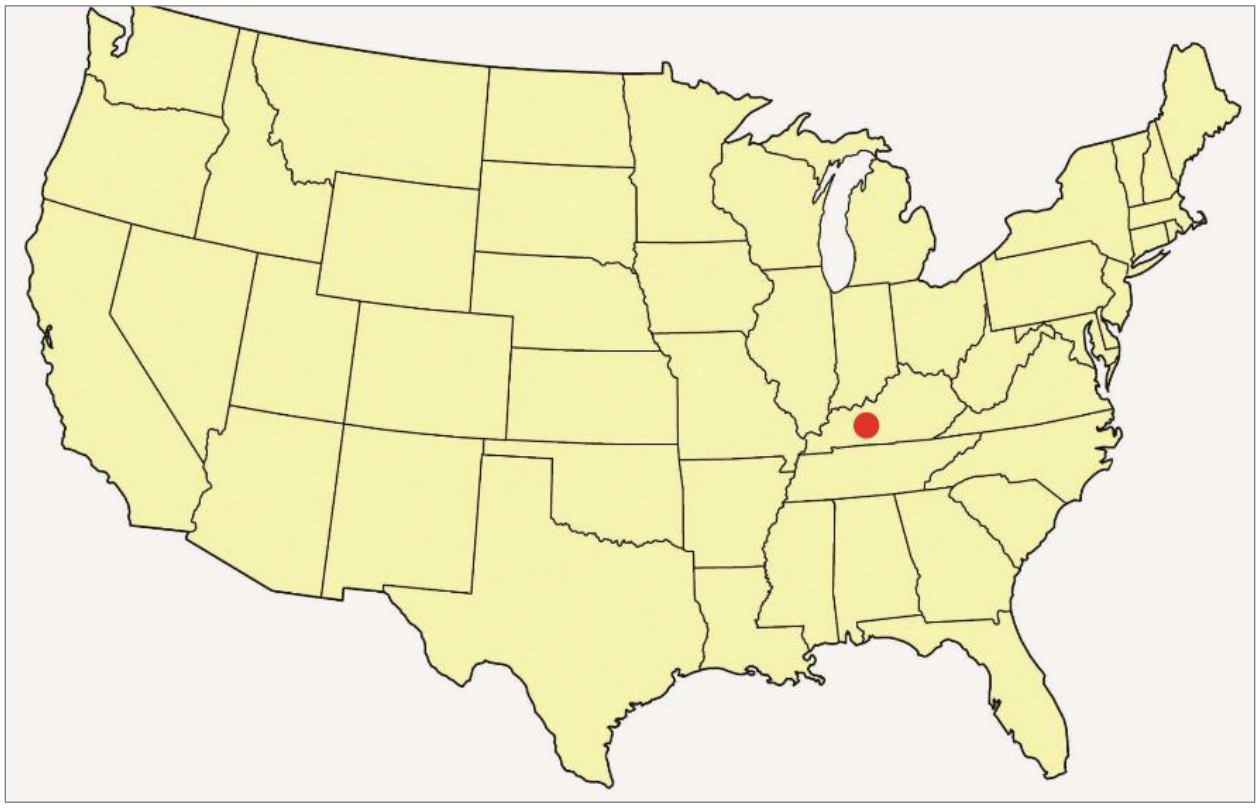


Figure 30. Location of Mammoth Cave National Park, in southwestern Kentucky. U.S. map adapted from Craig and Connor (1979: Plate 10). ADAPTED FROM USGS

[1] For this paper, miles, feet, and inches have been converted to km, m and cm, which are rounded off.

The report is divided into sections reflecting the background and level of interest of the reader. It is meant for the general public as well as for cavers, geologists and students interested in identifying the rocks in the cave. The general introductory section is followed by Appendix A, a detailed description of the geologic column, written specifically for cavers and geologists, and including descriptions of each unit based on observations in the cave. Appendix B is a geologic guide to the tourist route in Mammoth Cave for non-cavers who wish to identify the rocks from a tourist trail.

The Cave

The Mammoth Cave System consists of many integrated sections, mostly located within park boundaries. The best-known parts of the cave system are those within Mammoth Cave Ridge, which contain most of the trails open to the public. The entire cave system extends into adjacent Flint, Toohey, and Joppa Ridges, through passages beneath intervening valleys. A simplified map of the cave and its geologic cross-section are shown in Figures 31 and 32.

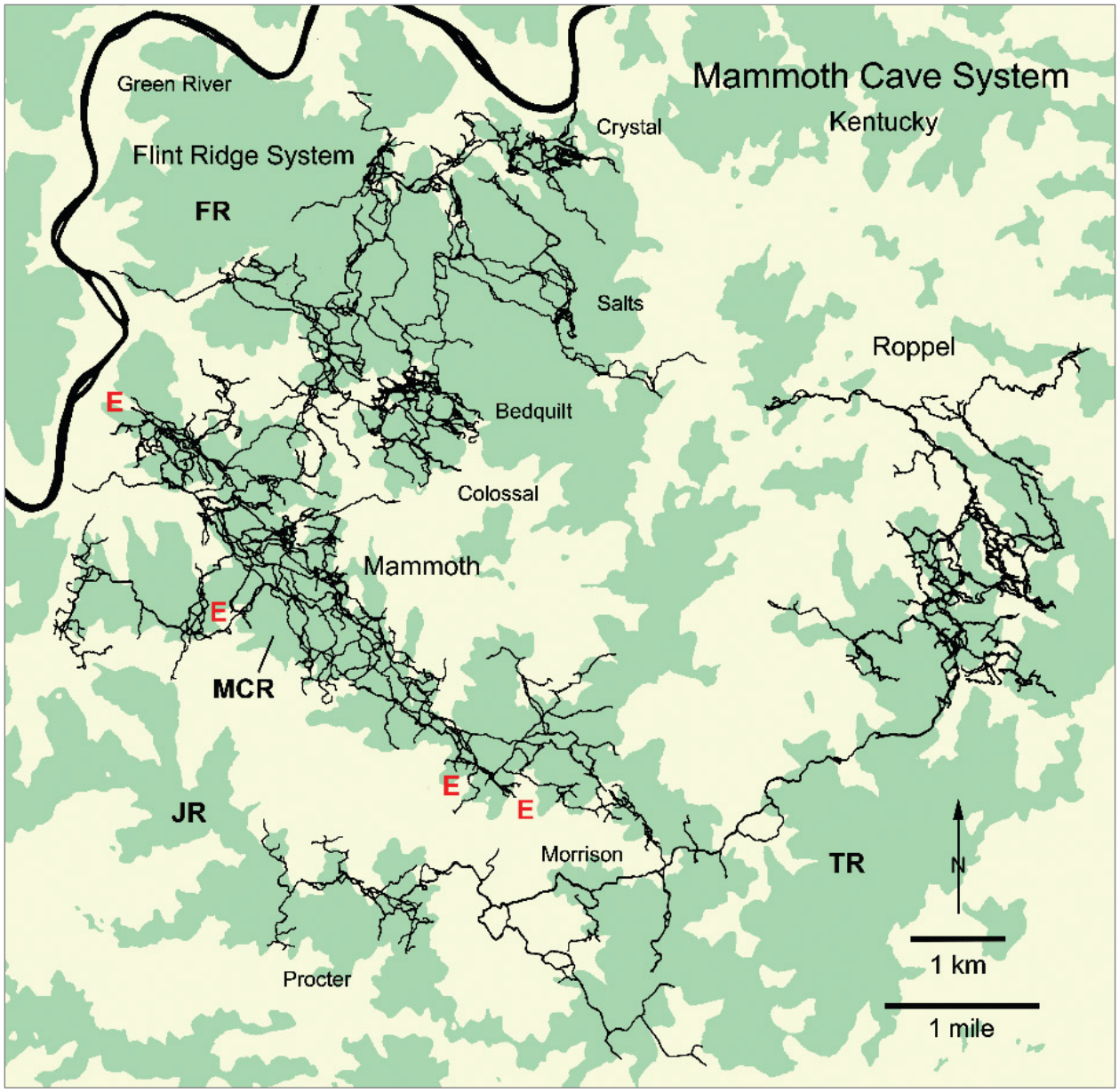


Figure 31. Generalized map of the Mammoth Cave System, Kentucky, based on surveys by the Cave Research Foundation and Central Kentucky Karst Coalition. Names are shown for caves explored separately but connected by later discoveries. Major passages are shown in black. **E** = entrances to tour routes in the main part of Mammoth Cave. Ridges capped by insoluble rocks are shown in green. **Ridge abbreviations: FR**, Flint Ridge; **JR**, Joppa Ridge; **MCR**, Mammoth Cave Ridge; **TR**, Toohey Ridge. Figure adapted from Palmer (2009). A. N. PALMER

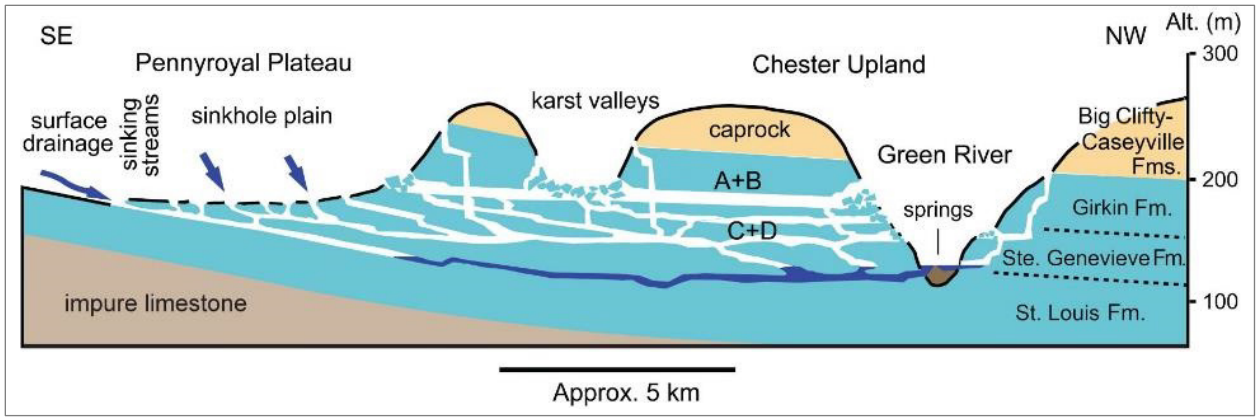


Figure 32. Highly simplified geologic cross-section through Mammoth Cave, showing its relation to the Pennyroyal Plateau, Chester Upland, and Green River Valley. The various cave levels (A, etc.) are shown in their approximate stratigraphic and topographic positions. Figure adapted from Palmer (2009).
A. N. PALMER

Geologic Setting

The park is located in the Interior Low Plateaus physiographic province (Figure 33) (Fenneman 1938). It covers about 58 km^2 (36 mi^2) on the southern flank of the Green River, a tributary of the Ohio River. The low-relief plateaus contain significant amounts of carbonate rock, and so the entire area is well known for its solutional landforms such as caves, sinkholes, and subterranean streams.

Mammoth Cave is located along the southeastern edge of the Illinois Basin, where the mean stratal dip averages about 0.3° toward the northwest. The low dip is largely responsible for the great lateral extent of Mississippian carbonate rock in the region. In the down-dip direction the carbonate rocks are overlain by a relatively insoluble caprock of sandstone and shale. The sandstone cap has protected much of Mammoth Cave from erosion by surface streams. Farther up-dip to the southeast, the resistant strata have been entirely removed by erosion, forming a broad karst plain, the Pennyroyal Plateau.

Most cave development follows the slight northwesterly dip. Bedding plane partings, joints and small faults guide the water flow; however, the cave has four major passage levels adjusted to former pauses in downcutting of the Green River (Figure 34). Entrenchment was controlled by changes in regional base level related to glaciation and were dated using isotopes of quartz in the cave sediment (Table 1). Any given cave level, as it cuts across the dipping strata, may be developed in different sections of the bedrock. Passages at levels A and B are the largest in the system and provide the easiest access (Figure 34). The tour routes in the Mammoth Cave System are developed mainly in levels B1 and B2, which makes observing the bedrock very convenient and will be used later to give an overview of the stratigraphy.

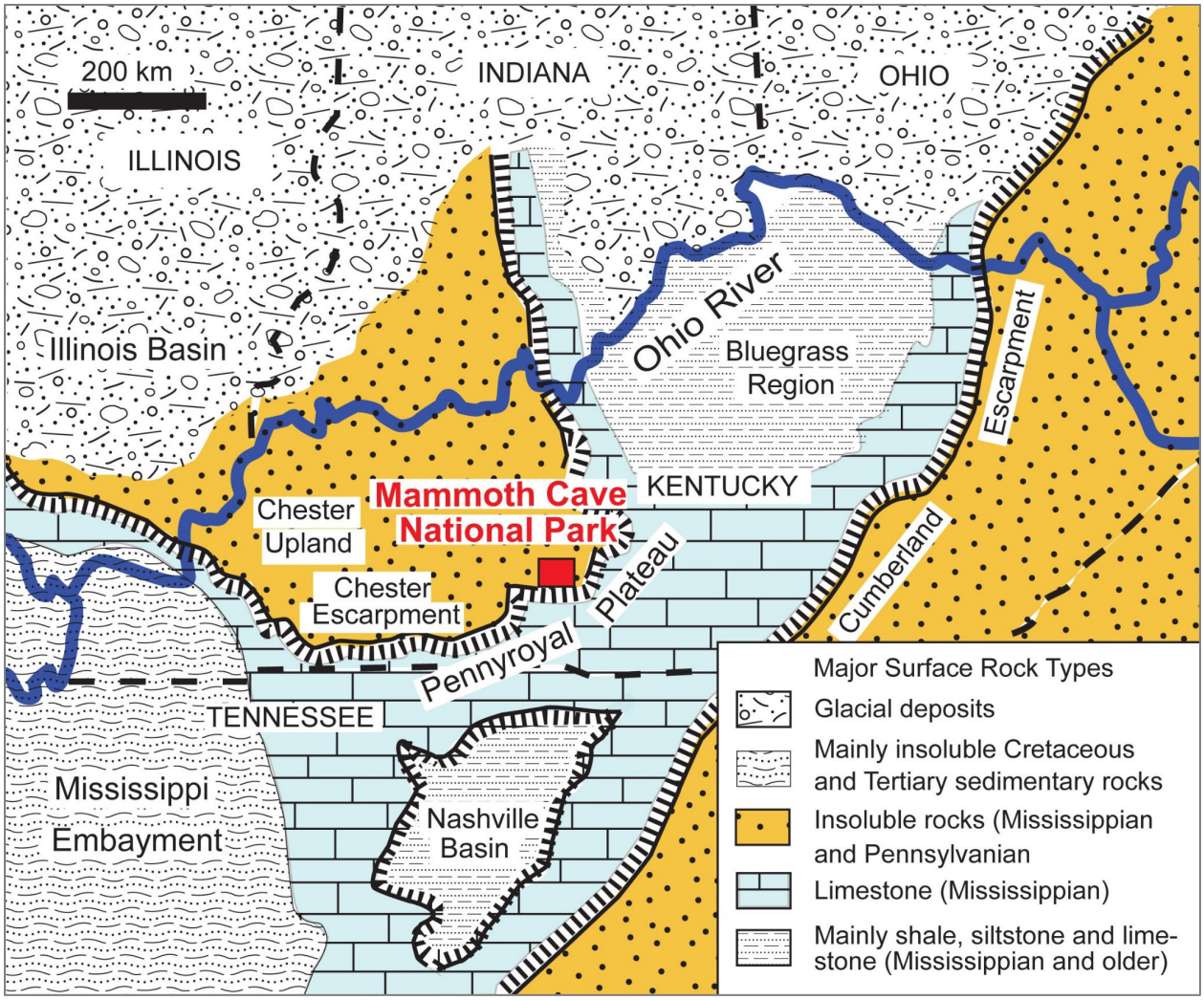


Figure 33. Topographic and geologic setting of the Interior Low Plateaus Province in the vicinity of Mammoth Cave. Figure adapted from Palmer (1981). A. N. PALMER

Table 1. Major passage levels and ages from highest and oldest to lowest and youngest, adapted from Granger et al. (2001) and adjusted for 2010 recalibration (Ma = millions of years ago). “Al” and “Be” are aluminum-26 and beryllium-10, radioisotopes used here to determine age.

Level	Altitude	Al/Be Age of Quartz Sediment
A	190–210 m (620–690 ft)	>6 Ma
B 1	183–190 m (600–620 ft)	6–4 Ma
B 2	174–183 m (570–600 ft)	5–3 Ma
C	168 m (550 ft)	1.6–1.5 Ma
D	152 m (500 ft)	~1.3 Ma

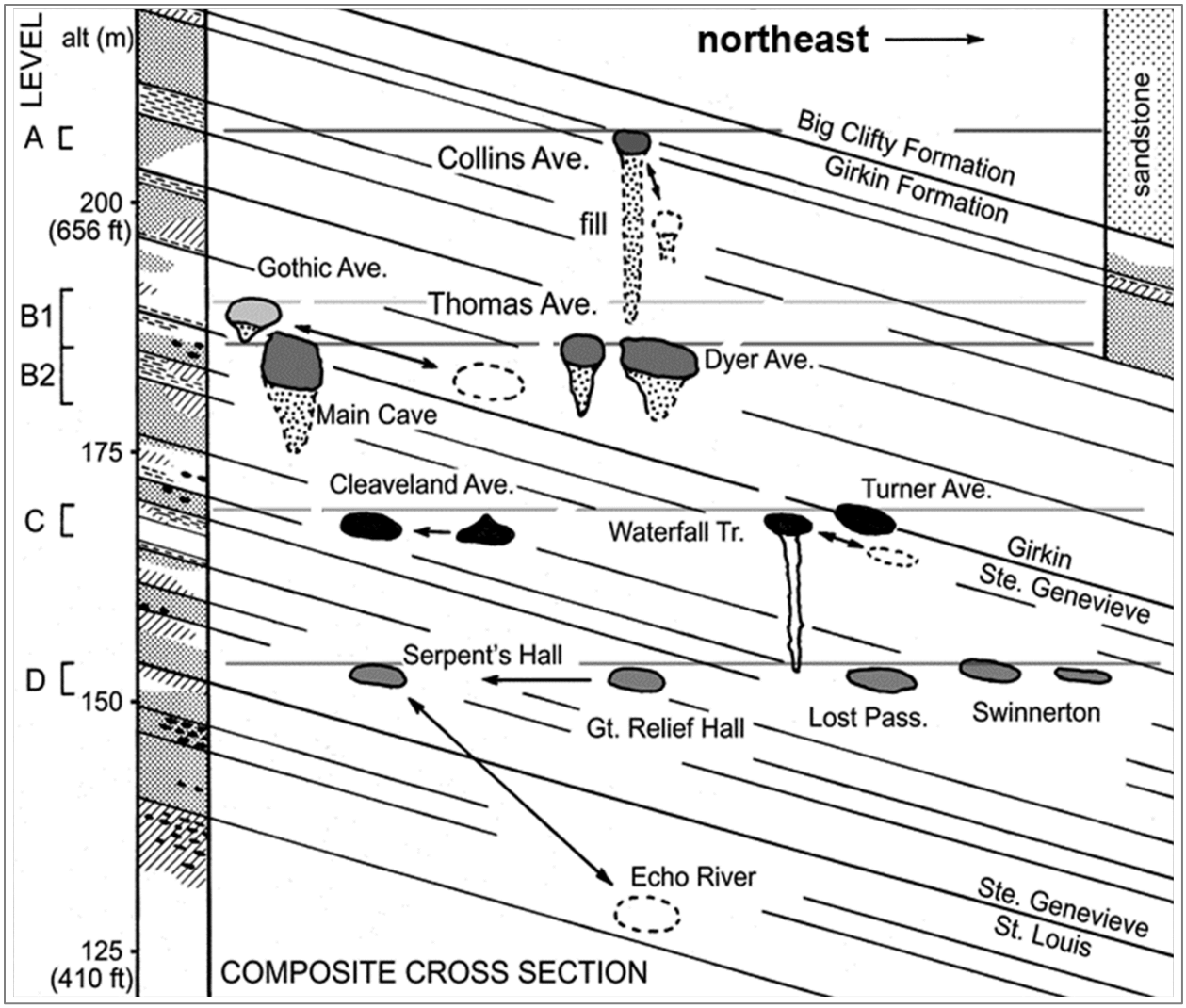


Figure 34. Passage elevations vs. stratigraphic position in the northern parts of Mammoth Cave Ridge and Flint Ridge, within ~2 km (1.2 mi) of the Green River, where levels are most clearly developed. To demonstrate that A, B1, B2, C, and D are true levels in the geomorphic sense (rather than controlled by favorable strata), we plotted the elevations of the major passages vs. their stratigraphic positions. The figure indicates where the formations are best exposed. Gothic Ave., Main Cave, Cleaveland (correct spelling) Ave., Serpent's Hall, Great Relief Hall, and Echo River can all be visited on tour trails. Figure adapted from Palmer (2009). A. N. PALMER

Rocks of the Carboniferous Period

Internationally, the Carboniferous Period is a subdivision of the Paleozoic Era that is dated to approximately 360 to 299 million years ago. In North America the Carboniferous is subdivided into the Mississippian and Pennsylvanian, which are treated as periods in their own right. The Mississippian dates to approximately 360 to 323 million years ago, and the Pennsylvanian dates to approximately 323 to 299 million years ago (International Commission on Stratigraphy 2023). (A geologic time scale is included as an appendix to this inventory, Appendix I.) The carbonate rocks in which Mammoth Cave developed were deposited during the Mississippian Period, while the

relatively insoluble caprock beds formed in the Late Mississippian and Early Pennsylvanian. During the Middle Mississippian, when the equator crossed North America and Canada (Figure 35) (Craig and Connor 1979), beds of gypsum, anhydrite, and algal-laminated dolomite were deposited. Warm, shallow, tropical seas covered much of the area, and marine fossils are common, especially crinoids, but also corals, bryozoans, brachiopods, pelecypods, gastropods, trilobites, ostracods, and skeletal remains (teeth, scales, spines, bone, and cartilage) of marine vertebrates such as sharks, ratfish, and bony fish. See Chapters 5 (invertebrates in general), 6 (echinoderms), and 7 (vertebrates) for more information on the fossils found in these rocks.

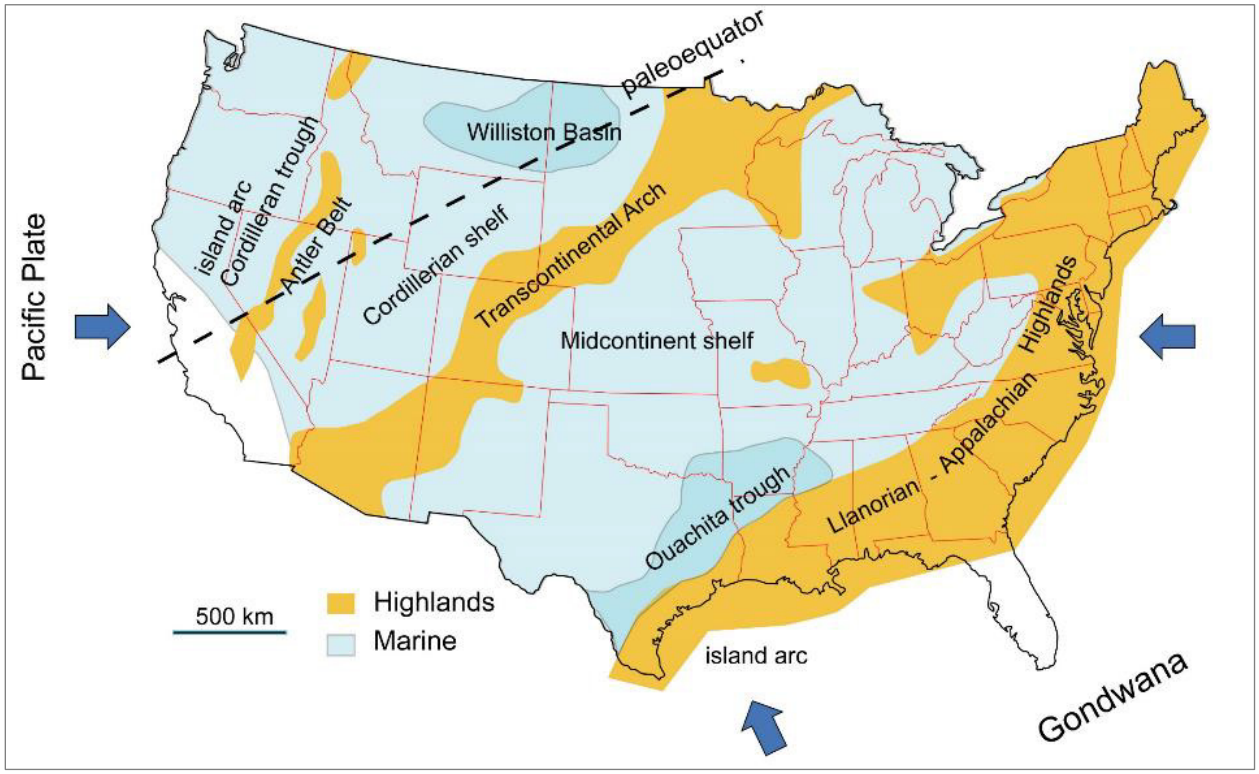


Figure 35. Middle Mississippian geography of the future continental USA. The map depicts the vast extent of the Mississippian sea throughout the midcontinent and the encroaching highlands that delivered increasing amounts of siliciclastic (insoluble), eroded sediment toward the end of the Mississippian. Adapted from Craig and Connor (1979: Plate 10). ADAPTED FROM USGS

During the latter part of the Mississippian, the supercontinent Gondwana began its collision course with what would become North America, leading to a phase of uplift of the Appalachian Mountain chain, and the long period of submergence came to an end. Soils developed, breaking up the succession of marine carbonates. Tidal deltas and low coastal plains to the north periodically invaded large parts of Kentucky, while the climate changed from tropical (hot and humid) to cool and arid, accompanied by glaciation near the south pole.

During the Pennsylvanian Period that followed, conglomerate, sandstone, shale, thin limestone, and coals were deposited. The siliciclastic rocks were derived from sediment eroded from higher land to

the north. In places the rocks reached a thickness of more than 244 m (800 ft), completely burying the deeply eroded surface of the Mississippian rocks above a major unconformity. For the entire 280 million years since the Late Pennsylvanian, the Mammoth Cave region has been above sea level, with the surface exposed to erosion rather than the accumulation of sediment.

Regional Stratigraphy

To construct a geologic column (Figure 36), rocks are divided into formations having similar characteristics; however, because most rocks change laterally from place to place, there is no unique rock type that fits everywhere. Rocks in the park most resemble those of similar age in Indiana and Illinois and can be correlated with some confidence (Sable and Dever 1990; Smith and Read 1999).

On the basis of field work in Crystal Cave (Figure 31), where a continuous exposure from the Big Clifty Formation down to the middle of the St. Louis Formation is present, a geologic column for the cave was created by A.N. Palmer (Figure 37). This column was based on rocks classified by Swann (1963) in Illinois and is similar to the local column of Pohl (1970), with a few exceptions. The regional nomenclature was followed to facilitate correlation of rocks in the park with those of Illinois and Indiana, where most of the rock units were first studied and named.

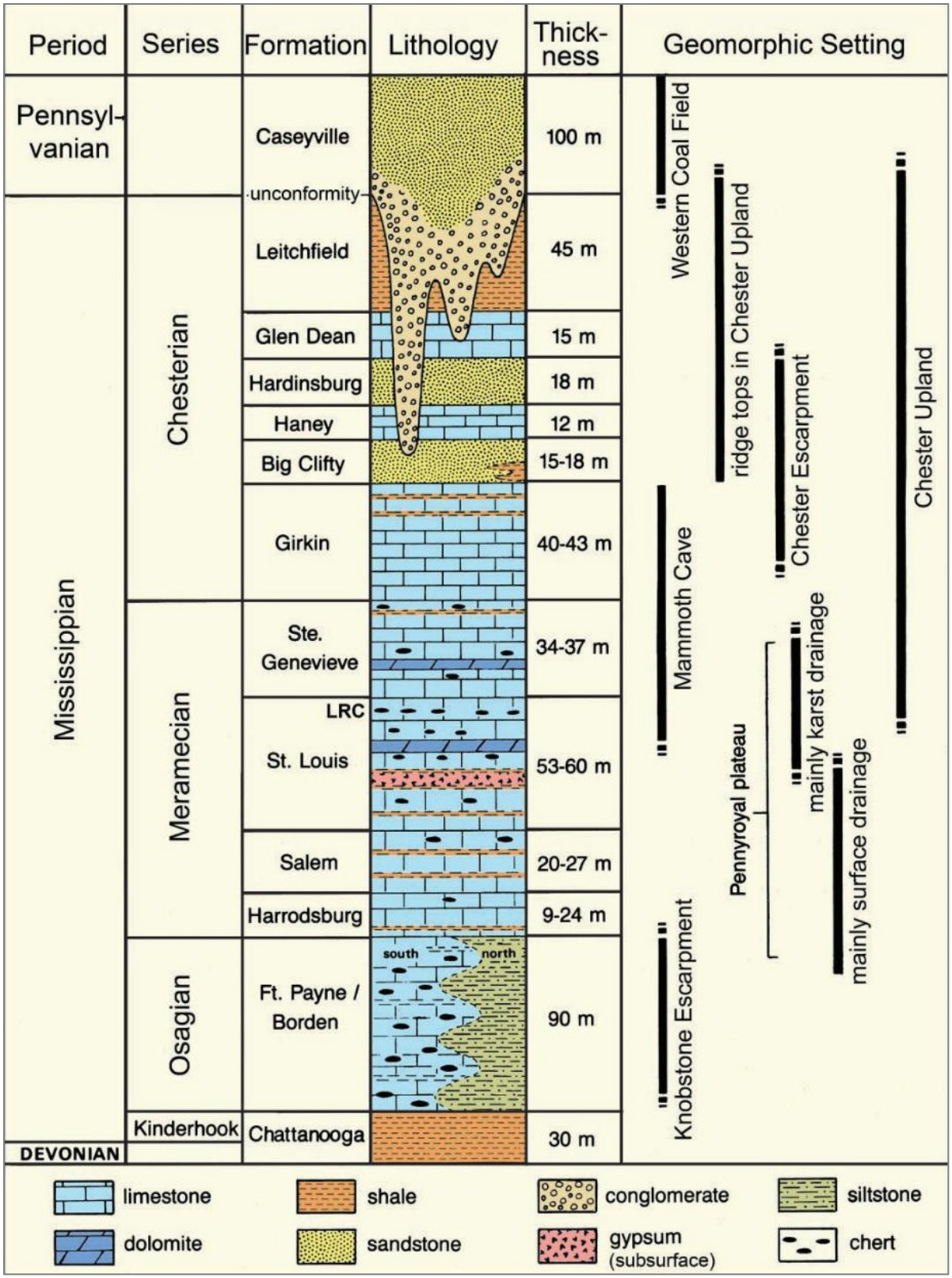


Figure 36. Regional stratigraphy of the Mammoth Cave region (Palmer 2009) indicating local exposures (see additional details in Pohl 1970; Palmer 1981, 2007). **LRC** = Lost River Chert Bed. The cave is developed in the Meramecian and Chesterian stratigraphic series. From Palmer (2009). A. N. PALMER

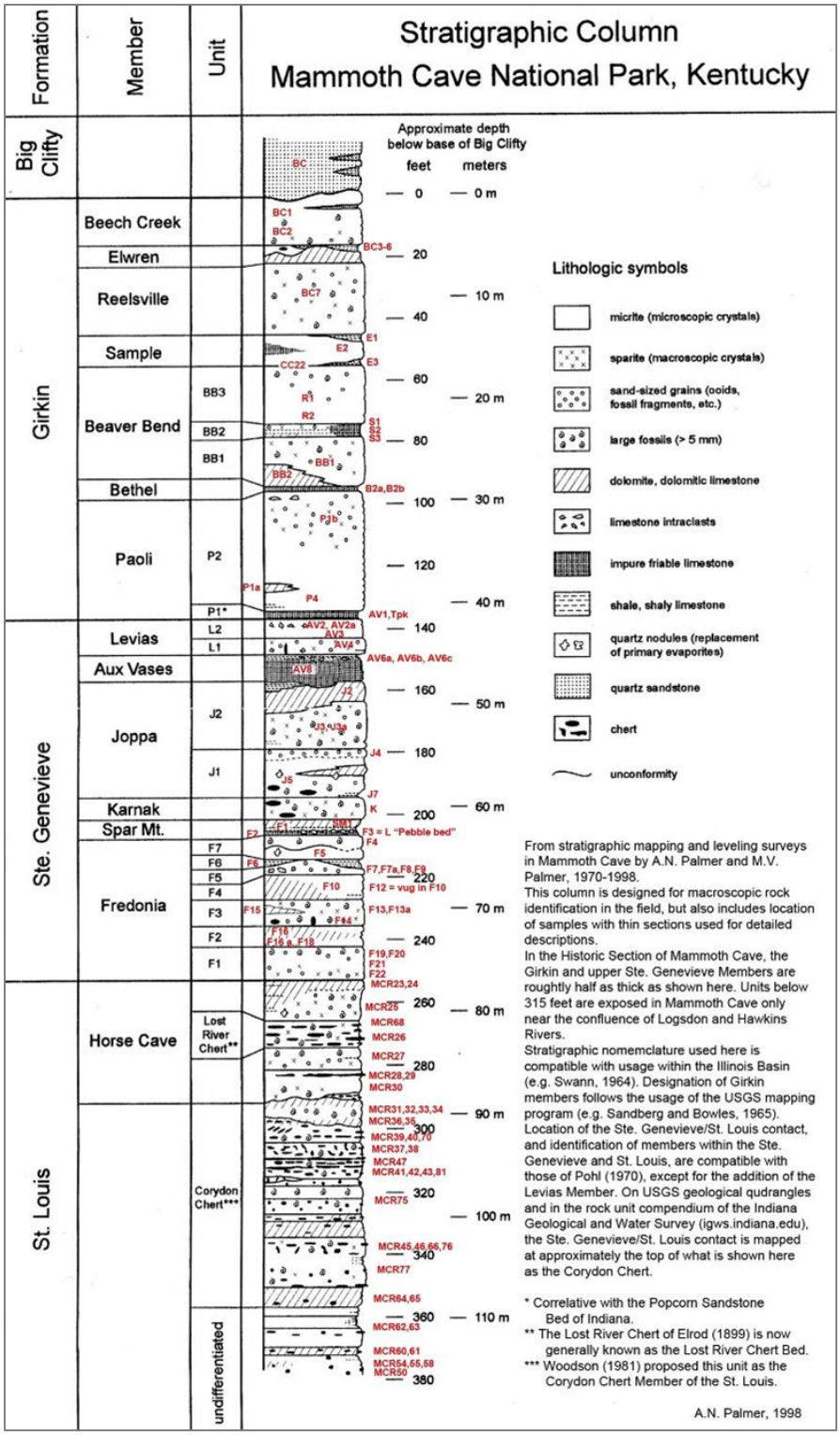


Figure 37. Stratigraphic column for the Mammoth Cave System. Because the cave covers so much area, there are many facies changes (many of them subtle) that appear in different sections of the cave. In describing the units, compromises were made to take facies changes into account. Thin sections were made of samples from various points in the section and are marked in red. They are referred to in the rock descriptions in Appendix A. © A. N. PALMER

Ridge-Forming Rocks in the Park

The ridges in the park are capped by siliciclastic rocks of Late Mississippian and Early Pennsylvanian age, although these include two thin carbonate formations sandwiched between thicker non-carbonate rocks. The thin limestone formations contain many springs and a few small caves perched on the resistant underlying beds. These rocks formed during North American collision with Gondwana, evidenced by increasing waves of siliciclastic sediment, characterized by cyclic marine deposition interrupted by exposure surfaces. The following descriptions (increasing in age) are based on information from the Kentucky Geological Survey Mammoth Cave Quadrangle Map (Haynes 1964). See also Figure 36. (Note that some references prefer names that specify rock types, e.g., Big Clifty Sandstone or Girkin Limestone.)

The Early Pennsylvanian-aged **Caseyville Formation,** although rare in the park, caps the ridges to the north. It can reach 27 m (90 ft) thick in places, where it fills deep valleys as much as 60 m (200 ft) deep with white-to-yellowish gray conglomerate, cobbles, sandstone, and siltstone. Caseyville Formation quartz pebbles carried into the caves have been used for radiometric dating of cave passages on the basis of cosmogenic isotopes (Granger et al. 2001). Although sparsely fossiliferous, the unit contains some plant remains.

The **Glen Dean Formation** consists of poorly exposed light-to-dark-gray limestone and shale. Where not intersected by the Caseyville, it can reach 14 m (45 ft) thick. The limestone contains abundant fossil casts and fragments.

The **Hardinsburg Formation**, 11–18 m (36–60 ft) thick, consists of locally cross-bedded, very light-gray to reddish-brown sandstone, siltstone, and shale. Interbedded siltstone and shale are present at the base. Weathering of the sandstone produces blocks separated by red clay that contains silicified fossil fragments.

The **Haney Formation** is light-to-medium gray limestone with fossil fragments cemented by calcite. Although only 3–15 m (10–50 ft) thick, it contains small caves. Lenses of gray shale occur throughout, and chert occurs locally. Extensive solution by groundwater has caused thinning of the limestone along with slumping of the overlying sandstone. Surface weathering leaves red-brown clay with silicified fossil debris and chert fragments.

It is common practice in Kentucky to combine the Haney, Big Clifty, and often the Beech Creek as members of the "Golconda Formation," but considering the lateral persistence in our study area of both the Beech Creek and Haney, it is appropriate to elevate the upper two units to formation rank, as is done in Illinois and Indiana. This also places the Beech Creek as the uppermost member of the virtually continuous limestone sequence of the Girkin Formation.

The **Big Clifty Formation** consists of light-gray to tan sandstone, 15–30 m (50–100 ft) thick, overlying the Girkin Formation. Thin layers of green-gray shale are present in some places near its base. The Big Clifty is the brown, resistant rock that stands out in low cliffs along the roads and paths leading to the major cave entrances. It is the oldest (and lowest) of the series of mainly insoluble, resistant rocks that cap the ridges in the park.

Rocks Exposed in Mammoth Cave

Major cave development occupies almost the entire thickness of the underlying Girkin and Ste. Genevieve Formations and roughly the upper half of the St. Louis (see Figure 37). The lower beds of the St. Louis lie below the local base level. The beds are characterized by their cyclic nature, in which a cycle includes rocks that form in submerged conditions and end in exposure. As evidence of exposure, Ettensohn et al. (1988) drew attention to recurrent paleosols (ancient soils) in the Middle and Upper Mississippian rocks in northeastern Kentucky. Smith and Read (2001) showed that major cycles correlated regionally with rocks in Kentucky and Indiana and proposed that these cycles are linked to changes in sea level and glacial ice volume. For detailed descriptions of the rocks in the cave system see Appendix A.

The **Girkin Formation** is the uppermost and youngest of the major cave-forming limestones in the park. It is generally 41–43 m (135–140 ft) thick but thins to only 23 m (75 ft) in the northwest part of Mammoth Cave Ridge. The Girkin consists of light-gray limestone with minor amounts of dolomite, separated at intervals of roughly 6 m (20 ft) by irregular beds of weak, crumbly, shaly or silty limestone generally less than 1 m (3 ft) thick that weather inward as recessed notches. In local areas near the top of the Girkin, these beds consist of greenish-gray shale. The increase in sandstone and shale shows that more detrital sediment was reaching the Mammoth Cave area. Paleosol development was periodic in the Girkin as well as the Ste. Genevieve, as evidenced by micritic layers (essentially lime mud), root casts, and laminated grains.

The **Ste. Genevieve Formation**, which underlies the Girkin, is 34–37 m (110–120 ft) thick in the park. By far the greatest number of passages in the Mammoth Cave System are located in this formation. The Ste. Genevieve consists mainly of dolomite and light gray, subtidal limestone. In the upper half of the formation, these rocks alternate with thin beds of dark, silty, granular limestone that weather inward as prominent notches in the cave walls. Breccia and limestone pebbles are scattered throughout many of these beds and have been interpreted as paleosols (Ettensohn et al. 1988). Their dark coloration is attributed to the accumulation of organic material in a topsoil. Traced toward the northwest into Illinois, these beds become much thicker and change into major formations of sandstone and shale. The Ste. Genevieve also contains isolated, irregular nodules of chert as much as 5 m (15 ft) long, especially in the middle and top beds.

The **St. Louis Formation** is the oldest and lowest stratigraphic rock formation exposed in the park. Even though not identified on the 1964 Mammoth Cave geologic quadrangle map (Haynes 1964), the St. Louis may be exposed at the base of the bluffs along the Green River and is exposed in the caves. The entire formation is more than 61 m (200 ft) thick, but only the top half can be seen. The deepest passages in the Mammoth Cave System are located in the St. Louis Formation. It can be recognized by the many beds and nodules of chert that stick out from the cave walls as black ledges and fins, or form irregular, resistant passage floors. The location of the Ste. Genevieve/St. Louis contact has long been controversial. Finding fossil ranges to be ambiguous, Pohl (1970) placed the contact at the top of a dolomite in the St. Louis, above the Lost River Chert and below an oolitic limestone (composed of small spherical concentrically layered grains) in the Ste. Genevieve. The uppermost 5–10 m (15–30 ft) of the St. Louis contain very little chert, but this same interval can be identified instead by the

dull, dark-brown color of its weathered surfaces and by thin layers of brown shale that protrude in many places. Beds of gypsum occur in the middle of the St. Louis in deep wells outside the park, but near the surface it has been dissolved away by fresh underground water. The gypsum formed at a time when the evaporation rate was very high and very little water was entering the continental sea through rivers.

Acknowledgments

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Appendix A: Guide to Mammoth Cave Stratigraphy

This detailed study is focused on field work in the cave and does not include the strata in the ridges. It is meant for use by cavers and geologists with access to the cave. Although the regional geologic setting of the park has been known for more than a century, it was only more recently that the Mississippian limestones of central Kentucky were studied in detail within the caves. Using Crystal Cave at the northeastern edge of the Mammoth Cave System as a prototype, a leveling survey of all passages and rock units was conducted from 1970–2000 by A.N. Palmer and M.V. Palmer, which provided a continuous stratigraphic section through the approximately 90 m (300 ft) of cavernous limestone in the park (Figure 38). Strata were identified using mainly the nomenclature of Swann (1963) and Pohl (1970), which were subdivided into individual beds or groups of beds of uniform rock type (members), most of which can be further divided into thinner units on the basis of minor variations in composition, texture, and thickness. Only a few of the thinner units have recognized names. The identity of individual members tends to become more distinct toward the north in Illinois and Indiana, where many attain the status of formations. Identifying specific rock units can be challenging owing to similarities in lithology and subtle contrast in grain type between beds. However, except for local anomalies in rock type and thickness, every unit identified in Crystal Cave has been recognized throughout the park. For a history of the nomenclature, correlation across changing facies, and the regional stratigraphy of Kentucky, see Sable and Dever (1990).

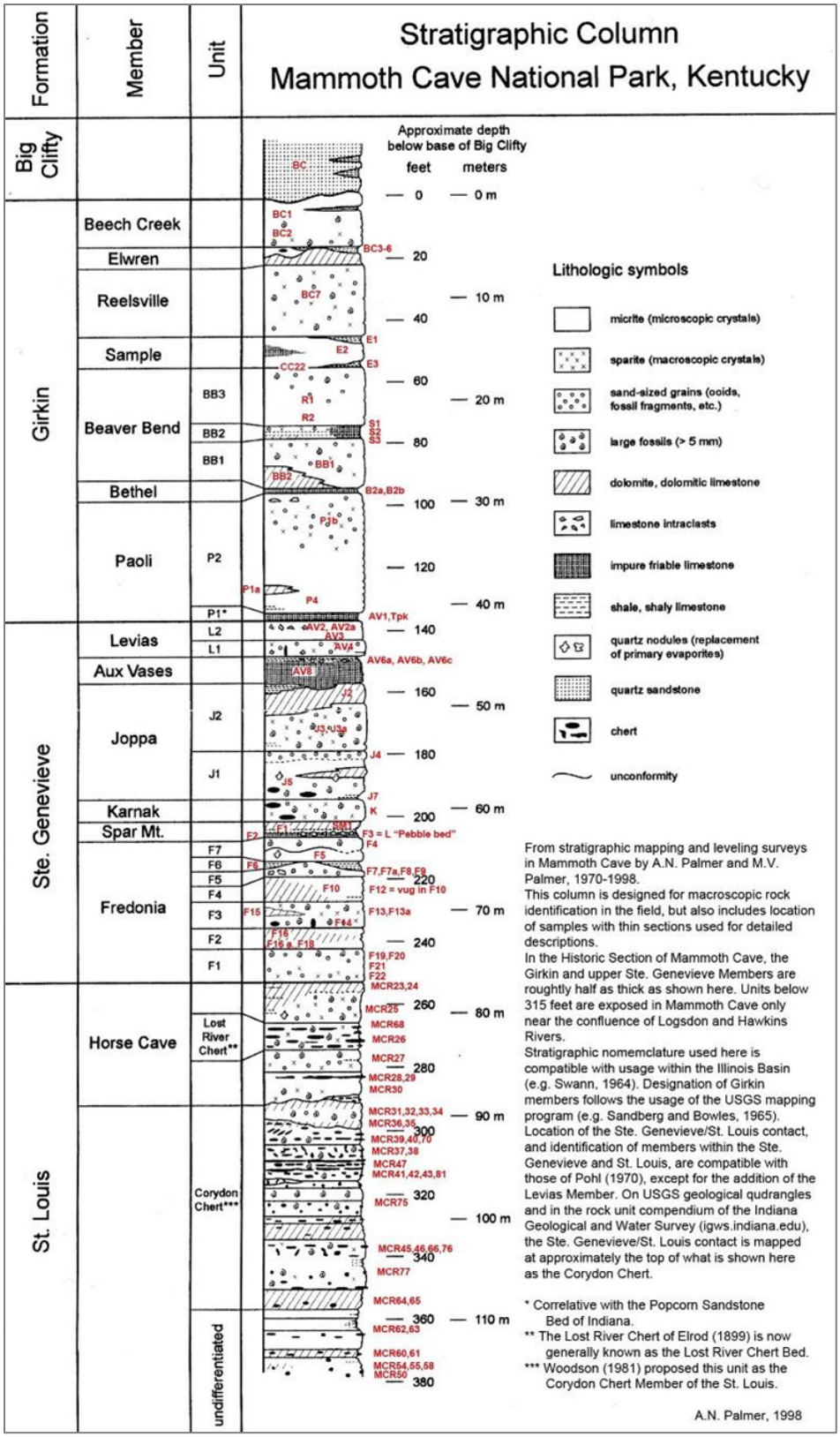


Figure 38. Stratigraphic column for the Mammoth Cave System. Thin sections labeled in red were made of samples from various points in the section as described in this appendix. © A. N. PALMER

In the vicinity of the Historic Entrance of Mammoth Cave, the various units in the Girkin and upper Ste. Genevieve Formations are about 30% to 50% thinner than shown in Figure 38, but all are still present. Stratigraphic mapping by A.N. and M.V. Palmer uses the names applied in the central Kentucky region by Pohl (1970), modified slightly according to recent adjustments by the USGS and Kentucky Geological Survey. For example, Pohl treated the Big Clifty and Haney as members within the Golconda Formation. However, as noted above it seems more appropriate to elevate the upper two units to formation rank, as is done in Illinois and Indiana, and to include the Beech Creek as a member of the Girkin Formation. Accepted names and contacts tend to change with time according to interpretation, but the physical strata remain the same! About 65% of the total thickness of the St. Louis Formation in central Kentucky is exposed in Mammoth Cave.

Recognition of Rock Units

Identifying rock units in the cave has rarely been done. An advantage is that the beds are more continuously exposed in caves. At first glance the rocks appear to be a rather uniform gray so that a detailed description of the limestone rock type requires examination of freshly exposed surfaces. However, rock sampling in the cave is rarely appropriate or allowed. It is strongly advised that bedrock samples not be broken off cave walls, for they possess as much aesthetic value as do speleothems. With a small amount of practice, however, it is possible to identify stratigraphic units simply from the appearance of their weathered surfaces. Familiarity with the individual rock units is best obtained by observing them in the locations described below.

Aids in Identification

Certain beds or rock sequences are quite distinctive. A guide to the most easily distinguished units follows. The identification of one or more of these characteristics within an exposure will normally allow the other less distinctive units to be recognized.

1. Thin, shaly, or sandy rocks that weather into recesses between more resistant beds:
    a. Containing limestone pebbles up to 5 cm (2 in) in diameter in a shaly matrix:
        i. Overlain and/or underlain by cross-bedded, dark gray, granular limestone (= Spar Mountain Member; Figure 39).
        ii. Included within light gray oolitic limestone (= unit F5 in Fredonia Member).
    b. Dark gray, granular limestone containing small dark limestone pebbles generally less than 1 cm (0.4 in) in diameter:
        i. Overlain by fine-grained, yellowish dolomite or by massive, coarse-grained, rough-weathering limestone (= Bethel Member).
        ii. Underlain by dull-weathering, fine-grained limestone; overlain by fine-grained, uniformly bedded limestone (= unit P1 in Paoli).
    c. Conglomeratic limestone, generally rather resistant, with prominent recessed bedding plane or shaly zone at top overlain by limestone that weathers rough and golden brown (= top of Aux Vases Member).

d. Soft, shaly:

    i. Green shale and yellowish dolomite (= upper Elwren Member).

    ii. Several beds of dark gray, shaly limestone with large fossils (= lower Elwren Member).

    iii. Light gray; overlain by fine-grained limestone (= unit F8 in Fredonia Member).

2. Dolomite:

    a. Dolomite bedrock often contains pyrite that weathers in the cave environment to a yellow-brown color: Thomas Ave., the Gypsum Rte., Crystal Cave (= unit BB2, Beaver Bend).

    b. Acquiring sulfur from the pyrite, gypsum is commonly found forming on dolomite: the Gypsum Route, Crystal Cave (= unit BB2, Beaver Bend).

    c. Weathering of pyrite to sulfuric acid can also create pores in the dolomite bedrock: Great Relief Hall (= unit F2, Fredonia Member).

    d. Very finely crystalline dolomite tends to peel off the walls in sheets: T survey between Five Passages and Mud Ave., Crystal Cave (= unit 4, Fredonia Member).



Figure 39. Intraclasts in the Spar Mountain Member at the junction of Boone and Rose's Pass, Mammoth Cave. © A. N. PALMER

Details of Rock Strata in Mammoth Cave

The following detailed descriptions were taken from stratigraphic columns made in the Mammoth Cave System and emphasize the carbonate bedrock. The general character of the strata is outlined from top to bottom (increasing in age), in the order in which they are normally viewed in the caves. Small samples, to be donated to the park, were collected with permit from the National Park Service and their stratigraphic positions were noted (red labels in Figure 38). Samples from the Girkin and Ste. Genevieve were obtained from Crystal Cave (for locations see Lawrence and Brucker 1955) and those from the St. Louis came from exposures accessed from the Doyle Valley entrance in Mammoth Cave. Sample descriptions are arranged by formation, followed by member, and then unit according to their occurrence in the geologic column. Sample characteristics are first described as seen in the cave, followed by a description of the sawed surface with additional detail from a corresponding thin section. Occasionally more than one sample was taken from the same stratum. Sample descriptions

end with a classification, first according to Folk and followed by that of Dunham (for a petrographic guide to carbonate rocks, see Scholle and Ulmer-Scholle 2003; for definitions of terms, see the same or the online SEPM guide available at http://www.sepmstrata.org/page.aspx?pageid=245). Fossil identification in this report is cursory and needs improvement by competent paleontologists. Photographs are by A.N. Palmer; photomicrographs by M.V. Palmer. In captions, **NP** = non-polarized light; **P** = polarized light; **RL** = reflected light.

Big Clifty Formation

The Big Clifty Formation forms a slope above cave entrances to Mammoth and Old Crystal Caves (Figure 40).



Figure 40. Shale at base of the Big Clifty Formation. © A. N. PALMER

Sample BC: ***Detail***: Medium-grained quartz arenite, porous, medium-yellowish brown to grayish brown on inside, weathers yellow-brown. Sparse clay matrix. Includes overgrowths on quartz, pressure solution between grains and few microcline grains. Grains ~0.4 mm (0.02 in).

Girkin Formation

The Girkin Formation is poorly exposed; Collins Ave. in Crystal Cave is the only passage that transects most of the formation. In that passage it is partly obscured by gypsum overgrowth. Short Cave, not far to the south of the park, contains much of the Girkin section. The Girkin Formation is as much as 41–43 m (135–140 ft) thick, but at the Historic Entrance of Mammoth Cave, it thins locally to as little as 20 m (65 ft), owing to a reduction in thickness of nearly all its members. (These values are not included in the thickness ranges described below.)

Beech Creek Member
Thickness 4–6 m (12–20 ft); fine-grained-to-granular limestone containing locally profuse fossils (particularly brachiopod shells), with beds roughly 0.2–0.3 m (6–12 in) thick; exposed directly beneath the lowest sandstone (Big Clifty Formation) of the caprock that forms the ridge crests in the park.

Sample BC1 = upper Beech Creek: From Crystal Cave entrance area. Medium-gray, very finely crystalline to lithographic limestone. Weathers light gray-brown. Beds 0.2–0.3 m (6–12 in). ***Detail***: Unsorted, grains range from 0.05–1.0 mm (2–39 mil [thousandths of an inch]). Bryozoans, ostracods, crinoids, and forams. Pellets disintegrate into mud. Spar cement in pores. Scattered dolomite rhombs (100 µm [3.9 mil]) especially in mud fraction. Biopelmicrite, wackestone.

Sample BC2 = Beech Creek: Crystal Cave, top of Collins Ave. canyon. Medium-dark gray, coarsely crystalline limestone. Locally foreset, fossils, weathers dark brown-gray, siliciclastic at base. Thin 3 cm (1 in) bands of coarsely crystalline, fissile limestone in undulating, irregular bands as interbeds. ***Detail***: Exposed surface is friable. Grains weather out, leaving raised matrix between pores, creating rough surfaces. Ooids and micrite-coated, rounded grains ~0.8 mm (0.03 in), well-sorted with finely crystalline to radially fibrous rim cement. Close packing, causing some broken grains. Calcite cement between grains. Oointrasparite, grainstone.

Elwren Member
Upper unit: 0.3–1.2 m (1–4 ft); soft, gray-green shale and yellow-to-gray dolomite, both of which, particularly the shale, form recessed niches in the cave walls.

Sample BC3 = upper Elwren: Crystal Cave, Collins Ave. canyon. Medium-light gray, very finely crystalline dolomite. Weathers shaly, friable, cream-to-light gray, local large fossils (corals, brachiopods), locally lithographic or oolitic. ***Detail***: Very finely crystalline, medium-gray. Silty, convoluted laminations with iron oxide crystals. Quartz silt is fairly uniform in grain size (~20 µm [0.8 mil] diameter). Dolomitic, micrite, mudstone.

Sample BC4 = Elwren: Crystal Cave, Collins Ave. canyon. Light-gray, shaly dolomite. Few crystals, irregular bed, gradational base. Mottled where weathered. ***Detail***: Some fractures, small vugs on surface, some pores filled with calcite spar. Very light-gray-to-white intraclasts appear between mud facies. Scattered fossil fragments are altered to calcite spar or dissolved, forming pores, some quartz grains. Grains (~0.2 mm [8 mil]) float in mud. Micritic dolomite, dolomitic mudstone.

Sample BC5 = Elwren: Crystal Cave, Collins Ave. canyon. Dolomite, light-brown, fine-grained. Porous where weathered. Weathers to massive blocks 15–30 cm (6–12 in) in diameter, mottled. ***Detail***: Light-gray, mudstone breccia with sparry calcite cement in openings between blocks, so blocks appear to float. Grains disintegrate into mud. Ostracods and crinoids. Dolomitic biomicrite, wackestone, breccia.

Lower unit: 1.5–3 m (5–10 ft); dark-gray, impure, shaly limestone containing large fossils (mainly brachiopod shells); weathers soft and crumbly, forming one or more recessed niches.

> **Sample BC6 = lower Elwren:** Crystal Cave, Collins Ave. (canyon). Very finely crystalline, medium-gray, recessive, weathers light-gray. Beds 2–15 cm (0.8–6 in) with some thin interbeds. ***Detail***: Some thin, dark, wavy laminations. Light, leached, weathered surface. Brachiopod fragments (50–1000 µm [2.0–39.4 mil]), trilobite, crinoid, echinoid, and other broken fossil fragments. Concentration of insolubles along stylolitic bedding-plane partings. Matrix consists of micritized grains. Biomicrite, wackestone.

Reelsville Member

Upper unit: 5–7 m (16–22 ft); granular, medium-coarsely crystalline, thick-bedded limestone; weathers rough; beds generally 1.5–3 m (5–10 ft) thick. **Lower unit:** 5–7 m (16–22 ft); slightly granular, finely crystalline limestone; beds generally 0.6–3 m (2–10 ft) thick; lower beds tend to be finer-grained than those higher in the unit.

> **Sample BC7 = Reelsville**: Crystal Cave, Collins Ave. canyon. Massive light-gray limestone, coarsely crystalline, weathers rough. ***Detail***: Fossils, ooids, massive texture. Fairly well sorted, tightly packed grains. Deformation of grains is common. Fossils have semi-distinct fibrous, concentric and radial crystalline coating. Large coated grains are ~1 mm (0.04 in) diameter. Grains have been micritized. Stylolites cut grains. Oobiosparite, grainstone (Figure 41).

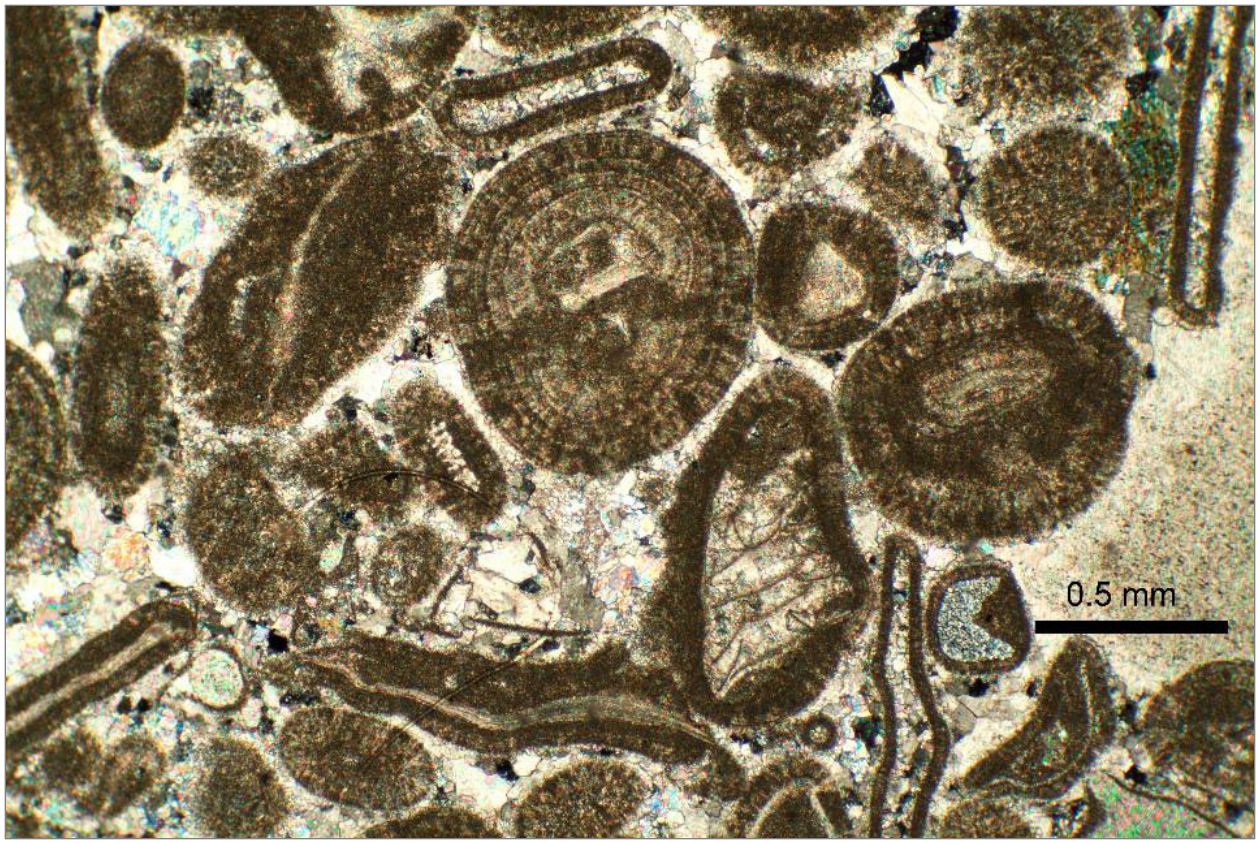


Figure 41. Coated grains in the Reelsville Member (BC7). Slightly micritized ooid and micrite-coated horn coral fragment near center. Micritization of grains is common throughout the Mississippian in the Mammoth Cave samples. P. © M. V. PALMER

Sample Member

Thickness 1.8–3 m (6–10 ft); dark-gray, granular, sandy limestone and fine-grained dolomite, thin-to medium-bedded; contains local beds of coarsely crystalline and/or fossiliferous limestone; forms recessed niches in cave walls.

Sample E1 = upper Sample Member: Crystal Cave, Collins Ave. canyon. Shaly, medium-gray, weathers light-gray, friable, medium-grained, finely crystalline; brachiopods. ***Detail***: Sparry fossils floating in finer-grained matrix. Limonite with some iron oxide crystals. Quartz grains ~10% (0.2 mm [8 mil] diameter). Secondary gypsum in veins replacing allochems and some matrix. Micrite-coated grains, peloids, crinoids. Grains are micritized. Scant saddle dolomite. Patchy dolomite, and sparse chert replacement. Sandy dolomitic biopelmicrite, wackestone.

Sample E2 = middle Sample Member: Crystal Cave, Collins Ave. canyon. Massive, dark-gray, granular, crystalline, weathers rough. ***Detail***: Abundant layered fossil fragments. Shell valves are filled with spar (shelter effect). Iron oxide staining in streaks. Allochem size varies (0.5–4 mm [0.02–0.2 in] diameter for large brachiopod fragments). Bryozoans, ostracods, possible trilobite fragment (Figure 42), forams, ooids, some quartz silt, intraclasts, some quartz replacement of

shells. Microspar matrix is dolomitized. Dolomitic biointramicrosparite to sparite matrix, packstone.

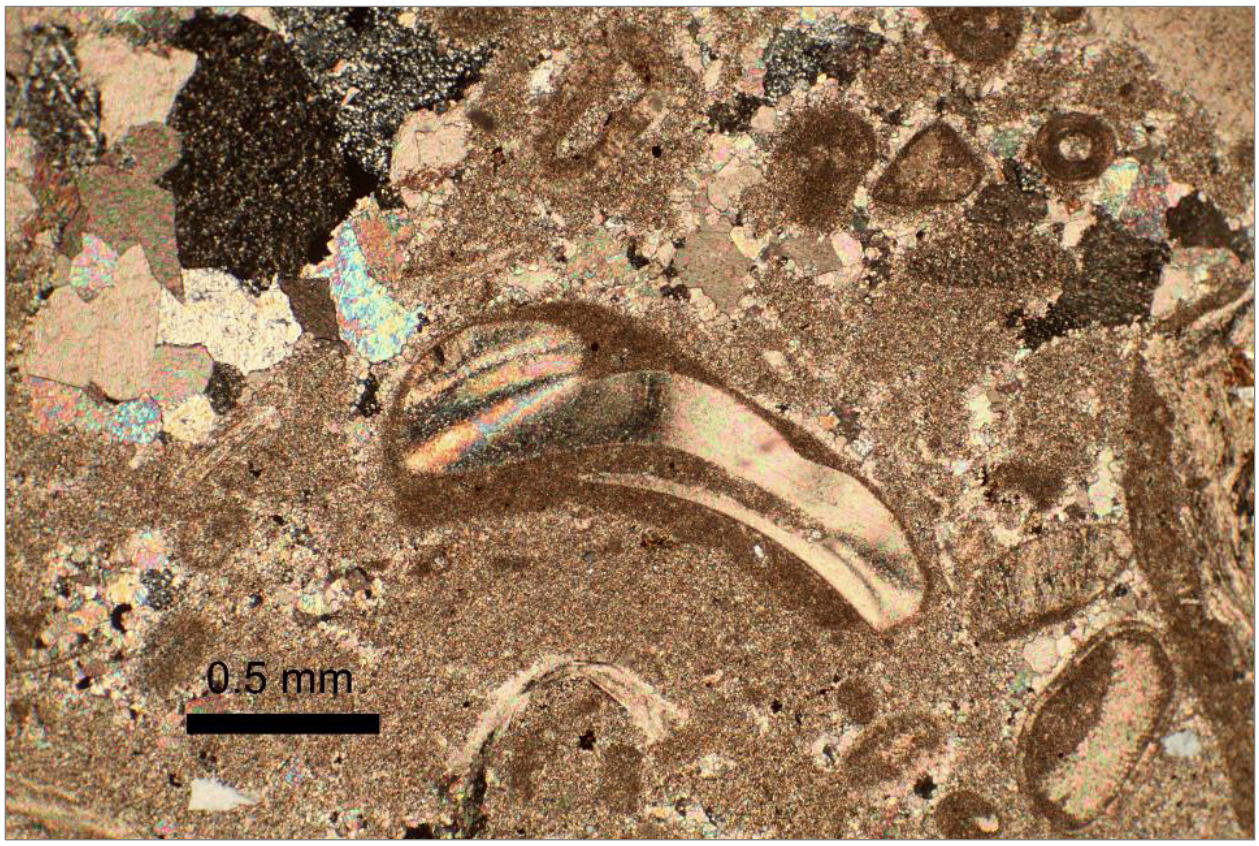


Figure 42. Possible trilobite fragment in E2. Undulose extinction can occur in pelecypod, trilobite, ostracod, and foraminifera shells (Scholle and Ulmer-Scholle 2003). P. © M. V. PALMER

Sample E3 = lower Sample Member: Crystal Cave, Collins Ave. canyon. Shaly, medium-light gray, weathers porous. Brachiopods. ***Detail***: Stained yellow. Friable, finely crystalline, no visible bedding. Scattered large brachiopods and iron oxide crystals. Moldic pores. Quartz silt ~0.05 mm (2 mil), dolomite rhombs <20 µm (0.8 mil). The few allochems are altered to spar, dolomitized or replaced by chert. Some secondary gypsum in pores. Silty, micritic dolomite, mudstone.

Sample/Beaver Bend Paleosol

The cyclic breaks in deposition that characterize the Late Meramecian-aged strata intensified through the Chesterian (Late Mississippian). Prominent breaks in the low-energy marine shoreline deposits have been interpreted as paleosols in northeastern Kentucky (Ettensohn et al. 1988). The paleosols are developed on discontinuity surfaces separating the predominantly limestone members and are characteristic of caliches, which are soils composed of calcium carbonate that form in arid to semi-arid climates. As a soil type, caliche has its own mode of formation and classification (Table 2). At the surface, with the aid of biological activity, supersaturated solutions form by dissolving the bedrock, and then move downward where they precipitate by evaporation as micrite. Micritization of

bedrock and grains is ubiquitous, as is the precipitation of micrite (as "cutans") in sheets below the surface or as rims around grains. Brecciation (breaking into angular fragments) is common, owing to root activity or evaporation after seasonal rain, while crystalline calcite typically fills the voids between clasts.

Table 2. Features in paleosols. Many of the soil terms are from Ettensohn et al. (1988). For other terms see Scholle and Ulmer-Scholle (2003) and SEPM (2013; available at http://www.sepmstrata.org/page.aspx?pageid=245).

Term	Definition
Caliche	Soils composed of calcium carbonate that form in arid to semiarid climates. During wet periods CO_2 dissolves the bedrock, while precipitation occurs during dry periods when evaporation occurs at the surface. Caliche is considered part of the B horizon of soils which is below the organic layer at the surface and in the root zone.
Cutan	A micritic precipitate in a soil profile.
Ooid	A spherical grain (0.2–2 mm [0.8–8 mil]) with a nucleus coated with one or more concentric laminations, can have a radial structure.
Oncoid	Irregularly laminated grain of microbial origin >2 mm (0.08 in).
Ped	A natural aggregate of soil particles formed as a result of pedogenic processes. Peds are separated from other peds by natural breaks such as joints.
Pellet	Generally elongated, structureless, micritic grain, <0.3 mm (300 µm [11.8 mil]). Thought to be fecal in origin.
Peloid	Any micritized grain. It includes the types intraclast and pellet.
Pisoid	Laminated spherical grain >2 mm (0.08 in). Larger than an ooid.
Silcrete	A hard crust formed especially in arid climates where surface material is cemented or replaced by dissolved silica.

A characteristic paleosol was sampled in Collins Avenue, Crystal Cave (Figure 38, CC21 and 22) and is described below (Figure 43). This sample was located along a disconformity at the base of the Sample Member and may have undergone several stages of soil development following changes in water level, eustacy, and/or climate.

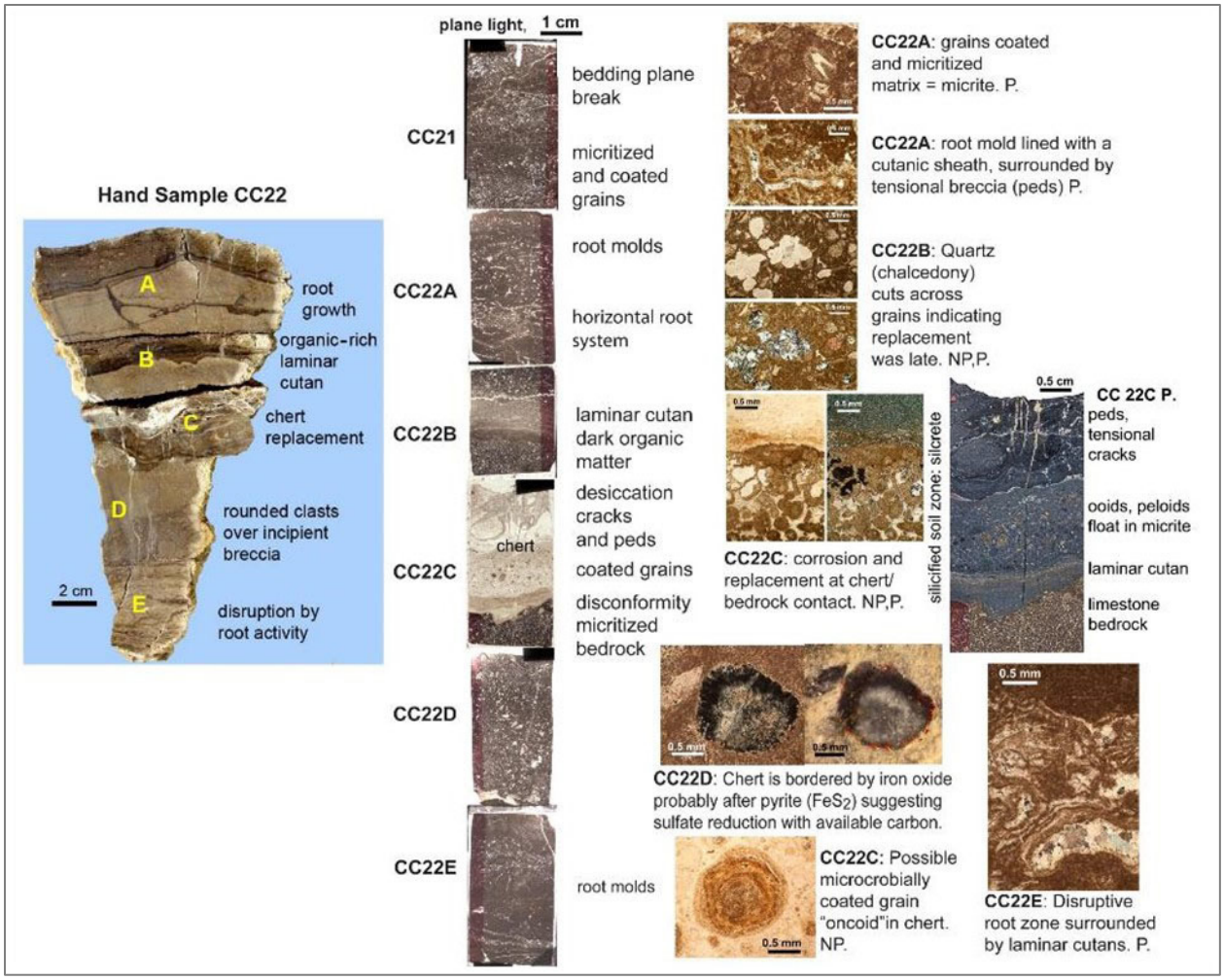


Figure 43. Features associated with subaerial exposure at the Sample/Beaver Bend contact. Hand sample CC22 on left hand side. Corresponding thin sections on right. There are at least two apparent exposure surfaces. Chert replaced former carbonate features and may represent a change from humid to arid conditions. © M. V. PALMER

Beaver Bend Member

Thickness 5–8 m (17–25 ft); granular, medium-bedded, medium-coarsely crystalline limestone; in places the lower beds are composed of yellow-brown dolomite to thicknesses up to 4.6 m (15 ft). The Beaver Bend and Sample Members are exposed in the sloping cave roof at the Historic Entrance of Mammoth Cave.

> **Sample R1 = main body of BB3 (upper Beaver Bend):** Crystal Cave, Collins Ave. canyon. Massive limestone, medium-gray, finely crystalline, granular. ***Detail***: Fossil hash, lacks distinct bedding, spotty limonite staining, large bryozoans on exterior, weathers granular, fossils project while matrix is dissolved, creating a rough surface. Unsorted fossil fragments float in very fine matrix. Dolomitic biosparite, packstone.

Sample R2 = base of BB3 (upper Beaver Bend): Crystal Cave, Collins Ave. canyon. Brown, micritic, weathers smooth. ***Detail***: Almost completely replaced by gypsum. Laminated black and yellow layers (leucoxene and iron oxide sediment residue). Gypsum expanding away from the walls leaves an incremental trail of sediment and residue.

Sample S1 = upper bed of BB2 (Beaver Bend): Crystal Cave, Collins Ave. canyon. Medium-dark-gray limestone. Finely crystalline with some zones of ooids and fossils. Weathers rough, light-gray and smooth. Massive. Locally coarsely crystalline near top. ***Detail***: Quartz grains >60 µm (2.4 mil) (sandy). Brachiopods, crinoids, echinoids, intraclasts, and coated grains, becoming micritized. Poorly sorted. Close packing. Sandy intrapelmicrosparite, packstone.

Sample S2 = middle bed of BB2: Crystal Cave, Junction of Dyer and Collins Ave. Limestone. Local 15 cm (6 in) green-gray shale lenses. ***Detail***: Massive texture, medium-gray, oolitic, fossiliferous, ostracods, intraclasts, close-packing. Weathers rough. Quartz grains >60 µm (2.4 mil) (sandy), minor microcline and chert grains. Sandy oointramicrosparite, sandy packstone.

Sample S3 = lower bed of BB2 (Beaver Bend): Crystal Cave, junction of Dyer Ave. and Collins Ave. Dark-gray limestone and dolomite. Fissile, medium-grained. Weathers light-gray-yellow, recessive. Burrows. ***Detail***: Highly porous. Light-yellow-brown. Intraclasts and small pebbles. Matrix is uniform, very finely crystalline (10 µm [0.4 mil] dolomite rhombs). Widely scattered grains floating in micrite. Grains: quartz sand, brachiopods, ostracods, crinoids, echinoids, and micritic allochems (0.3–0.5 mm [0.01–0.02 in]). Microcline grain. Scattered iron oxide crystals in matrix. Unsorted. Dolomitic, sandy intramicrite, packstone.

Sample BB1 = unit BB 1 (main body) Beaver Bend: Crystal Cave, Thomas Ave. White-to-light-gray oolitic limestone, massive, grading down into coarsely crystalline to medium-crystalline and oolitic at base. Top 1–1.8 m (3–6 ft), locally medium-gray, medium-finely crystalline. Resistant beds (10–20 cm [4–8 in]) weather blocky, light-gray or light-brown. ***Detail***: Deeply stained iron oxide zone above stylolite. Silty wisps. Allochems are micritized in part of the sample. Scattered dolomite. Part of sample has recognizable grains (brachiopods, ostracods, ooids, coated grains, intraclasts). Unsorted grains vary from 0.2–5 mm (8–200 mil). Sheltering effects show grain support in some areas. Biointramicrosparite, packstone.

Sample BB2 = basal bed of unit BB 1: Crystal Cave, Thomas Ave. Base commonly dolomitized, locally extending upward as much as 4.5 m (15 ft). Fine-to-medium crystalline, limy dolomite to dolomitic limestone. Less resistant than overlying rock. Medium-gray but weathers light-gray with yellowish stain. Blocky. Former pyrite in dolomite was source for gypsum in Thomas Ave. Gypsum occurs in tensional veins and replacing grains. ***Detail***: Dolomite rhombs 20 µm (0.8 mil). Former wackestone with fossils and intraclasts. Micritic dolostone, mudstone.

Bethel Member

Thickness 0.3–1 m (1–3 ft); dark-gray, impure sandy limestone containing small rounded limestone pebbles; weathers with crumbly texture, forming prominent recessed niches. The Bethel forms the indentation just below the ceiling level in Broadway and Audubon Avenues in Mammoth Cave.

Sample B2a = Bethel: Crystal Cave, Scotchman's Trap. Dark-gray, granular, sandy with rounded intraclasts. Weathers light-gray, friable, incompetent. ***Detail***: Close packing of grains. Grains are very micritized. Coated grains, ooids, sparse quartz silt, intraclasts, echinoderms, crinoid plates, forams. Dolomitic intrapelmicrosparite, wackestone.

Sample B2b = Bethel: Same bed as B2a, but different location, Crystal Cave, Dyer Ave., Valley of Decision. Dark-gray, granular, sandy limestone with rounded intraclasts. Weathers light-gray, friable, incompetent. ***Detail***: Massive texture, sparse intraclasts 0.4 × 0.1 cm (0.2 × 0.04 in), elongate and angular. Somewhat bedded. Unsorted. Micritized peloidal grains (100–1000 μm [3.9–39.4 mil]). Very sparse fossils. Quartz sand (grains ~100 μm [3.9 mil]) and clay between grains. Some chalcedony replacement. Scattered iron oxide crystals. Scattered 50 μm (2.0 mil) dolomite rhombs. Sandy intramicrosparite, wackestone.

Paoli Member

Thickness 11–15 m (35–50 ft); thin-to-medium-bedded limestone, grading upward from fine-grained to moderately granular and finely crystalline. Beds are generally 5–30 cm (2–12 in) thick. The Paoli is only 6.4 m (21 ft) thick at the Rotunda in Mammoth Cave, where it forms nearly the entire passage wall. In Long Cave, the upper half of the Paoli is a massive, cross-bedded, oolitic limestone. It is exposed at the base of the entrance slope below the recessed, crumbly, 0.1 m (0.3 ft)-thick Bethel.

Sample P1b = uppermost Paoli (unit P2): Crystal Cave, Crawlway at Scotchman's Trap. Medium-gray, fine-grained ooids cemented by spar. Limonite stain cuts across rock. ***Detail***: Some dolomite along bedding planes. Micritized grains, most are rounded intraclasts >1 mm (0.04 in) composed of peloids in mud matrix. Closely packed, poorly sorted, sparry matrix. Intrapelsparite, packstone.

Sample P1a = Dolomite near base of P2 (Paoli): Crystal Cave, Crawlway at Scotchman's Trap. Medium-gray-brown to yellow, crinkly laminations. Scattered, sparry fossil fragments. Very fine-grained matrix with laminations. Weathered surface is yellow. ***Detail***: Grains are unsorted: peloids, bryozoans, brachiopods, crinoids, echinoids, and intraclasts (0.2–5 mm [8–200 mil] diameter). Scattered 50 μm (2.0 mil) dolomite rhombs. Dolomitic intrabiomicrosparite, wackestone.

Sample P4 = basal P2 unit: Crystal Cave, above Dining Room. Light-gray-brown, medium-bedded-to-massive, lithographic limestone. Weathers creamy, breaks into thin resistant slabs (4–15 cm thick). ***Detail***: Cut by spar-filled veins. Stylolites along bedding planes. Mostly peloids, ooids, fossil fragments with micritic rims (grains ~200 μm [7.9 mil]). Spar matrix. Pelintrasparite, packestone.

Sample AV1 = unit P1 (basal Paoli): Crystal Cave, Straddle Canyon. Dark-gray limestone, incompetent. Weathers to calcareous dark-gray sand. Friable, shaly, thin-bedded, mottled gray. Sparse intraclasts (~5 mm [0.2 in]). ***Detail***: Micritized, rounded grains (50–1000 μm [2.0–39.4 mil]), ooids, peloids, scattered quartz sand, clay, clay matrix. Sandy intrapelmicrite, wackestone.

Sample Tpk = unit P1, 30 cm (12 in)-thick base of Paoli: Same bed as AV1, but different location. Crystal Cave, recessed bed used for Turnpike crawlway around pit overlooking Turnpike Room (Figure 44). Friable, mottled gray-to-dark-gray, calcareous shale, massive. ***Detail***: Quartz sand and clay matrix. Micritized grains, rounded intraclasts, peloids, crinoids, and echinoid plates. Sandy intrapelmicrite, wackestone.



Figure 44. The friable, calcareous shale (unit P1) forms a recessed layer, enlarged here to create a bypass over a pit in the Turnpike Room, Crystal Cave. © A. N. PALMER

Ste. Genevieve Formation

The vast majority of the cave passages in Mammoth Cave National Park are developed in the Ste. Genevieve Formation, which is 33.5–36.6 m (110–120 ft) thick and can be distinguished from the Girkin Formation by the following characteristics: (1) variations in rock type in the Ste. Genevieve occur over more closely spaced intervals; (2) except for those in the Bethel, beds in which pebbles are incorporated into the limestone are confined almost exclusively to the Ste. Genevieve; and (3) nodular chert is common at several stratigraphic horizons in the Ste. Genevieve.

Levias Member

Thickness 3.7 m (12 ft); prominent incompetent lithology typically forming recessed bedding.

Sample AV2 = Upper Levias (unit L2): Crystal Cave. Dining Room. Dark-gray, sandy, oolitic limestone. Weathers light-gray or mottled dark-gray and friable. Generally foreset beds. Dark-

gray, subrounded intraclasts up to 2 cm (0.8 in). Sparse white chert and silicified zones. Local lenses (2 × 30 cm [0.8 × 12 in]) and angular clasts (up to 5 cm [2 in]) of green shale. ***Detail***: Very close packing, calcite spar matrix. Medium sorting, intraclasts, rounded peloids, pellets, fossil fragments and micrite-coated grains, ooids, bryozoans, crinoids, echinoids. Scattered quartz silt. Micritic-to-finely crystalline calcite matrix. Silty intrabiopelmicrosparite, packstone/wackestone.

Sample AV2a = Upper Levias (unit L2): Crystal Cave, Turnpike**.** Dark-gray, sandy, oolitic. Weathers light-gray or mottled dark-gray, friable. Generally foreset beds. Dark-gray, sub-rounded intraclasts up to 3 cm (1.2 in). Sparse white chert and silicified zones. Local angular clasts of greenish shale up to 5 cm (2 in) long. Local lenses of green shale 1 × 2.5 cm (0.4 × 1 in). ***Detail***: Weathers granular with protruding grains. Calcite matrix varies from spar to micrite. Chalcedony forms core of sparse micrite-coated clasts. Abundant clusters of peloids, pellets and ooids. Crossed by a laminar cutan. Scattered iron oxide crystals. Close packing. Angular, elongate, dark intraclasts (0.3 × 1 cm [0.1 × 0.4 in]). Intrapelmicrosparite, packstone/wackestone.

Sample AV3 = lower L2 (Levias): Crystal Cave, midway in crawl to east beyond Scotchman's Trap. Finely crystalline-to-lithographic, medium-dark gray, rather massive, weathers light-gray, shaly, competent but breaks into thin, irregular slabs. Small horn corals, local silicified zones and boxwork. ***Detail***: Wispy zones in mudstone. White siliceous projections with reddish inner siliceous zones. Sparse, scattered, small (100 µm [3.9 mil]) fossil fragments in calcite mud matrix (fragments altered to spar and partly micritized). Abrupt but interfingering contact with chert containing scattered iron oxide crystals. Quartz has replaced mud matrix, leaving scattered, ragged, coarsely crystalline allochems. Scattered dolomite rhombs. Biopelmicrite, wackestone.

Sample AV4 = unit L1 (Levias): Crystal Cave, Camp II. Light-medium-gray, massive, cross-bedded limestone. Ooids and horn corals. Weathers golden-brown with rough, granular surface. Chert nodules and siliceous dikes are gradational with each other, generally discordant to bedding, especially near base. ***Detail***: Massive; ooids. Rounded, fiber-coated grains (~300 µm [11.8 mil]). Oopelsparite, grainstone.

Aux Vases Member

Thickness 5–8 m (16–26 ft); locally only 3 m (10 ft) at Mammoth Cave. Occurrences of the Aux Vases Member include: a limestone pebble bed that forms recessive ledges, such as one near the floor level of Audubon Avenue in Mammoth Cave; cross-bedded limestone with shale fragments forming the ceiling of most of Turner Avenue in Flint Ridge; granular limestone with local chert nodules that forms the walls of the Frozen Niagara Entrance of Mammoth Cave; and crumbly limestone, shale, chert and limestone pebbles that form a deep wall recess near the ceiling of most of Mather Avenue in Flint Ridge. Pohl (1970) considered the Aux Vases Member was deposited under turbulent conditions. This might be reassessed as an exposure surface.

Sample AV6a = top of Aux Vases: Crystal Cave, Camp II. Medium-gray, shaly, somewhat granular, competent, fissile, thin-bedded at top to 30 cm (12 in)-thick beds above a shale break. Locally conglomeratic with micritic clasts, rounded to 15 cm (6 in) diameter in shaly limestone

matrix, which is brecciated and incompetent. ***Detail***: Spar separates mudstone into intraclasts (possible peds). Zones of scattered 50–100 µm (2.0–3.9 mil) dolomite rhombs are replaced by quartz. Mud matrix is slightly replaced by dolomite. Cherty intrasparudite, wackestone.

Sample AV6b = top of Aux Vases: Crystal Cave, Dining Room. Medium-gray, weathers granular, large angular intraclasts with wavy edges, in shaly, granular, lighter-colored matrix. Intraclasts range to more than 8 cm (3 in) diameter. ***Detail***: Intraclasts are separated by wispy seams of clay and calcite spar in dolomitic mudstone. Scattered 30 µm (1.2 mil) dolomite rhombs in mudstone. Fossil fragments include brachiopods, ostracods, crinoids, and echinoids. Fossils and coated grains are replaced by dolomite and chalcedony. Cherty, dolomitic intramicrosparudite, wackestone.

Sample AV6c = top of Aux Vases: Crystal Cave, Big Dining Room. Medium-gray, angular, elongated, micritic intraclasts (1 × 2 cm [0.4 × 0.8 in]) in light-yellow matrix which contains smaller intraclasts (0.2 cm [0.08 in]). Forms a breccia. ***Detail***: Anastomotic spar and clay surround intraclasts. Sparse chalcedony in grains. Intraclasts contain scattered fossil fragments and micritized grains in mud matrix. Brachiopods, ostracods, crinoids, echinoid plates, unsorted. Scattered 30 µm (1.2 mil) rhombs. Intrasparudite, wackestone (Figure 45).

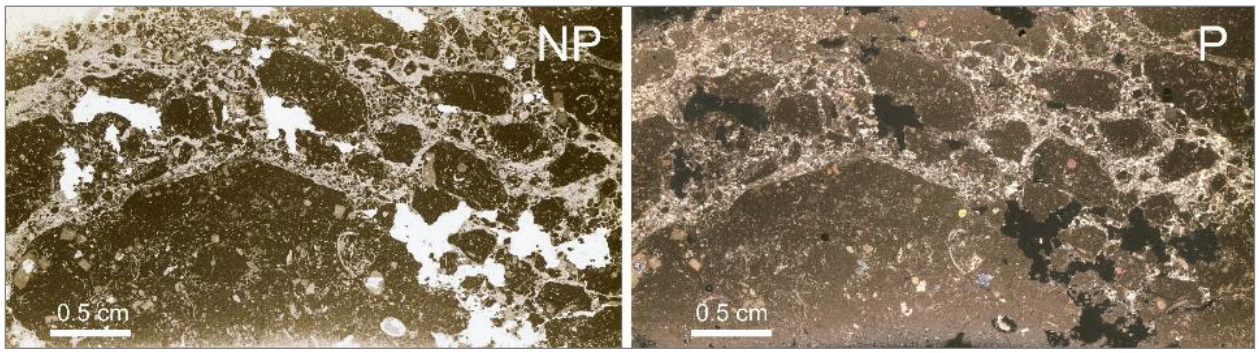


Figure 45. Intraclasts in AV6c, at the top of the Aux Vases. © M. V. PALMER

Sample AV8 = main body of Aux Vases: Crystal Cave, Camp II. Cross-bedded, dark-gray, granular, shaly limestone. Beds ~10 cm (4 in). Weathers light-gray, friable, rough texture. Locally finely crystalline. Can grade into mudstone or contain quartz silt. ***Detail***: Porous. Weathers light-tan with sandy texture. Grains mainly micritized (100–300 µm [3.9–11.8 mil] diameter). Tightly packed peloids and fossil fragments. Intrabiosparite, packstone.

Joppa Member
Thickness 8–12 m (26–40 ft); the Joppa Member can be subdivided into the J2 and J1 units.

Unit J2 = upper unit of Joppa, 4–8 m (13–25 ft): Massive, granular, coarsely crystalline limestone containing large fossils, particularly crinoid fragments; a dolomitic zone occurs at the top, in places including most of the unit. Thin beds of shale are common at the top and near the base. The coarse beds weather rough and golden-brown and commonly exhibit cross-bedding. This unit forms the

walls of Mather Avenue in Flint Ridge. In several areas, J2 contains layers of fossil hash. Each is more than a meter (several feet) thick. They are grain-supported biosparites with almost all grains consisting of fossils. Most of the fossils are crinoid fragments, but horn corals, bryozoans, brachiopods, and vertebrates are all common in places. The fossil-hash zones are separated by matrix-supported biosparite to biomicrite. At Forks of the Cave at least two fossil-hash zones are visible. In Genie's Pass, there appear to be at least three fossil-hash layers. The fines appear to be winnowed out of the fossil-hash zones. Other areas with fossil-hash layers are Fossil Ave. (in New Discovery), Specimen Ave., Solitary Cave, Serena's Arbor, and Marion Ave. (Rick Toomey, MACA, pers. comm., December 2022).

Sample J2 = dolomite in unit J2: Crystal Cave, Camp II. Dolomite, limy, locally shaly, directly underlies shale or is separated from shale by up to ~1 m (4 ft) of granular limestone. Dark medium-gray-to-light-gray-brown. Weathers dull, smooth, often light-gray and shaly. Local stylolites. Medium-bedded-to-massive. Thinnest beds ~30 cm (12 in). Total thickness 0–3 m (0–10 ft). Base interfingers with biosparite. ***Detail***: Crinkly laminations, finely laminated, scattered iron oxide, buff, massive. Mud-size dolomite rhombs ~20 µm (0.8 mil), with scattered 200 µm (7.9 mil) rhombs. Scattered quartz silt. Dolostone, mudstone.

Sample J3 = main part of unit J2: Crystal Cave, Fool's Delight, Bottomless Pit. Medium-gray, massive limestone. ***Detail***: Unsorted (large fossil fragments ~4 mm (0.2 in) and small fragments ~50–500 µm [2.0–19.7 mil]). Fossils: *Schoenophyllum aggregatum* (*Siphonodendron genevievensis* of older references, such as Pohl 1970; Figure 46) and other corals, bryozoans, brachiopods, gastropods, echinoid plates, and forams. Partly micritized ooids. Calcite spar in shelters under large grains and in fossil molds, closely packed. Some chert in fossils. Weathers rough. Biointrasparite, packstone.

Sample J3a = main part of unit J2: Crystal Cave, Camp II. Sample is from below dolomite. Locally is light-gray, oolitic limestone. Weathers white. Up to 0.8 m (2.5 ft) thick. Grades laterally into biosparite. Abundant shark fossils have been found in Fossil Ave., New Discovery (JP Hodnett, Maryland National Capital Parks and Planning Commission, pers. comm., November 2022; R. Toomey, pers. comm., December 2023). ***Detail***: Broken fossil fragments aligned parallel to bedding. The matrix consists of smaller fossil fragments, granular texture (grains protrude) on weathered, very rough surface. Unsorted allochems float in crystalline matrix. Fossil fragments with spar overgrowths: corals, bryozoans, brachiopods, echinoid plates, and intraclasts. Tightly cemented overgrowths on many grains form sutured contacts. Large overgrowths >3 mm (0.1 in). Chert has replaced parts of grains. Biosparite, grainstone.



Figure 46. Colonial rugose coral *Schoenophyllum aggregatum* (=*Siphonodendron genevievensis*) in wall, Joppa Member, near Foundation Hall, Flint Ridge. © A. N. PALMER

Unit J1 = lower unit of Joppa, 4–5 m (13–18 ft): fine-grained, medium-bedded limestone with a white-to-light-gray oolitic bed at the top 0.3–1 m (1–3 ft), a 0.6 m (2 ft) dolomitic bed commonly near the middle, and a shaly zone more than a meter (several feet) thick at the base. Large but sparse fossils (particularly horn corals) project from cave walls in the lower half of the unit. Nodules and discontinuous beds of chert are common in the lower half of the unit in Flint Ridge. This unit forms Cleaveland Avenue in Mammoth Cave. The J2/J1 contact is very clearly exposed in the upstream half of Swinnerton Avenue in Flint Ridge and in Fossil Avenue (New Discovery).

> **Sample J4 = oolitic bed at top of unit J1**: Crystal Cave, Camp II. Light-gray-to-white limestone, weathers cream-colored, smooth, with locally sandy texture, local stylolites at base or at transition with underlying beds (0.3–1 m [1–3 ft] thick). ***Detail***: Grains weather out forming rough surface. Large irregular bodies are cemented by spar; surrounding rock has a micritic matrix. Micritized ooids with radial-fibrous coating are most common (Figure 47). Also intraclasts, bryozoans, a trilobite fragment, crinoids, echinoids, and forams. Patches of grains with overgrowths recrystallizing to poikilotopic calcite spar. In other areas, grains grade into micrite and may be intraclasts. Biointrasparite, wackestone to packstone.

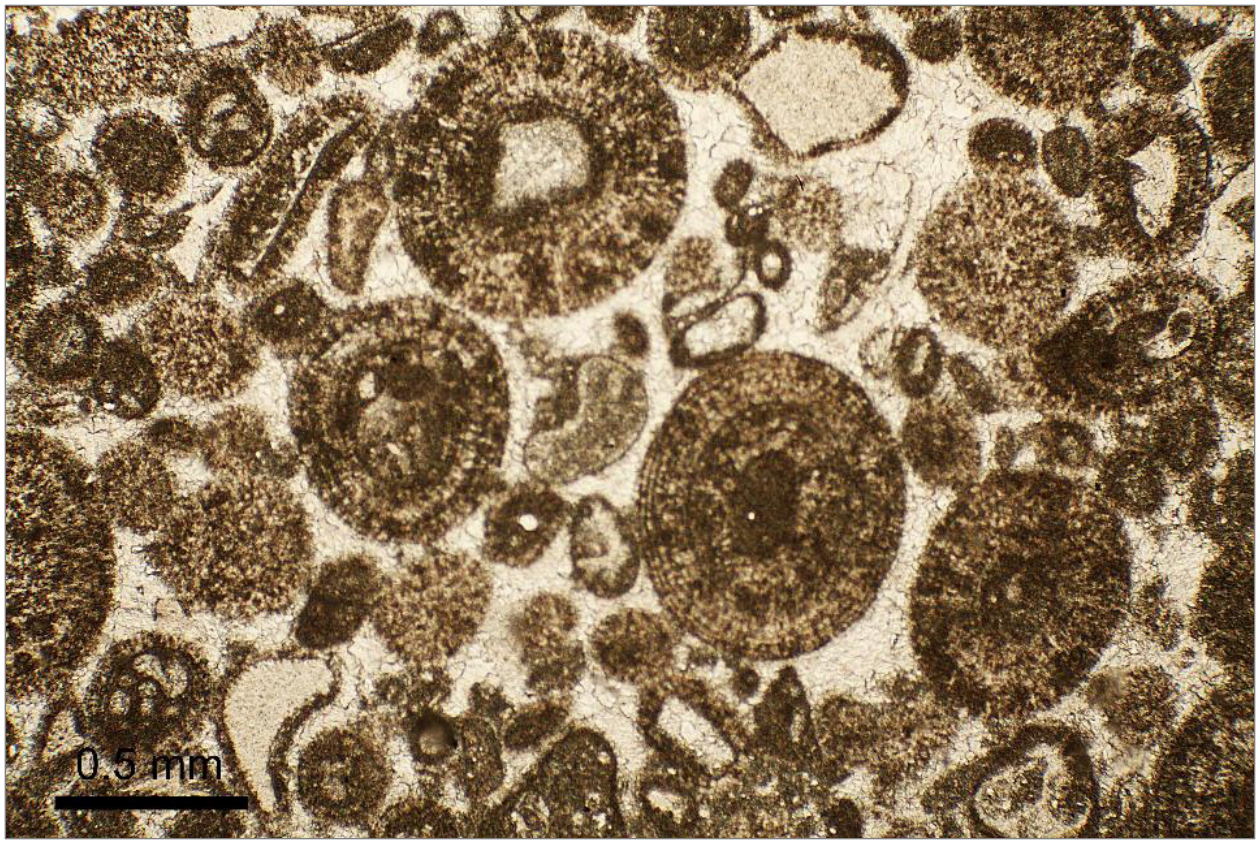


Figure 47. Ooids in J4. NP. © M. V. PALMER

Sample J5 = main part of unit J1: Crystal Cave, Canyon from Floyd's Jumpoff to Bottomless Pit. Finely crystalline to lithographic, medium-bedded, medium-light-gray-brown dolomite. Weathers same or light-gray. Beds 0.5–1 m (1.5–3 ft). Some exfoliation of massive beds; locally slightly shaly; local stylolites. Thinner-bedded toward base. Chert nodules. ***Detail***: Weathers smooth, very finely crystalline. Dolomite rhombs (50 µm [2.0 mil]) with scattered, micritized grains and iron oxide crystals, quartz silt, fossil fragments and peloids. Dolomitic biopelmicrite, mudstone.

Sample J7 = shaly basal bed of unit J1: Crystal Cave, Canyon from Floyd's Jumpoff to Bottomless Pit. Friable, dark-to-medium gray, shaly, finely crystalline limestone commonly found at base of J1. No visible crystals on exposed cave surfaces. Weathers lighter gray. Locally irregular bedding planes up to 0.3 m (1.0 ft) apart. ***Detail***: Wispy laminations, shaly with less shaly areas stretched out parallel to bedding. Poorly sorted grains floating in mud matrix. Indistinct rounded, mudstone peloids merge with mud matrix. Grains: Bryozoans, brachiopod fragments, and ostracods. Sparse quartz silt. Intrabiomicrosparite, wackestone.

Karnak Member

Thickness 1.5–3 m (5–10 ft); granular, medium-to-coarsely crystalline limestone, containing nodular chert in parts of Flint Ridge (Figure 48). Weathers rough and golden brown, with protruding fossils (particularly horn corals). Cross-bedding is common.



Figure 48. Chert bodies (possibly algal) in the Karnak Member, in the former downstream direction from Floyd's bean cans, Lost Passage of Crystal Cave. Blue pen on ledge for scale. © A. N. PALMER

> **Sample K:** Crystal Cave, From Bottomless Pit to Mud Ave. Medium-light gray, massive, foresets, generally coarsely crystalline, but locally medium-fine-grained, darker gray. Large abundant chert nodules. Weathers rough with protruding fossils, golden-brown to cream or light gray. Local geodes at base. Local shale stringers. Diagonal joints common, low angles to 30° that are gradational with bedding plane partings—perhaps influenced by cross-beds. ***Detail***: Unsorted, closely packed, micritized grains with spar between grains. Grains 0.1–2 mm (4–80 mil) diameter. Grains: Peloids, ooids, intraclasts, brachiopods, crinoids, and echinoids. Intrabiosparite, grainstone.

Spar Mountain Member

Thickness 1–2 m (3–7 ft); the Spar Mountain Member is exposed at the ceiling level of Pohl Avenue in Flint Ridge and the Steps of Time on the Historic Tour of Mammoth (Rick Olson, MACA, pers. comm., 2022). A thin bed of limestone pebbles in a matrix of shaly limestone is commonly found within the unit or at its base.

> **Sample SM1 = upper bed of Spar Mountain:** Crystal Cave, Mud Avenue. Shaly, dolomitic, light-gray limestone. Locally medium-dark-gray-brown, lithographic. Weathers smooth, light-

brown, tan or light-gray. Beds 15–30 cm (6–12 in). ***Detail***: Light-yellow brown, silty-textured mudstone, with large brachiopods. Dolomite rhombs ~50 µm (2.0 mil) diameter. Scattered iron oxide crystals. Scattered fossil fragments (altered to spar). Dolomite, wackestone.

Sample F1 = middle bed of Spar Mountain: Crystal Cave, Mud Avenue. Medium-gray, very finely crystalline, shaly limestone, mottled by possible burrows (Figure 49). Weathers light-brown or light-gray. Stylolites common at base. ***Detail***: Contains scattered quartz silt and iron oxide crystals. Silt is concentrated in burrows. Rhomb size is greater in burrows (~50 µm [2.0 mil]) than in matrix (~10 µm [0.4 mil]). Silt supports the assumption that the structures are not fossils but fill voids. Matrix is gray, burrows are tan. "Burrowed" dolostone mudstone.

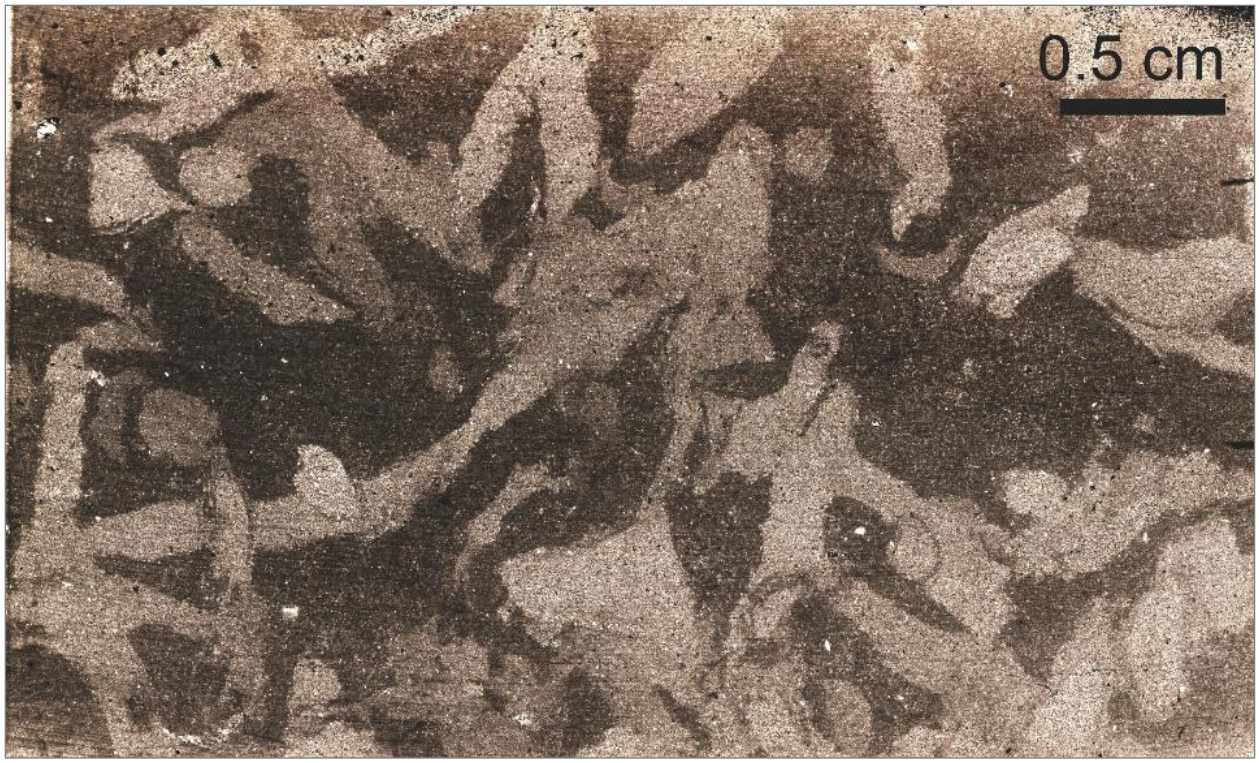


Figure 49. "Burrows" in dolomitic middle bed of Spar Mountain Member. P. © M. V. PALMER

Sample F2 = lower bed of Spar Mountain: Crystal Cave, X Pit. Medium-light-gray, coarse-grained, granular limestone. Prominently foreset, thin-bedded. Weathers light-gray, friable, rough texture. Generally contains 6–24 cm (2–9.4 in) recessive bed of rounded, micritic intraclasts in granular or shaly matrix. ***Detail***: Few vugs. Alternating bands of fine (200 µm [7.9 mil]) and coarse (500 µm [19.7 mil]) grains. Grains aligned parallel to bedding. Scattered quartz silt and iron oxide crystals. Grains: mainly peloids, ooids, crinoids, and echinoids. Overly close packing. Pelmicrosparite, packstone.

Sample F3 = pebble bed in Spar Mountain: Crystal Cave, Upper level of Mud Avenue. Dark-medium-gray with dark matrix. Weathers light-gray. Pebbles up to 4 cm (1.6 in) generally at the

bottom or top of the unit. Locally small intraclasts up to a few mm occur throughout. May grade into underlying unit. ***Detail***: The sample is a single pebble. Pebbles are 0.3–0.7 cm (0.1–0.3 in) long by 0.2 cm (0.08 in) thick. They are very friable and elongate, subangular, medium-brown and weather granular. Scattered quartz silt, iron oxide crystals, clay streaks: tightly packed, peloids, intraclasts, bryozoans, brachiopods, gastropods, crinoids, and echinoids. Cracks (<5 μm [0.2 mil] wide) separate intraclasts, indicating poor cementation. Lithoclastic intrapelmicrosparite, packstone.

Fredonia Member

Thickness 10.7–21.3 m (35–70 ft); the Fredonia is clearly exposed in Mammoth Dome in Mammoth Cave. According to Pohl (1970: Figure 2), "Member begins with mature oolith-bearing calcisiltite and ends with algal-associated dismicrite and pelletoidal calcarenite possessing a rhomb matrix. Main mass is most often an alternation of oosparites grading above to dolostones, in three rhythms about 20, 30 and 10 feet [6, 9, and 3 m] thick. Each partial cycle starts on an undulating scoured surface. Sparse chert nearly restricted to uppermost 7 feet [2 m]." Although the member possesses many lateral variations in rock type, several subdivisions can generally be recognized:

Unit F7: 1.5–3 m (5–10 ft). Unit F7 is exposed in the walls of Mammoth Dome.

Sample F4 = upper bed of unit F7: Crystal Cave, X Pit. Medium-gray to gray-brown, finely crystalline limestone, sparse fossils (particularly brachiopods), thin-to-medium-bedded at top (forms projecting ledges), massive below. Generally there is a wavy disconformity between the thin and massive beds, with relief up to 1 m (3 ft) (exposed at Grand Central Station at the base of the New Entrance, Mammoth Cave). ***Detail***: Massive texture, very finely crystalline, medium-gray. Weathers with yellow tinge. Grains were micritized or altered to spar. Boundary between grains and mud matrix is indistinct. Scattered quartz silt. Fossil fragments are indistinct. Biopelmicrite, packstone.

Sample F5 = lower bed of unit F7: Crystal Cave, ¼ of the way up the wall of Mud Ave., near the junction with Lost Passage and B Trail. Medium-gray, very fine-grained, wavy, gray-brown, wispy laminations. Weathers smooth. In dry passages this unit commonly spalls off in thick slabs concentric to the cave walls. ***Detail***: Very unsorted, sparse grains (altered to spar). One mm (0.04 in) brachiopod; remaining fossils are scattered fragments. Some quartz replacement in fossils. Dolomite (rhombs ~50 μm [2.0 mil]) and fine quartz sand in wispy laminations. Dolomitic biomicrosparite, wackestone.

Unit F6: 0.3–1.5 m (1–5 ft). Light-gray, thin-bedded, shaly limestone; weathers soft and recessive, particularly at the top. It appears as a recessed niche in the wall of Mammoth Dome.

Sample F6: Crystal Cave, lower walls of Mud Avenue. Thin-bedded, medium-light-gray, fissile, shaly limestone, upper 15 cm (6 in) strongly recessive. Grades down to shaly, but more competent and massive beds (1–30 cm [0.5–12 in] thick). Darker gray and locally crystalline toward base. Locally weathers rough with shale interbeds. Locally gradational with overlying

unit. ***Detail***: Fossil fragments are very micritized and/or altered to spar. Ostracod shells. Scattered fine quartz sand grains. Biopelmicrite, wackestone.

Unit F5: 0.3–1 m (1–3 ft). Granular, finely crystalline, oolitic limestone, in places containing a pebble bed (as in unit L).

Sample F7 = unit F5: Crystal Cave, top of X Pit at overlook from Five Passages. Light-medium gray, finely crystalline beds, 5–30 cm (2–12 in) thick. Locally intraclastic, entirely granular, dark-gray. Thin shaly interbeds common where bedding is thin. Weathers coarse, granular, light-medium gray. Top generally = 0–8 cm (0–3 in) thick intraclastic bed, shaly, friable, recessive. Bedding increases in thickness downward. Oolitic content increases downward. Local burrows at base. ***Detail***: Scattered quartz sand, iron oxide crystals and quartz replacement in fossils. Micritic seams around grains. Ooids, intraclasts, peloids, bryozoans, brachiopods, and echinoids. Micrite fraction may be dolomitic. Packed biopelmicrite, packstone.

Sample F7a = bottom of unit F5: Crystal Cave, X Pit. Medium-gray, weathers to friable white crust. Very finely crystalline with small but visible sparry allochems. ***Detail***: Dolomite rhombs (~10 μm [0.4 mil]) compose the matrix. Floating grains are altered to spar with sweeping extinction (may be saddle dolomite). Scattered iron oxide crystals. Possibly burrowed. Dolomitic dismicrite, mudstone.

Sample F8 = unit F5: Crystal Cave, X Pit. Oolitic, light-gray, finely crystalline. ***Detail***; Unsorted, intraclasts, ooids, peloids, bryozoans, brachiopods. Oopelbiosparite, packstone.

Sample F9 = unit F5: Crystal Cave, Mud Avenue. Locally intraclastic, granular, dark-gray. Top 0.5–1 cm (0.2–0.4 in) is generally an intraclastic bed, shaly, friable, and recessive. ***Detail***: Medium-gray, granular, oolitic with dark-gray, angular intraclasts (0.5–1 cm [0.2–0.4 in] diameter). Intraclasts are large and unsorted in a matrix of densely packed, sorted, and unbedded round grains. Scattered quartz sand. Some chert replacement of fossils. Intraclasts, ooids, peloids, bryozoans, and echinoids. Scattered iron oxide crystals. Dolomite in micritic matrix. Dolomitic intraoomicrite, wackestone.

Unit F4: 2–3.7 m (7–12 ft). Fine-grained limestone and dolomite, medium-to-thick-bedded. It is exposed in the wall of Mammoth Dome. A local, recessed, shaly zone occurs at the base of the unit at this location.

Sample F10 = unit F4: Crystal Cave, X Pit. Shaly, massive, limestone and dolomite. Limestone is lithographic, medium-dark-gray or gray-brown, weathers to light-gray and grades into limy dolomite. Thin-bedded at base. ***Detail***: Dolomite is very porous, light-yellowish-gray with uniform texture. Scattered iron oxide crystals. Weathers to creamy color. Dolomite rhombs (~5 μm [0.2 mil]). Mud matrix. Scattered quartz silt. Fifty μm (2.0 mil) grains altered to spar. Moldic pores. Dolomitic micrite, wackestone.

Sample F12 = unit F4: Crystal Cave, Storm Sewer. Shaly, massive dolomite and limestone. Limestone is locally coarsely crystalline with calcite vugs. Thin sparse chert layers at base. ***Detail***: Calcite spar from vug has undulose extinction and crenulated edges. Scattered quartz silt and iron oxide crystals. Likely hydrothermal fill and replacement. Calcite spar.

Unit F3: 2.4–3 m (8–10 ft), up to 7 m (23 ft) in northwestern Mammoth Cave Ridge. Medium-to-coarsely crystalline, granular, fossil-rich limestone (Figure 50), thin-bedded to massive; weathers with rough texture. This unit forms the pillars of the Ruins of Karnak in Mammoth Cave, where it is atypically massive. The "capitals" of the pillars are formed by the thinner-bedded F4 unit. F3 is also exposed in Jessup Ave. in Mammoth Cave, where shark fossils have been identified (R. Toomey, pers. comm., December 2022).

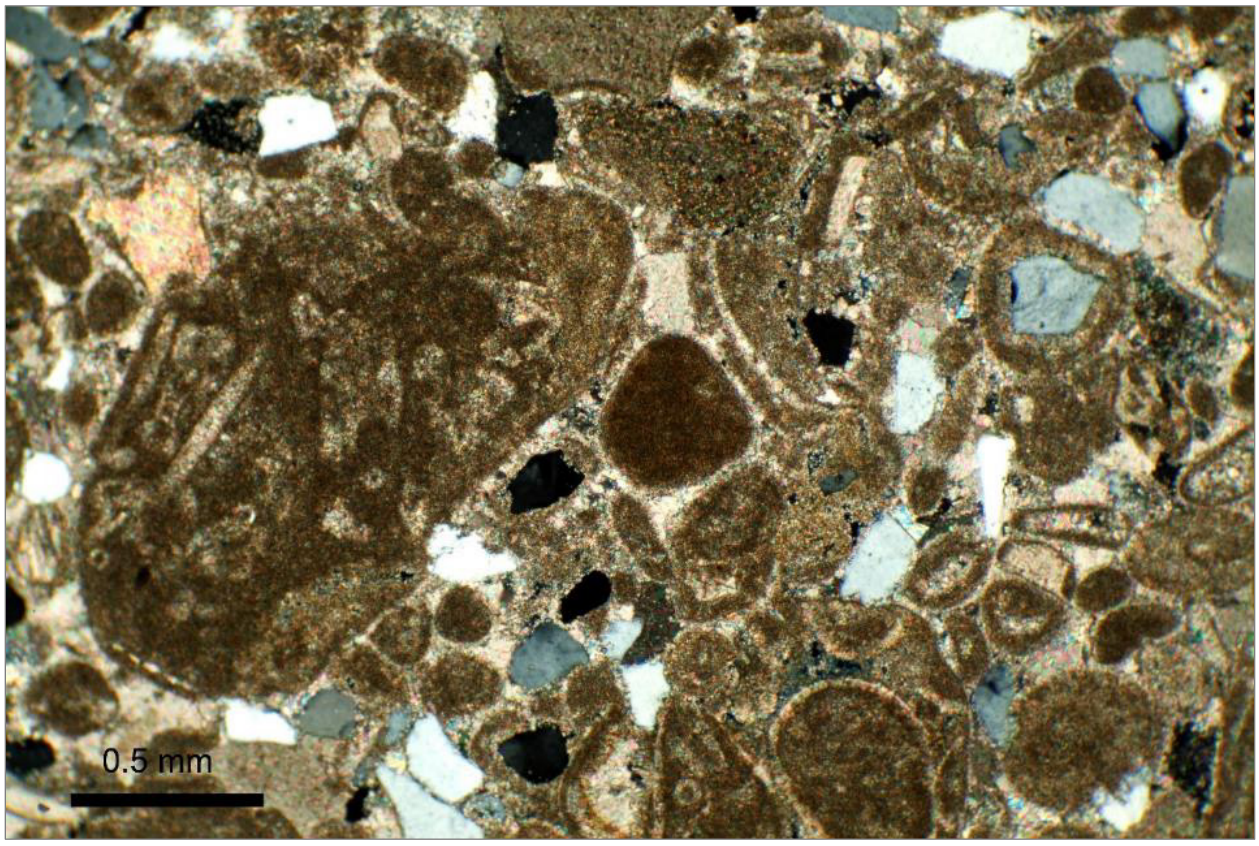


Figure 50. Intraclast and coated grains in silty packstone in F3. White-to-light gray grains are quartz. P.
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Sample F13a = unit F3: Crystal Cave, X Pit. Usually medium-coarsely granular, oolitic, medium-to-light gray. Beds 10–30 cm (4–12 in), recessed. Generally coarser toward middle. Weathers rough. ***Detail***: Medium-gray, very finely crystalline, small scattered intraclasts and sparry fragments in much finer matrix. Weathers buff. Unsorted grains: peloids, ostracods, echinoids, and forams. Tabulate coral *Syringopora* (at Ruins of Karnak). Grains highly micritized. Scattered 15–40 μm (0.6–1.6 mil) dolomite rhombs, iron oxide crystals, and quartz

silt in micritic matrix. Scant quartz replacement in fossil fragment. Dolomitic pelmicrite, wackestone.

Sample F13 = unit F3: Crystal Cave, Camp II Pit, climbing down in drain. Medium-to-coarsely granular, oolitic, medium-to-light gray, generally fine-to-coarsely crystalline. Beds 8–30 cm (3–12 in), recessed. Generally coarser toward middle. Weathers rough. ***Detail***: Massive, some clear cement between tightly packed ooids, intraclasts, grains with micritic rims, peloids, bryozoans, and forams. Some echinoderm and/or crinoid plates with overgrowths. Oobiosparite, packstone.

Sample F15 = dolomitic unit in F3: Crystal Cave, X Pit. Local dolomite bed, massive. Medium-to-light gray, beds 30–60 cm (12–24 in), finely crystalline. ***Detail***: Yellow-brownish gray. Fifty µm (2.0 mil) dolomite rhombs partly replace scattered grains that were altered to calcite spar. Sparse, clusters of iron oxide crystals. Dolomite, mudstone.

Sample F14 = fossil bed at base of unit F3: Crystal Cave, X Pit. Base = fine-to-coarsely crystalline, medium-granular texture. Oolitic, medium-gray, weathers rough. Bed 30 cm (12 in) thick with fossils, especially small brachiopods. ***Detail***: Closely packed ooids and some fossil fragments, peloids, intraclasts, bryozoans, brachiopods, echinoids, and forams. Sparse, scattered iron oxide crystals. Oobiosparite, packstone (Figure 51).

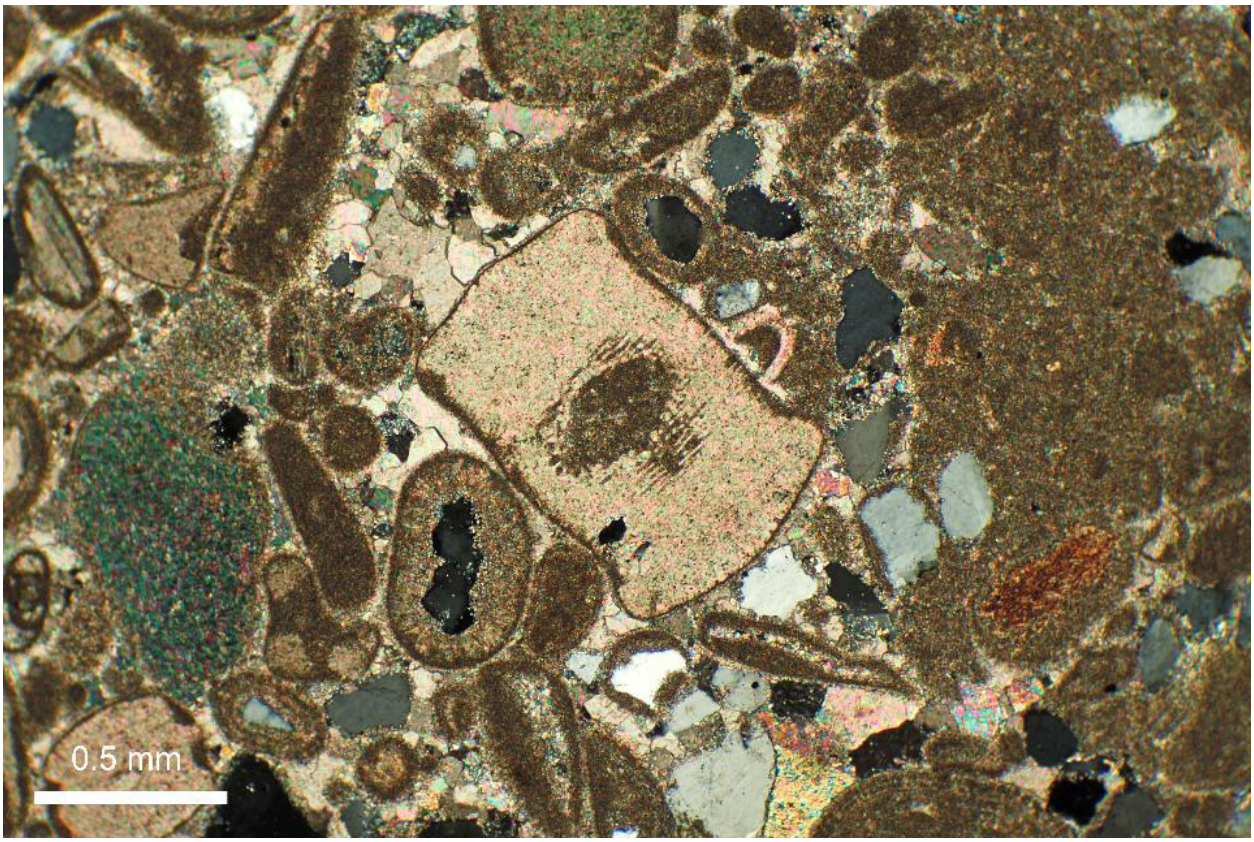


Figure 51. Fredonia unit F3. Grains to right merge into micrite. Echinoderm plate in center. P.
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Unit F2: 1.5–3 m (5–10 ft). Fine-grained limestone and dolomite, similar to unit F4.

Sample F16 = dolomite (unit F2): Crystal Cave, X Pit. Locally light-medium-gray, very finely crystalline dolomite. ***Detail***: Sparse quartz silt and iron oxide crystals with grains altered to calcite spar. Massive. Rhombs 20–100 µm (0.8–3.9 mil). Dolomite, mudstone.

Sample F16a = dolomite (unit F2): Crystal Cave, X Pit. Medium-gray, very finely crystalline, weathers light-gray with brown coating. ***Detail***: Dolomite rhombs 20–100 µm (0.8–3.9 mil). Scattered grains altered to calcite spar. Scattered iron oxide crystals. Dolomite, mudstone.

Sample F18 = Basal bed (unit F2): Crystal Cave, X Pit. Medium-to-gray-brown, very finely crystalline matrix with large spar-filled grains. Surface weathers white. Gypsum crust. Long, linear ridges (possible burrows) stand out on the weathered surface. Porosity occurs in sparry areas. ***Detail***: Scattered iron oxide crystals and quartz-filled pores in dolomite (20–50 µm [0.8–2.0 mil]) matrix. "Burrows" are filled with calcite spar, scattered dolomite rhombs and pyrite crystals. Dolomitic mudstone.

Unit F1: 2.7–4.9 m (9–16 ft). In northwestern Mammoth Cave Ridge unit F1 thickens, as at Mammoth Dome, where the unit is located at the level of the lowest landing. Sparks Avenue in Mammoth Cave is developed along the contact between the base of unit F1 and the underlying St. Louis Formation. *Syringopora* occurs in sample from Pinson's Pass.

Sample F19 = Unit F1: Crystal Cave, X Pit. Medium-to-dark gray, medium-grained. Weathers rough, granular, coarse, sandy texture. Massive with 2–4 cm (0.8–1.6 in) sub-beds. Recessed 30–60 cm (12–24 in) below F2. ***Detail***: Grains stand out in relief. Dark, discontinuous laminations. Fossil hash, grains broken, many grains altered to calcite spar. Brachiopods, echinoid plates, forams. Sparse quartz replacement of grains. Biomicrite, wackestone.

Sample F20 = Unit F1: Crystal Cave, X Pit. Local facies. Light-gray, shaly limestone. Texture finely crystalline. Grades downward with no major break. ***Detail***: Coated grains, intraclasts, ooids, and peloids. Broken bryozoans, brachiopods, crinoids, and echinoids (fossil hash). Micritized area with mud matrix grades into packstone with calcite spar matrix. Bio-oomicrosparite, packstone.

Sample F21 = Unit F1: Crystal Cave, X Pit. Very finely crystalline limestone, medium-gray-brown. Weathers rather rough, lighter gray. Massive texture, vugs. ***Detail***: Cluster of spar-replaced forams. Bimodal: bryozoans, ostracods, forams. Biomicrite, wackestone.

Sample F22 = Unit F1: Crystal Cave, X Pit. Oolitic. Some large crystals up to 2 mm (0.08 in). Light-gray. Weathers granular, slightly rough. Dark-brown shale at base. ***Detail***: Large cavity partly filled with calcite spar. Areas of grains with finely crystalline matrix adjacent to areas with no cement (porous) or spar cement. Iron oxide crystals lined stylolites formed at the contact of spar versus finely crystalline cement matrix. Grains: ooids, intraclasts, and echinoderm plates. Porous oomicrosparite, packstone (Figure 52).

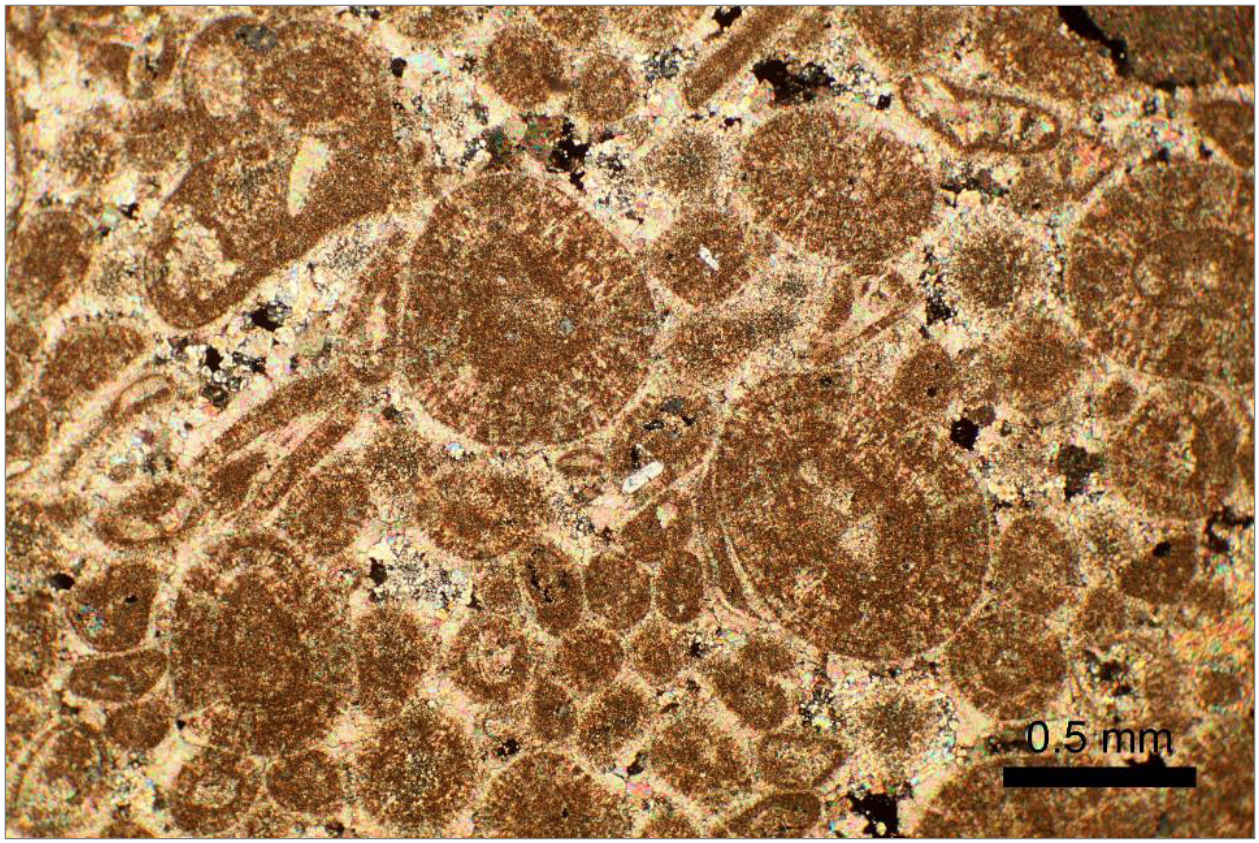


Figure 52. Ooids going to micrite in F22. Note tiny euhedral quartz crystals. P. © M. V. PALMER

St. Louis Formation

Only the uppermost 24.4 m (80 ft) of the St. Louis Formation are exposed in the presently known parts of the Mammoth Cave System. This stratigraphic interval can be distinguished from the overlying Fredonia beds by several characteristics: (1) the dark-brown color of most weathered surfaces, in contrast with the predominantly light-gray color of the Fredonia; (2) thin interbeds of dark-brown shale near the top of the St. Louis; and (3) abundant bedded and nodular chert in the lower beds of the exposed section (Figure 53). An 8.8-m (29-ft) section of the St. Louis is exposed at the bottom of Mammoth Dome that shows the typical character of the non-cherty upper beds, but with an abnormally large thickness. The lowest beds observed to date appear in Hawkins River.



Figure 53. Manganese-dioxide-coated, bedded and nodular chert standing out from a wall, Martel Ave., Mammoth Cave; Lost River Chert Unit, Horse Cave Member of the St. Louis Formation. © A. N. PALMER

Horse Cave Member

Thickness 10.7–14 m (35–46 ft); this unit, proposed by Pohl (1970), was previously included within the Ste. Genevieve Formation. It consists largely of moderately granular and crystalline limestones grading upward to dolomites. Thin beds of dark-brown shale are common in the upper 3–6 m (10–20 ft). Two prominent zones of bedded and lenticular chert occur within the limestone. The upper chert zone, which attains an overall thickness as great as 3 m (10 ft), is called the Lost River Chert Bed and is exposed in passages slightly above the general ceiling level of Mystic River. Several of the access crawlways to Mystic River (in the lower levels of Mammoth Cave) are perched on the lower of the two chert zones. The uppermost bed in the Horse Cave Member is a fine-grained dolomite 0.8–2 m (2.5–7 ft) thick, which generally protrudes slightly into passages because of its comparative resistance, although where shaly, it forms a recessed niche, as in Mammoth Dome. The bed is exposed more than a meter (several feet) above the floor throughout most of the length of Emily's Avenue, Mammoth Cave, where it appears as a resistant unit containing dark laminations on weathered surfaces.

The meter or so (a few feet) of the St. Louis found in the cave below the Horse Cave Member consists of fine-grained dolomite and limestone. The top of this sequence is defined by a prominent zone of lenticular chert (exposed in the bed of Mystic River).

Per Pohl (1970), the entire formation is nearly devoid of terrigenous material, except toward the top of the Horse Cave Member. Present are ostracod-bearing micrites, highly fossiliferous lithostrotionid-bearing limestone, and abundant but irregularly present stromatolites. Other fossils in the St. Louis include the foram *Eoendothyranopsis*.

The following is a detailed description of the upper 24.4 m (80 ft) of the St. Louis Formation exposed in Hawkins River, below the Doyle Valley entrance to Mammoth Cave.

Horse Cave Member: 12.2 m (40 ft). Prominent chert beds and nodules (Figure 54). The Lost River Chert near the top of the member forms a resistant unit over much of the sinkhole plain to the south of Mammoth Cave and in the cave forms black ledges coated with manganese and iron oxides (White 2017). It was named for Horse Cave, Kentucky. In Mammoth Cave, saddle dolomite is commonly found as veins and pore-filling cement. The following samples are in stratigraphic order rather than numeric order (see Figure 38 for stratigraphic positions).



Figure 54. Chert-filled burrows in Bransford Ave. East, Mammoth Cave. Lost River Chert, St. Louis Formation. © A. N. PALMER

Sample MCR23: Medium-gray, finely crystalline, dolomite, beds 2–30 cm (1–12 in). ***Detail****:* 50 µm (2.0 mil) dolomite rhombs, few quartz silt grains, allochems replaced by saddle dolomite. Micritic dolomite, mudstone.

Sample MCR24: Dark-gray, granular, thin-bedded limestone. Scattered iron oxide crystals. ***Detail***: Fossil fragments in mud matrix. Bryozoans, brachiopods, echinoderm plates, and forams. Packed biomicrite, packstone.

Sample MCR25: Top of Lost River Chert. Discontinuous 15 cm (6 in) zone of light-gray nodules in micritized limestone matrix. ***Detail***: Matrix = micritized fossil fragments in mud. Scattered iron oxide crystals line matrix/nodule boundary. Calcite grains disintegrate into quartz matrix and form nodules. Bryozoans, brachiopods, echinoderm plates, and forams. Chert replacement in the St. Louis samples appears to progress along grain contacts, so that grains appear to float in the chert matrix. Biomicrite, packstone with chert replacement (Figure 55).

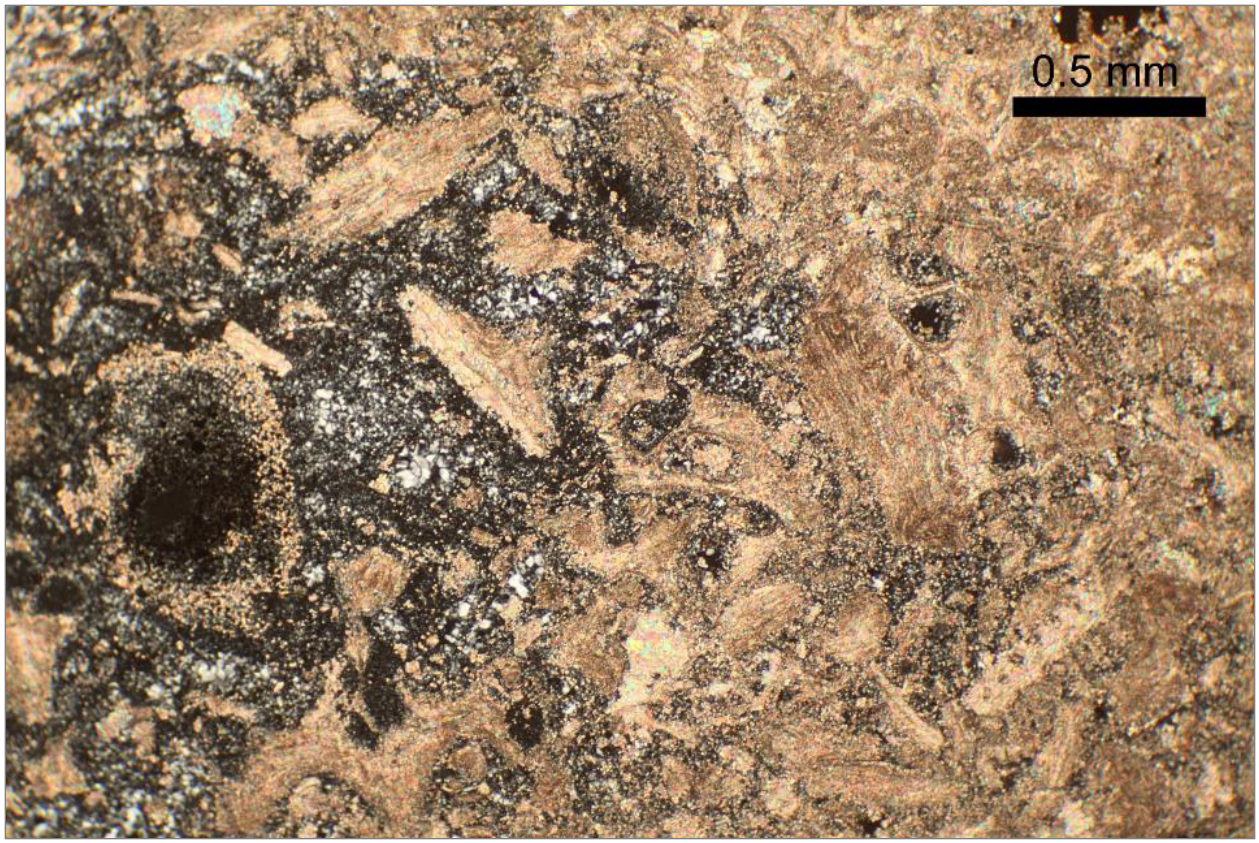


Figure 55. Chert in MCR25 illustrates progressive replacement of calcite along grain borders leaving disintegrated calcite fragments floating in chert. P. © M. V. PALMER

Sample MCR68: Cherty, light-gray limestone just below ceiling level at confluence of Hawkins River in the Lost River Chert. ***Detail***: Bryozoans, crinoids. Closely packed fossil hash. Chert has replaced micritic grains leaving larger fragments in ovoid areas up to 1 cm (0.4 in) diameter. Biomicrosparite, packstone.

Sample MCR26: Near base of Lost River Chert. Irregular lenses of chert. ***Detail***: Unsorted, closely packed, micritized fossil fragments. Bryozoans, brachiopods, echinoderm plates, and

forams. Overgrowths are common as well as large, intact fossil fragments. Packed biosparite, grainstone.

Sample MCR27: Massive limestone bed (~3 m [10 ft]). Grades downward from granular to biomicrite and chert bed at base. ***Detail***: Unsorted, overly tight packing, micritized fossil fragments (0.5–5 mm [0.02–0.2 in]). Few scattered quartz sand grains. Ooids, bored, coated grains, bryozoans, brachiopods, and echinoderm plates. Biomicrite, packstone.

Sample MCR28, 29: Chert bed at base up to 30 cm (1 ft) thick in gray-brown mottled limestone. No visible fossils. ***Detail***: Grains (<0.5 mm [0.02 in]), closely packed, broken, micritized, and recrystallized fossil hash. Possibly former breccia. Scattered iron oxide cubes in calcite grains in chert. Silty clay seams. Chert replaces micrite. Grains are recrystallized, shredded, dissolved in chert. Manganese dioxide lines the surface exposed to the cave. At the cave wall, calcite is dissolved from the chert and iron oxide and clay builds up (Figure 56). Manganese-coated dendrites suggests microbial activity is participating in the manganese wall coating (Spilde et al. 2005). Cherty biomicrite, wackestone.

Sample MCR30: Gray, bedded, granular limestone. ***Detail***: Grain size >1 mm (0.04 in), unsorted, large overgrowths. Algae, recrystallized crinoids, echinoids, forams. Biomicrite, packstone.

Sample MCR31: Light-gray dolomite. ***Detail***: Rhombs 50–100 µm (2.0–3.9 mil). Calcite matrix. No grains. Dolomite, mudstone.

Sample MCR32: Granular, gray-brown limestone, possibly burrowed. ***Detail***: Bryozoans, echinoids, forams. Biosparite, grainstone (Figure 57).

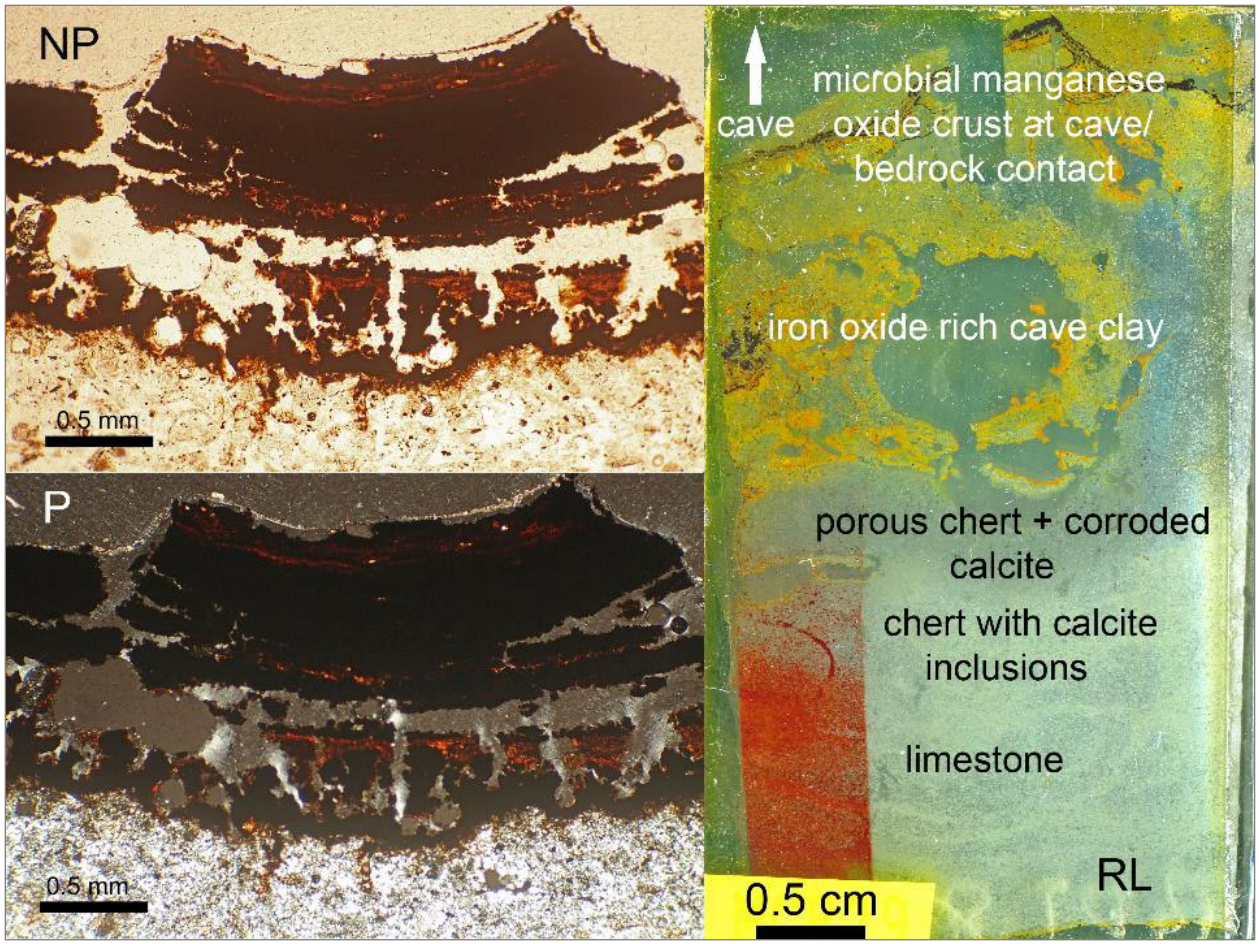


Figure 56. Shrub-like probable microbial structures coated with manganese dioxide line the cave wall and penetrate chert bedrock. Calcite inclusions in chert are dissolved leaving porous crust in MCR29. NP, P. Thin section is stained with Alizarin Red for calcite and is viewed in reflected light to highlight the iron and manganese oxides. The exposed cave wall is toward the top. © M. V. PALMER

Sample MCR33, 34: Light-gray dolomite, rhombs 50–100 µm (2.0–3.9 mil). Calcite matrix. No grains. Saddle dolomite balls up to 1 cm (0.4 in). Dolomite, mudstone.

Sample MCR35: Porous dolomite. Light-gray, smooth surface. ***Detail***: Rhombs 100 µm (3.9 mil). Calcite spar matrix. No grains. Dolomite, mudstone.

Sample MCR36: Corydon Chert. Medium-light-gray chert. ***Detail***: Ostracods, forams, possible spicules, micritized grains, unsorted. Chert replaces micritized rounded calcite grains (100–200 µm [3.9–7.9 mil]), probably a former packstone. Calcite grains in chert are dissolved to form porous zone adjacent to clay, which coats the cave wall. Where exposed, clay is lined with shrub-like (probably microbial) manganese dioxide.

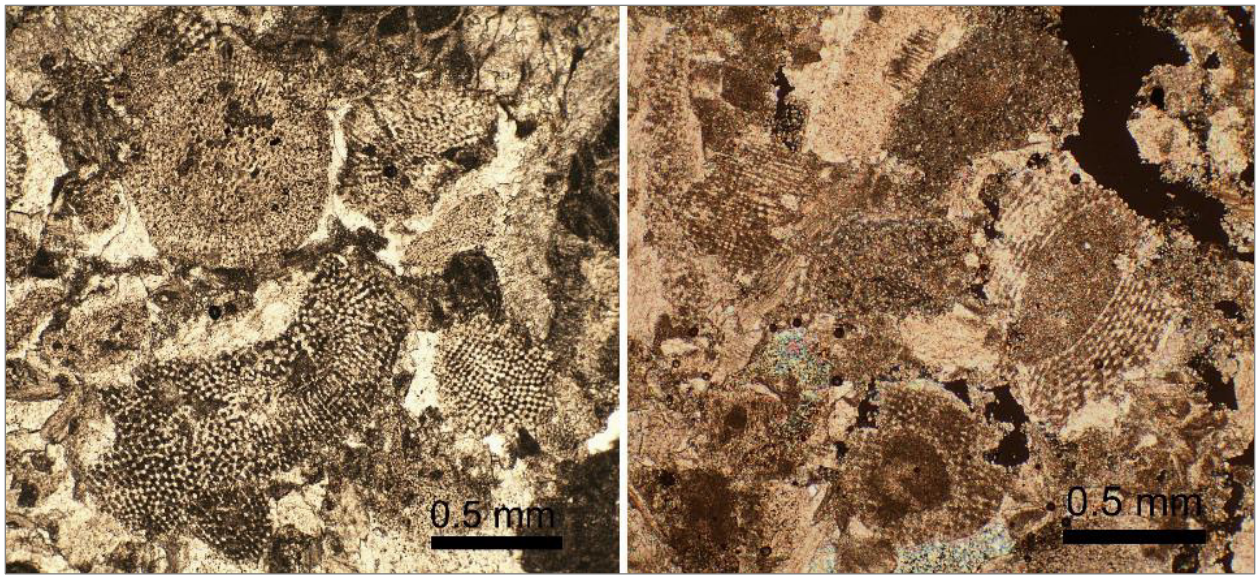


Figure 57. Grains in MCR32. NP, P. © M. V. PALMER

Sample MCR39: Chert. steeply dipping thin layers. ***Detail***: Closely packed fossils replaced by calcite spar in chert matrix with alternating laminations of possible siliceous filaments and grains (Figures 58 and 59). Micritized grains: ooids, echinoderm plates, and forams.

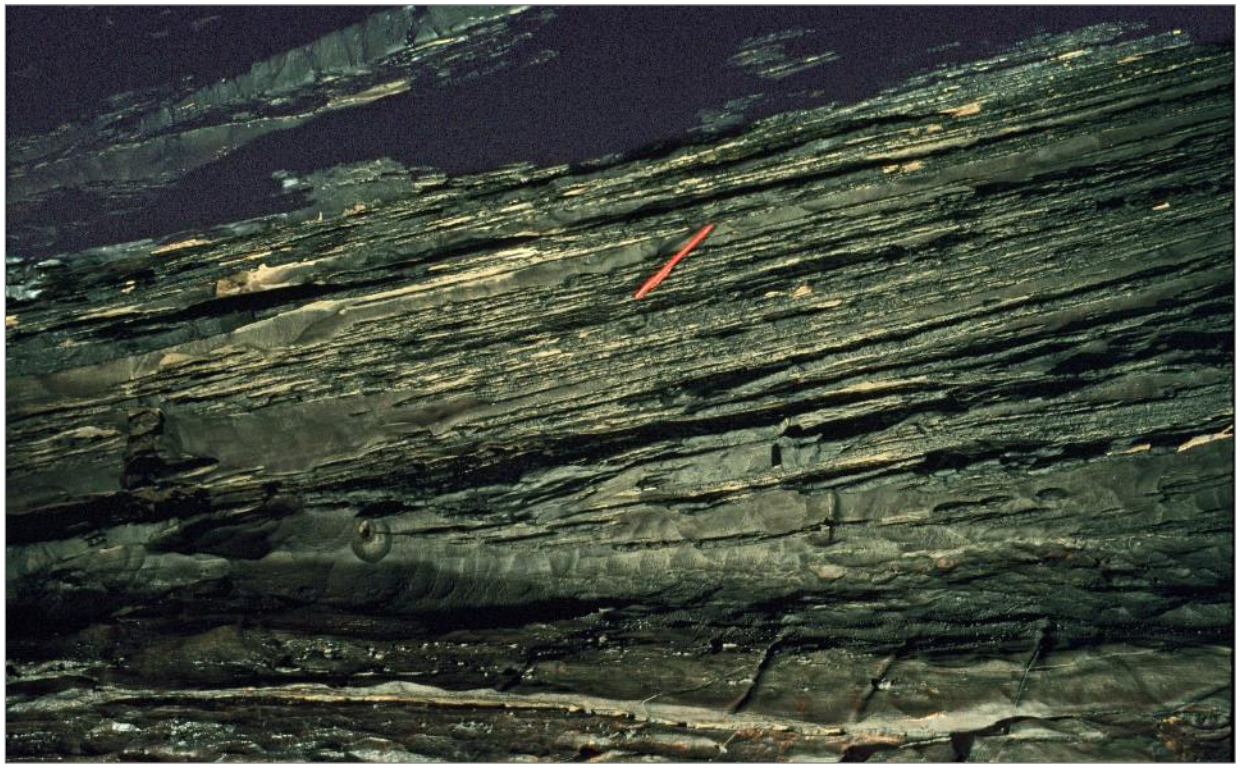


Figure 58. Hawkins River, inclined siliceous layers containing samples MCR39 and MCR70. Gloomy cave wall is coated with manganese dioxide. © A. N. PALMER

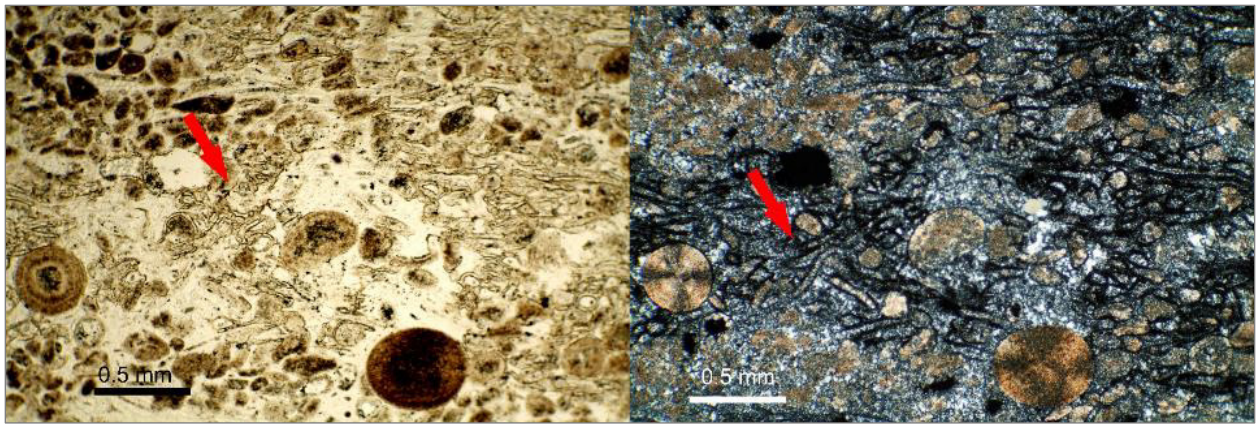


Figure 59. St. Louis Formation. Possible algal filaments and coatings (arrows) may have formed alternating mats separating layers of carbonate sediment. Sample MCR39. NP, P. © M. V. PALMER

Sample MCR70: Top of laminated zone (Figure 58). ***Detail***: Laminations containing siliceous bodies in fossiliferous limestone (Figure 59). Well-sorted forams, ooids and possible filaments. Closely packed biosparite, grainstone.

Sample MCR40: Uniform-gray limestone between chert beds. ***Detail***: Partly micritized, closely packed fossil hash: scattered quartz silt, pellets, forams, and fossil fragments. Packed biomicrite, wackestone.

Sample MCR37, 38: ***Detail***: Limestone merges with chert. Grains are altered to calcite spar. Poorly sorted, mostly intact forams, mollusk shells, ostracods. Widespread replacement leaves 1 µm (0.04 mil) micritic calcite outlining grains. Chert bodies possibly replace burrows. Biosparite packstone.

Sample MCR47: Chert. ***Detail***: Granular quartz replaced former biomicrite, packstone. Ostracods, echinoid plates, forams, possible spicules. Some chalcedony fills horizontal stringers of moldic pores. There is a prominent horizontal, porous layer where molds are lined with iron oxide. Some chalcedony in pores.

Sample MCR41: Area with apparent chert burrows. ***Detail***: 3 cm (1.2 in) chert ball. Center = dedolomite in finely crystalline quartz. (Dedolomite: calcite replaces dolomite. Common where calcium sulfates are present). 1 mm (0.04 in) ring of porous quartz. Micrite, dedolomite rhombs, and grains altered to calcite spar in chert. Four mm (0.2 in) outer layer of very finely crystalline quartz after biomicrite.

Sample MCR81: Example of chert ball in Hawkins River from same area as **MCR41** (Figure 60).

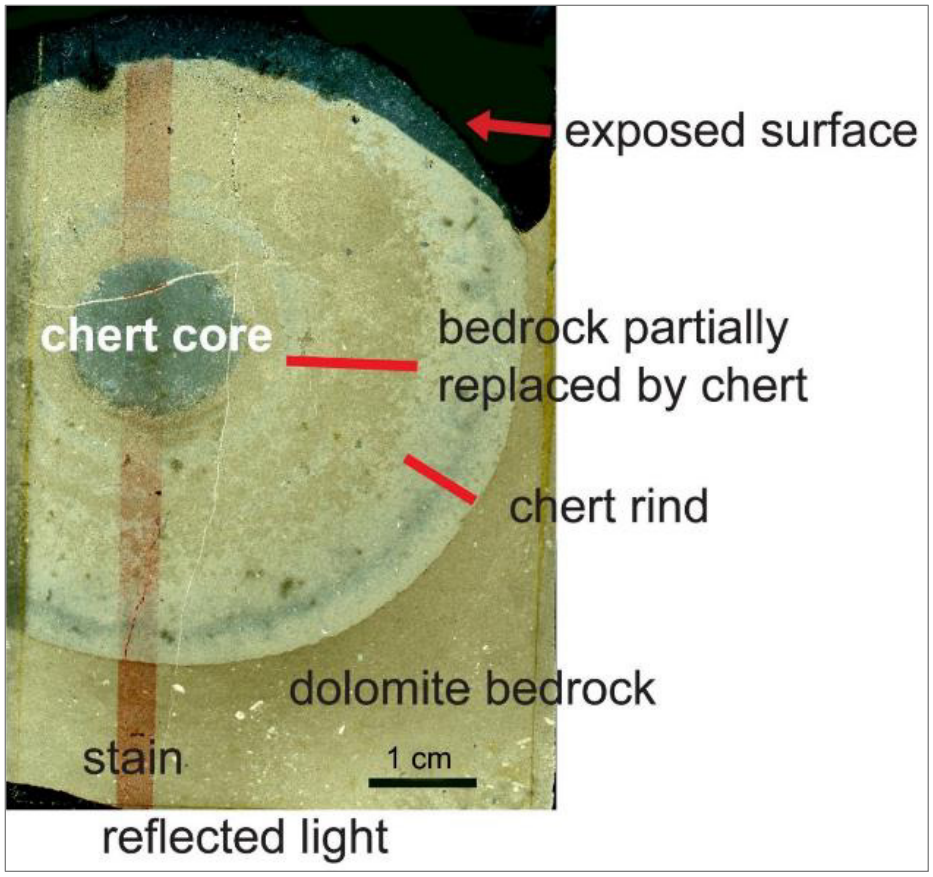


Figure 60. Ball chert in St. Louis Formation (MCR81, from same area as MCR41). Possible algal ball. Alizarine Red stain for calcite. Reflected light illustrates the large amount of iron oxide in both the ball and the dolomite bedrock. Weathering of pyrite in the dolomite produces iron oxide crystals, which can give the cave walls a yellow-brown color. Arrow points to corroded surface exposed to cave and overlain by sediment. © M. V. PALMER

Sample MCR42, 43: Apparent burrows (Figure 61). ***Detail***: Original matrix = 100 µm (3.9 mil) dolomite rhombs in calcite spar cement and dolomitic wackestone. There are concentric zones of chert replacement. Grains in fossil hash include possible spicules. Sparse chalcedony replacements of euhedral evaporite crystals.

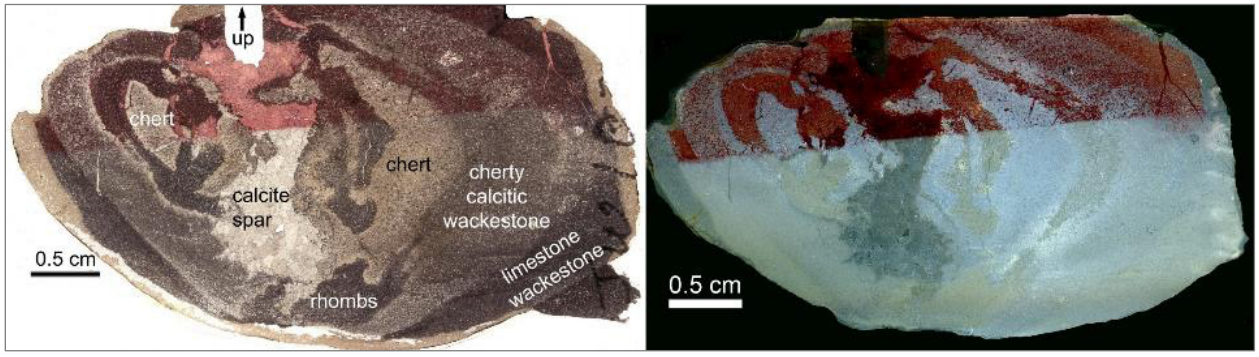


Figure 61. Apparent burrow in MCR 42. Alizarin red stain for calcite. NP, RL. © M. V. PALMER

Sample MCR75: Medium-gray, massive limestone. Below are irregular lenses of chert 1–2 cm (0.4–0.8 in) thick. ***Detail***: Some quartz silt, bryozoans, echinoderm plates, forams. Micrite fills voids in shells. Packstone, packed grains (Figure 62).

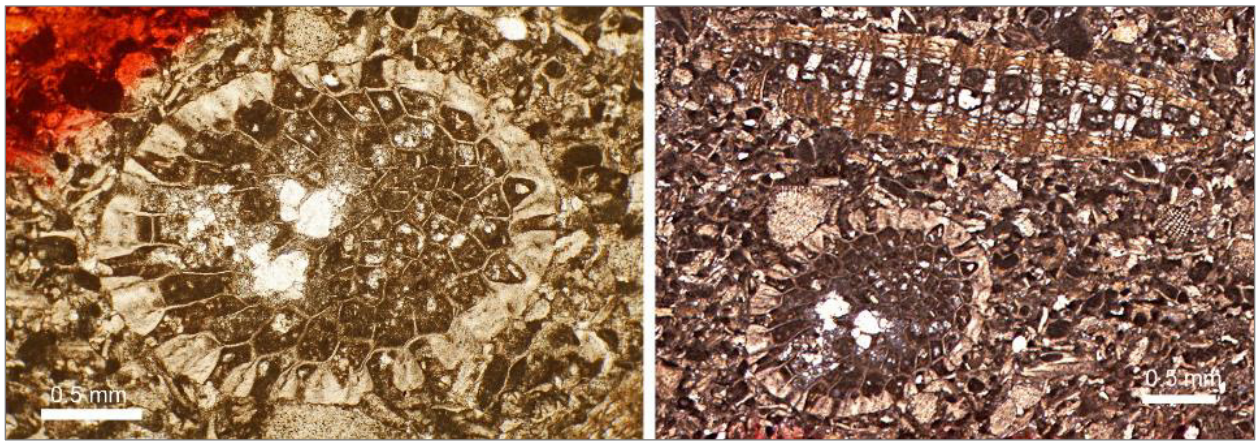


Figure 62. Bryozoans (MCR75). NP, NP. © M. V. PALMER

Sample MCR45: Chert ball in dolomitic bedrock. ***Detail***: Bedrock is dolomitic mudstone with scattered echinoderm plates and possible spicules.

Sample MCR46: White chert next to light-gray-brown dolomite. At water level at Hawkins Formation. There are chert after anhydrite dikes in the cave wall. ***Detail***: Cubic to pinacoidal, zebraic chalcedony in very finely crystalline quartz matrix (Figure 63), interfingers with dolomite (rhombs <10 µm [0.4 mil]). Iron-rich stringers of saddle dolomite and calcite in dolomite.

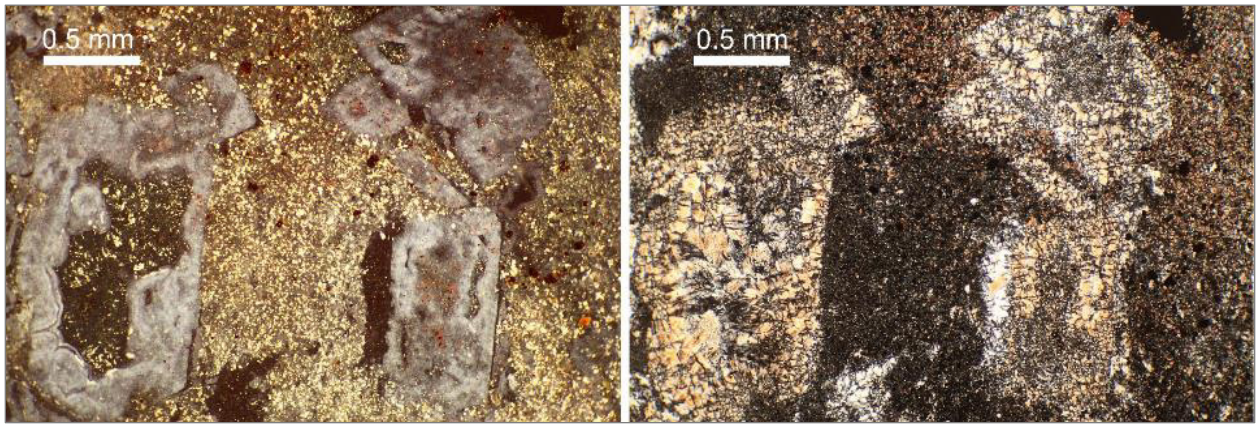


Figure 63. Zebraic chalcedony replaced perimeter of former euhedral, prismatic evaporite crystals in MCR46. Reflected light brings out red, former pyrite crystals in replaced evaporite crystals. RL, P. © M. V. PALMER

Sample MCR76: Abundant chert lenses up to 5 cm (2 in) thick (Figure 64). ***Detail***: Merges with silty dolomite where rhombs float in calcite spar matrix.

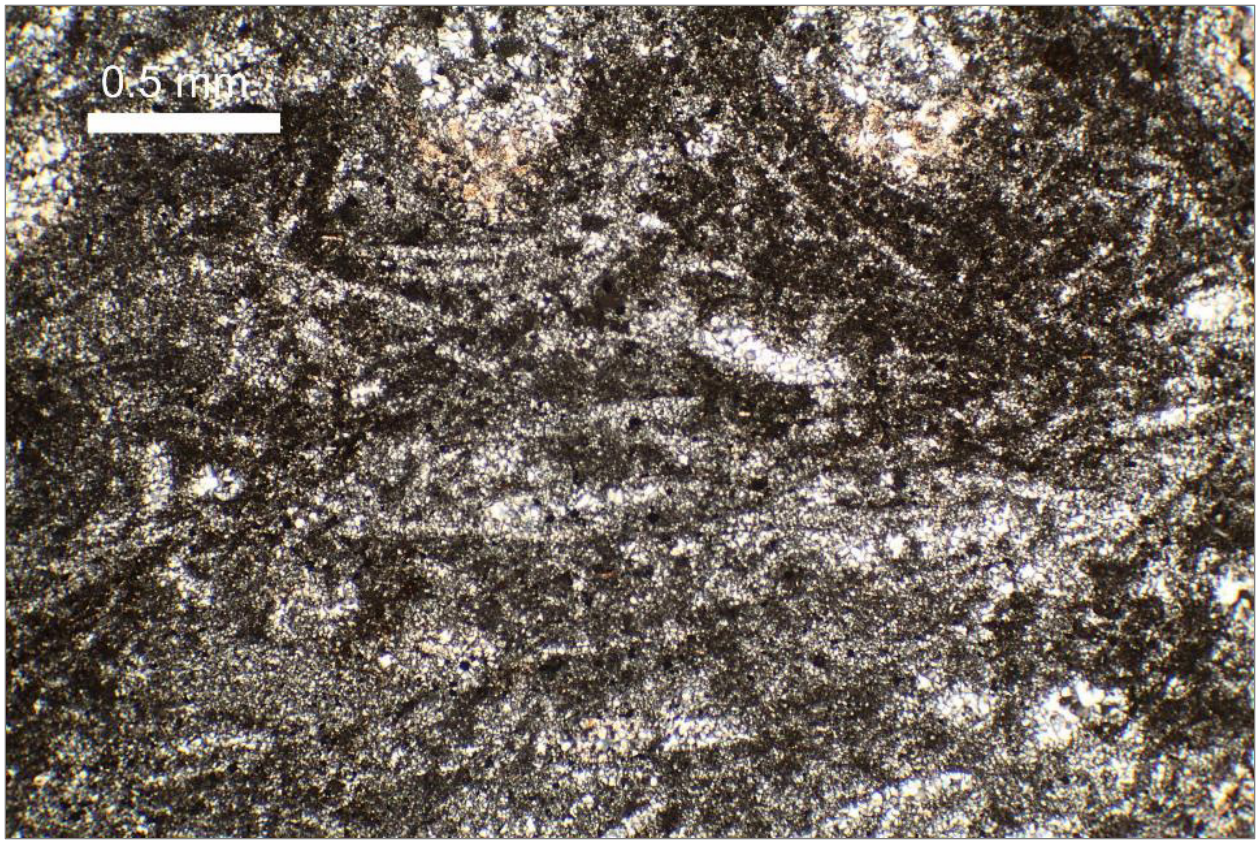


Figure 64. Possible spicules in MCR76. Resolution is affected by chert replacement. P. © M. V. PALMER

Sample MCR66: Chert lenses in the lowest part of the Corydon Chert (Figure 65). ***Detail***: Closely packed wackestone is cut by irregular lens of rectilinear calcite crystals (100 × 100 µm [3.9 × 3.9 mil]) merging into poikilotopic spar with patchy chert replacement and iron oxide crystals. Bryozoans, echinoids, forams, and fossil fragments in surrounding limestone.

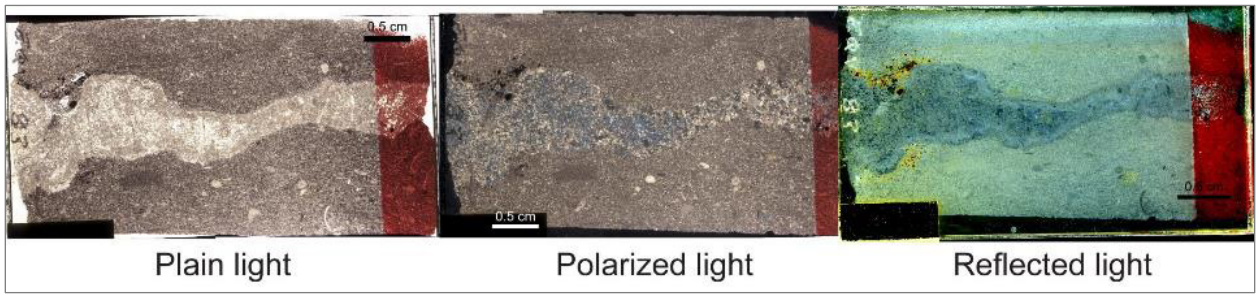


Figure 65. Irregular lens of rectilinear calcite and chert in calcareous wackestone bedrock (MCR66). Alizarin red stain is for calcite. Grey is chert in polarized light. Black iron oxide crystals and yellow limonite are highlighted in section viewed in reflected light. © M. V. PALMER

The rectilinear shape of the calcite crystals suggests replacement of anhydrite which has cubic cleavage, while the square shape of many of the iron oxide crystals suggests former pyrite. Micritic calcite surrounding iron oxide (Figure 66) may be the result of oxidation of former pyrite

to sulfuric acid. The combination of former pyrite and calcite after anhydrite suggests sulfate reduction occurred, where the combination of carbon and sulfate yields pyrite and calcite. Carbon to drive the reaction may have been hydrocarbons during a Mississippi Valley-type event that produced saddle dolomite, fluorite, pyrite, and sparse sphalerite in Mammoth Cave samples.

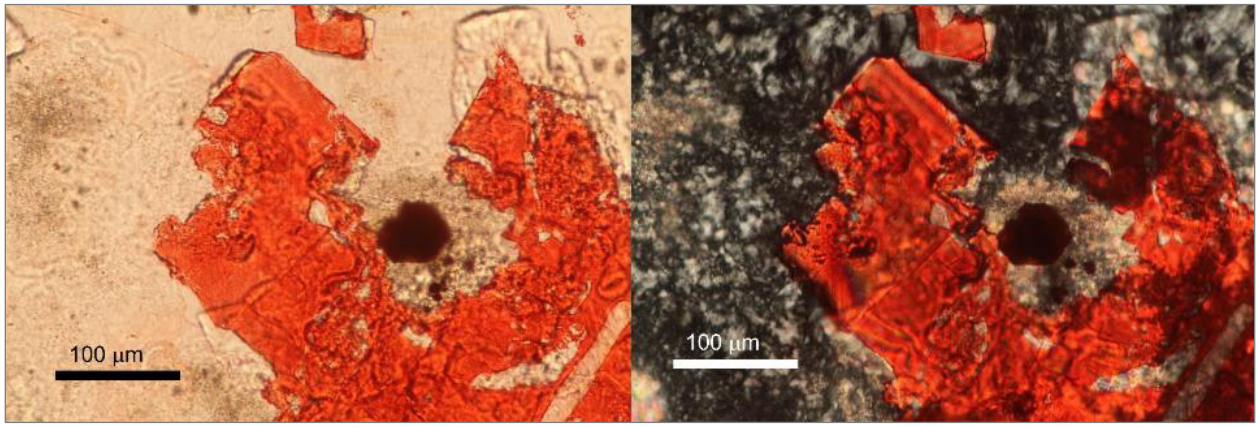


Figure 66. Calcite spar overgrowths in chert MCR66. Former pyrite oxidized to FeO_2 corroding the spar. Rectangular shape of calcite suggests sulfate reduction of anhydrite. NP, P. © M. V. PALMER

Sample MCR77: Massive chert bed. ***Detail***: Veins of calcite spar and saddle dolomite cut across chert. Stylolites cut across calcite cement. Much of chert is chalcedony. Chert replaced wackestone bedrock with bryozoans, echinoids, and other highly replaced fossil fragments.

Sample MCR65, 64: Light-gray, massive, finely crystalline dolomite. ***Detail***: Rhombs 10 µm (3.9 mil). Some quartz silt. No chert. Few grains replaced by saddle dolomite.

Sample MCR62, 63: Shaly, light-gray limestone. Laminated. ***Detail***: Clay in stringers colored yellow by iron oxide. Scattered, corroded grains altered to calcite spar. Clay and limestone interfinger. Limestone with bryozoans, crinoids, and forams. Partial micritization of grains. Scattered iron oxide crystals. Biomicrite, wackestone.

Sample MCR60: Light-gray, finely crystalline, silty limestone with balls of chert in discontinuous zones. Weathers with granular surface. ***Detail***: Scattered iron oxide crystals and quartz silt. Possible burrows filled with wackestone. Mudstone with packed biomicrite in "burrows".

Sample MCR61: 5–10 cm (2–4 in) balls of chert in **MCR60. *Detail*:** Ball has concentric zebraic chalcedony surrounding calcite spar (Figure 67). Very finely crystalline chert contains 300 µm (11.8 mil) rectilinear calcite crystals with scattered iron oxide crystals. Balls appear to have replaced evaporite nodules.



Figure 67. Rectilinear calcite in very finely crystalline chert on left. Zebraic chalcedony lines calcite spar that filled former void on right in MCR61. Calcite is after former evaporite. P. © M. V. PALMER

Sample MCR58: Yellow shale (1 cm [0.4 in] thick). ***Detail***: Shale overlies very finely crystalline, silty chert containing spicules (Figure 68).

Sample MCR55: Light-gray dolomite. Chert bed, 5 cm (2 in) thick and 0.3 m (1 ft) above base, grades into chert lenses. Nodules begin above the chert bed. ***Detail***: Dolomite rhombs 20 µm (0.8 mil), scattered quartz silt and 100 µm (3.9 mil) iron oxide cubes. Dolomite mudstone.

Sample MCR54: Pendulous chert hanging from base of overlying bed. ***Detail***: Balls of zebraic chalcedony with anhydrite inclusions and needle-shaped pores. Also contains fluorite. Saddle dolomite and fluorite commonly occur with quartz after evaporites in Mammoth Cave (Figure 69).

Sample MCR50: Light-gray limestone. ***Detail***: Highly micritized grains. Ostracods, scattered forams, possible spicules, pellets, quartz silt, and 50 µm (2.0 mil) dolomite rhombs. Dolomitic biopelmicrite, wackestone.

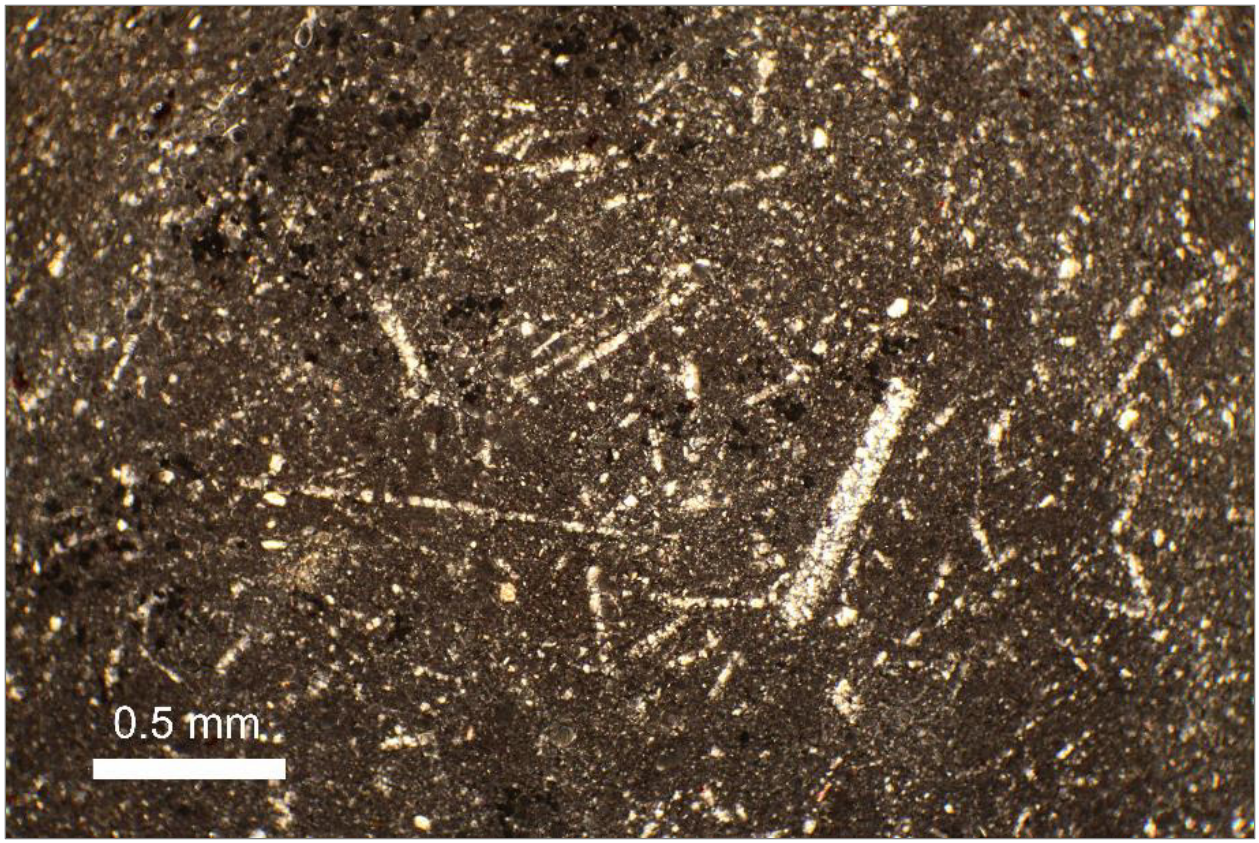


Figure 68. Probable spicules in very finely crystalline chert in MCR58. P. © M. V. PALMER

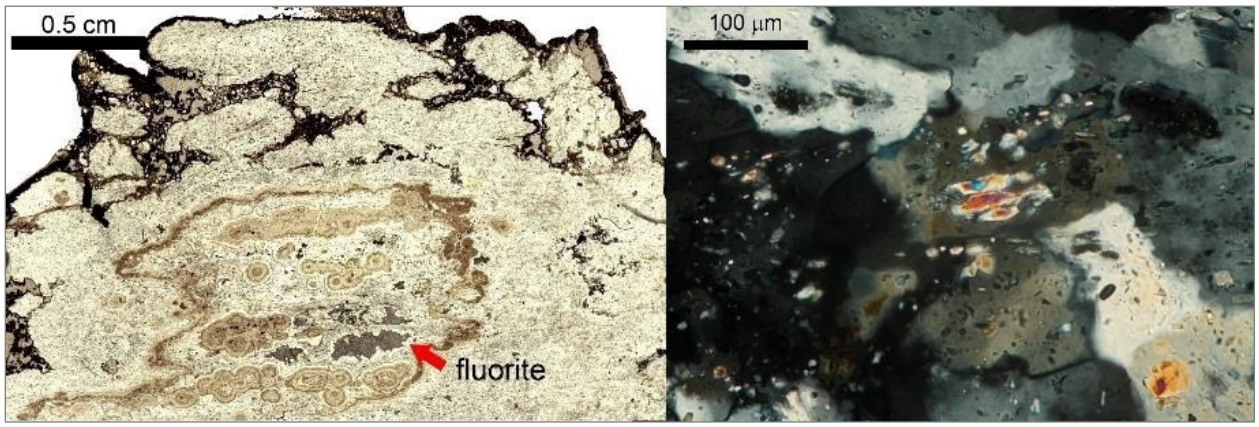


Figure 69. Chert with nodular shapes suggests replacement of evaporites. Anhydrite inclusions in quartz confirms evaporite replacement (MCR54). P, NP. © M. V. PALMER

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Appendix B: Geologic Guide to the Historic Route

This tour gives the clearest view of the various passage types, levels of cave development, and limestone strata in the cave, and is meant for a non-caver who would like to identify the rocks on a tourist route. It includes a long loop, which eliminates almost all retracing of the path (see map, Figure 70). It also extends through almost the entire sequence of limestone beds shown in the stratigraphic column (Figure 37). These include (from top to bottom, in the order seen on the tour), the Girkin Formation, the Ste. Genevieve Formation, and about the upper 9 m (30 ft) (roughly 17%) of the St. Louis Formation. On the Historic Tour, the various units in the Girkin and upper half of the Ste. Genevieve are only about half as thick as they are elsewhere in the cave. On the other hand, the underlying strata are thicker than average, so the total limestone thickness exposed on the tour is not substantially different from that shown in Figure 37.

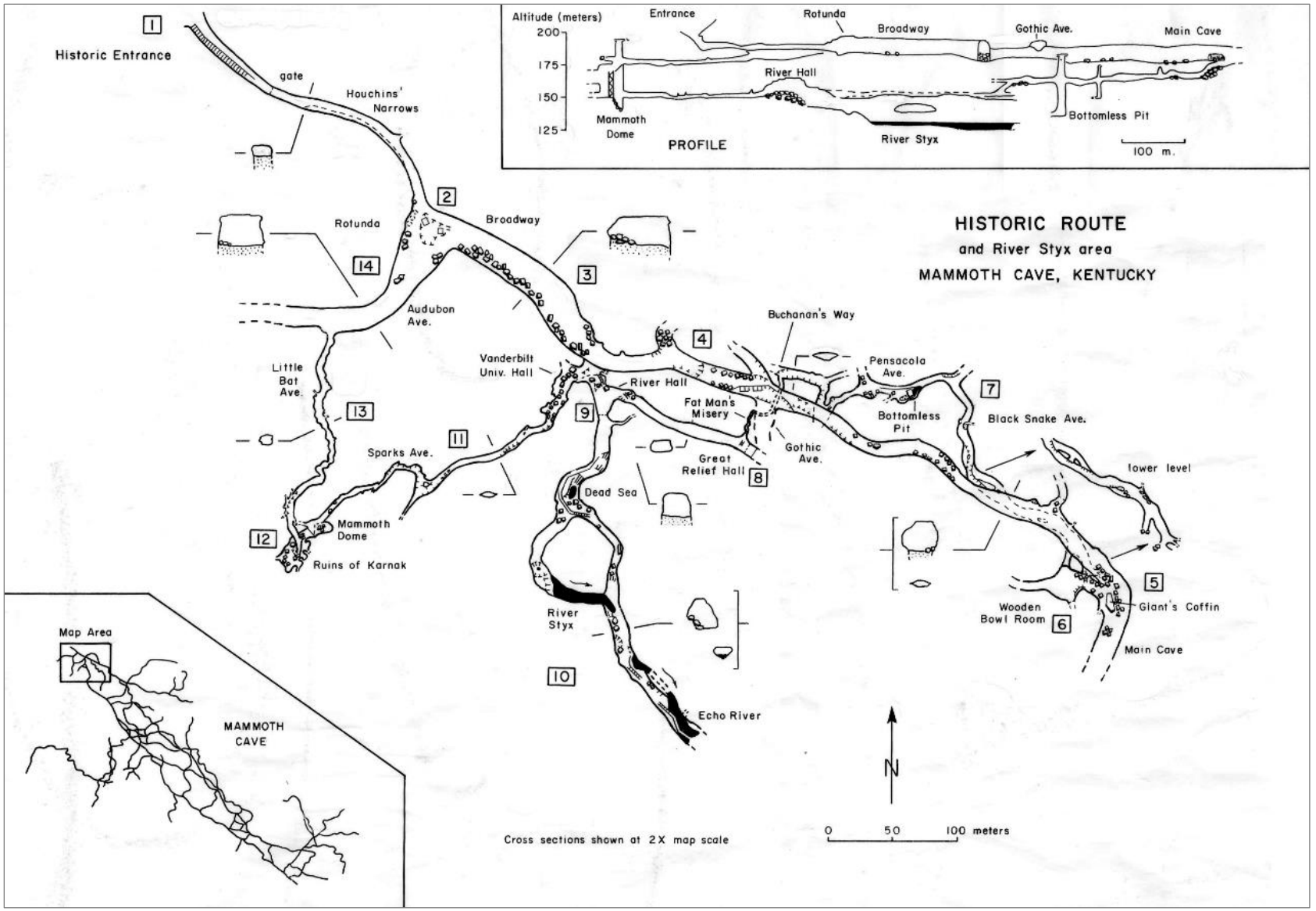


Figure 70. Simplified map and profile of the Historic Route, from the authors' surveys (1970s), showing locations of features described in the text. From Palmer (1981). Much more detailed maps have been produced since by the Cave Research Foundation. A. N. PALMER

Historic Entrance

The tour begins at the Historic Entrance (Figure 71), which formed when a small tributary valley of the Green River intersected one of the main cave passages. A poor exposure of the sandy Big Clifty Formation can be found, mainly as float, in the valley wall above the entrance. The entrance descends steeply through the Girkin Formation and leads to the main level of the cave at an altitude of about 183 m (600 ft). A short passage (Houchins Narrows), located mainly in the Paoli Member, leads to an impressive junction, the Rotunda.



Figure 71. Historic Entrance, in the middle Girkin beds. © A. N. PALMER

Rotunda

The medium-bedded unit of the Paoli Member occupies nearly the entire height of the Rotunda (Level B1). It consists of 6.4 m (21 ft) of light-gray, finely crystalline limestone. Near the ceiling is an irregular recessed ledge formed by the Bethel Member, a shaly and relatively weak limestone only

a meter or so (a few feet) thick, with the thicker-bedded Beaver Bend Member forming the ceiling. The bottom unit of the Paoli, a silty limestone, is very crumbly and forms a sharply recessed niche of dark-gray rock a meter or so (a few feet) above the floor of Audubon Avenue. This bed can be traced throughout the cave and is a good indicator of relative passage altitudes and stratigraphic position. It correlates with the Popcorn Sandstone Bed of the Paoli Limestone in Indiana.

Gothic Avenue Junction

The tour follows the passage known as Broadway in the original upstream direction. Here the sediment has been partly removed through lower-level routes by stream action late in the history of the passage, so the floor descends into the Ste. Genevieve as far down as the Joppa Member, while the ceiling remains at the base of the Beaver Bend Member of the Girkin. Some sediment was also moved around by saltpeter miners early in the 19th century.

Gothic Avenue and Main Cave are each only about half the height of Broadway. Gothic Avenue is located in the Paoli Member. The lower passage, in the upper Ste. Genevieve, is just called Main Cave. When Main Cave formed, it intersected Gothic Avenue in two places: at the "Church" and farther upstream where it cuts across Gothic Avenue (Figure 72), where the ceiling height represents the combined height of the two different cave levels.



Figure 72. Gothic Avenue (Level B1, at ceiling level) enters the Main Cave (Level B2). Gothic is in the Paoli Member (Girkin), and the Levias Member (Ste. Genevieve) lies below. Note the recessed bed at the base of the Paoli. © A. N. PALMER

Note how dry this part of the cave is. This is because it is overlain by the Big Clifty Formation and the entire thickness of the Girkin. Both of them contain thin shale beds that tend to shunt infiltrating water laterally to the edges of the ridge. Crusts of gypsum ($CaSO_4 \cdot 2H_2O$) have formed on some of the walls by evaporation of sulfate-rich water seeping in from the surrounding rock. Most of the sulfate is produced by oxidation of small crystals of pyrite (FeS_2) in the limestone, as confirmed by relatively negative sulfur isotope values in the gypsum. Moister parts of the cave contain no gypsum because the conditions are not evaporative enough, and the sulfates are carried away in solution by seeping water.

Black Snake Avenue

The Historic Tour continues a short distance beyond Gothic Avenue to a large breakdown block ("Giant's Coffin"). Here the tour exits to the right through a narrow canyon that formed when the last remnants of the original cave stream abandoned the Main Cave to form lower levels. The canyon descends through the light-gray Joppa and Karnak Members into the Wooden Bowl Room, which was named for a Native American artifact discovered there. Several passages intersect at this point. The resistant Karnak Member forms the flat ceiling of this wide, low room. The walls are composed of the Spar Mountain Member, which is smooth and dolomitic in its upper bed and dark-gray, sandy, and crumbly below.

A short but steep staircase descends through the upper Fredonia Member to a tubular passage at level C called Black Snake Avenue, so named for its dark walls and wiggly pattern. This passage, and others at this level, were formed about 1.5 million years ago during a long stable period in the continent. This is the most persistent and uniform level in the cave and includes some of the largest passages. Black Snake is one of the smallest, because it had only a small source area for water. It is at the same elevation as Cleaveland Avenue.

Mammoth Dome

Sparks Avenue leads to the impressive Mammoth Dome (Figure 73), one of the tallest vertical shafts in Mammoth Cave, 58.5 m (192 ft) high. It extends from about the Reelsville Member in the Girkin Formation at the top, through the entire Ste. Genevieve Formation, and 9 m (29 ft) into the St. Louis Formation. The top of the St. Louis lies 2 m (7 ft) below the public trail. Note the difference between the gray Ste. Genevieve and the brownish St. Louis. The thick-bedded, coarse-grained, highly fluted bottom bed of the Ste. Genevieve contrasts with the thin, shaly, dolomitic beds of the St. Louis. Incoming water sprays from the top of the shaft and filters out at the bottom through rocks that choke the floor. During wet weather the trickle becomes an impressive waterfall. Its source is apparently a sinkhole at the edge of Mammoth Cave Ridge, not directly above the dome.



Figure 73. Mammoth Dome. The Ste. Genevieve–St. Louis contact is presently considered to be the irregular horizontal notch in the wall several cm (a few inches) below the level of the walkway.
© A. N. PALMER

Mammoth Dome is part of what can be called a shaft complex. Instead of a single pit, several sources of water have formed a maze of interconnecting shafts and canyons. Several canyons open from the walls of the shaft, and, by peering straight up through a haze of descending water drops, we can see a narrow, wiggly canyon at the very top that supplies the water.

Climbing the stairs out of Mammoth Dome brings us to a tall room lined by openings to other shafts and canyons. To the left are the Ruins of Karnak, which consist of massive pillars of the Fredonia Member of the Ste. Genevieve sculpted by descending water (Figure 74). A coral can be found in the wall. At the top of the pillars is 1 m (3 ft) of the dull gray, granular Spar Mountain Member, overlain by a flat ceiling formed by the base of the more resistant Karnak Member.

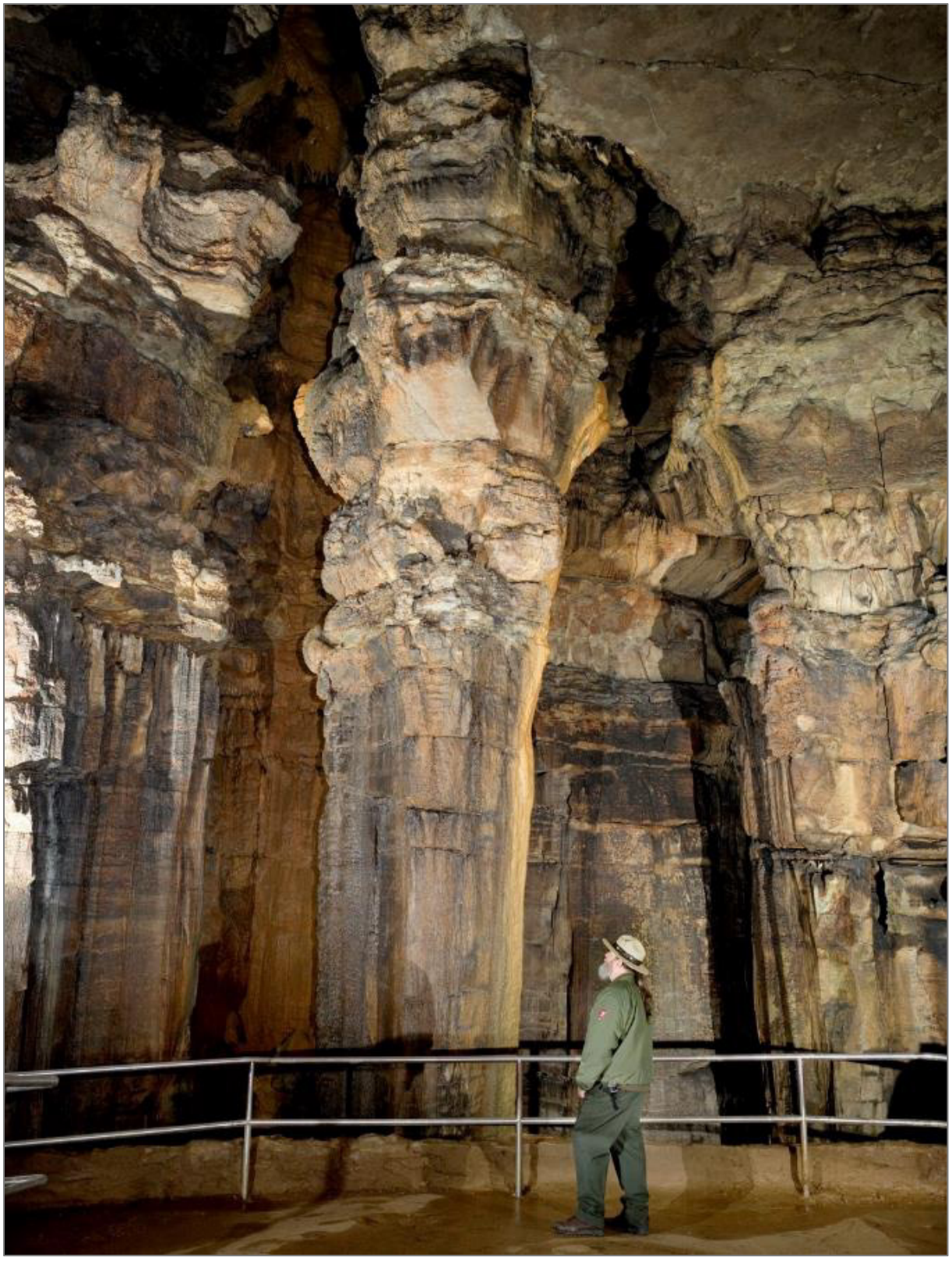


Figure 74. The Ruins of Karnak, in an alcove of Mammoth Dome, consists of solutional pillars of the Fredonia Member (Ste. Genevieve Formation) capped by beds of Spar Mountain and Karnak. See stratigraphic column (Figure 38) for reference. © A. N. PALMER

Return to the Surface

By now we are well aware of the most striking part of the room—a massive metal staircase that leads almost to the top of Mammoth Dome. The view is spectacular, at least as underground views go. The tour leaves the metal staircase at the shaly recessed base of the Joppa unit, but continues its ascent along a straight staircase through the Joppa to a final overlook into Mammoth Dome. The trail doubles back into a dry upper-level passage, Little Bat Avenue. Little Bat Avenue follows the contact between the Aux Vases and Joppa Members of the Ste. Genevieve. The Aux Vases (upper part of the passage) is unusually thin here, consisting of only 0.5 m (1.7 ft) of dark-gray, granular limestone. The underlying J2 unit of the Joppa Member is thick-bedded, fine-grained dolomitic limestone that forms rather smooth walls. We have seen these beds before, in the Main Cave, but not so clearly. The tube suddenly opens into the great void of Audubon Avenue (Figure 75**)**. Audubon Avenue leads directly to the Rotunda, to complete a long and intricate loop through the cave. The tour exits through the Historic Entrance.



Figure 75. Little Bat Avenue leads straight into Audubon Avenue. From here it is a short walk to the cave entrance. © A. N. PALMER

Literature Cited

Palmer, A. N. 1981. A geologic guide to Mammoth Cave National Park. Zephyrus Press, Teaneck, New Jersey.

Chapter 4. Paleozoic Paleobotany of Mammoth Cave National Park

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Abstract

In Mammoth Cave National Park (MACA), Carboniferous sandstones protect the underlying cave's enormous passageways from surface erosion. These resistant caprocks also preserve fossil evidence of Carboniferous plants that grew near fluvial environments when Kentucky was located close to the equator. Paleozoic fossil plants from MACA are documented here for the first time. Fossil plants from the Upper Mississippian Big Clifty Formation include arborescent (tree-like) lycopsid rhizomorphs (rooting structures) and possible cordaitalean woody stems, and historical field notes indicate the presence of fossil lycopsid axes (stems or branches). Similarly, the Lower Pennsylvanian Caseyville Formation preserves axes and rhizomorphs of arborescent lycopsids, calamitalean axes, and possible cordaitalean woody axes. New Caseyville plant-fossil localities have been documented during recent cave surveys, and fossils exposed in the walls of rock shelters and caves that intersect the formation are common. The Hardinsburg Formation may also produce fossil plants based on reports from outside of the park, but no Hardinsburg paleobotanical specimens have been found in situ in MACA. Paleozoic plant fossils from MACA survived fluvial transport before fossilization and are typically preserved as sandstone casts or impressions. Together, the fossil floras of MACA indicate the presence of wetland plant communities in the region during the Late Mississippian and Early Pennsylvanian.

Introduction

Mammoth Cave National Park (MACA) in south-central Kentucky is home to the longest known cave system in the world. The cave intersects three limestone units deposited in a shallow sea during the Mississippian. During the Late Mississippian and Early Pennsylvanian, sediments were deposited in deltaic and fluvial environments, which eventually led to the formation of erosion-resistant sandstone caprocks that now overlie Mammoth Cave. (A geologic time scale is included as an appendix to this inventory, Appendix I.) Since then, the region has been above sea level and exposed to erosional forces (Livesay 1962). Around 10 million years ago, the Mammoth Cave System began to form as groundwater seeped into cracks and dissolved the limestone (Palmer 2016). Mississippian and Pennsylvanian sandstone caprocks, including the Big Clifty and Caseyville formations, protect the soluble limestone of the cave system from erosion by surface streams, allowing some passageways to grow to massive sizes (Thornberry-Ehrlich 2011). The caprocks also preserve fossil evidence of ancient floras that lived in wetland environments during the Mississippian and Pennsylvanian (Figure 76) when Kentucky was close to the equator. Paleozoic fossil plants from

MACA have been collected since the mid-1800s, but no studies have been published on the fossil floras of the park. In this report, I provide an overview of the MACA Paleozoic fossil plant collection, fossil plant localities, and recent discoveries.

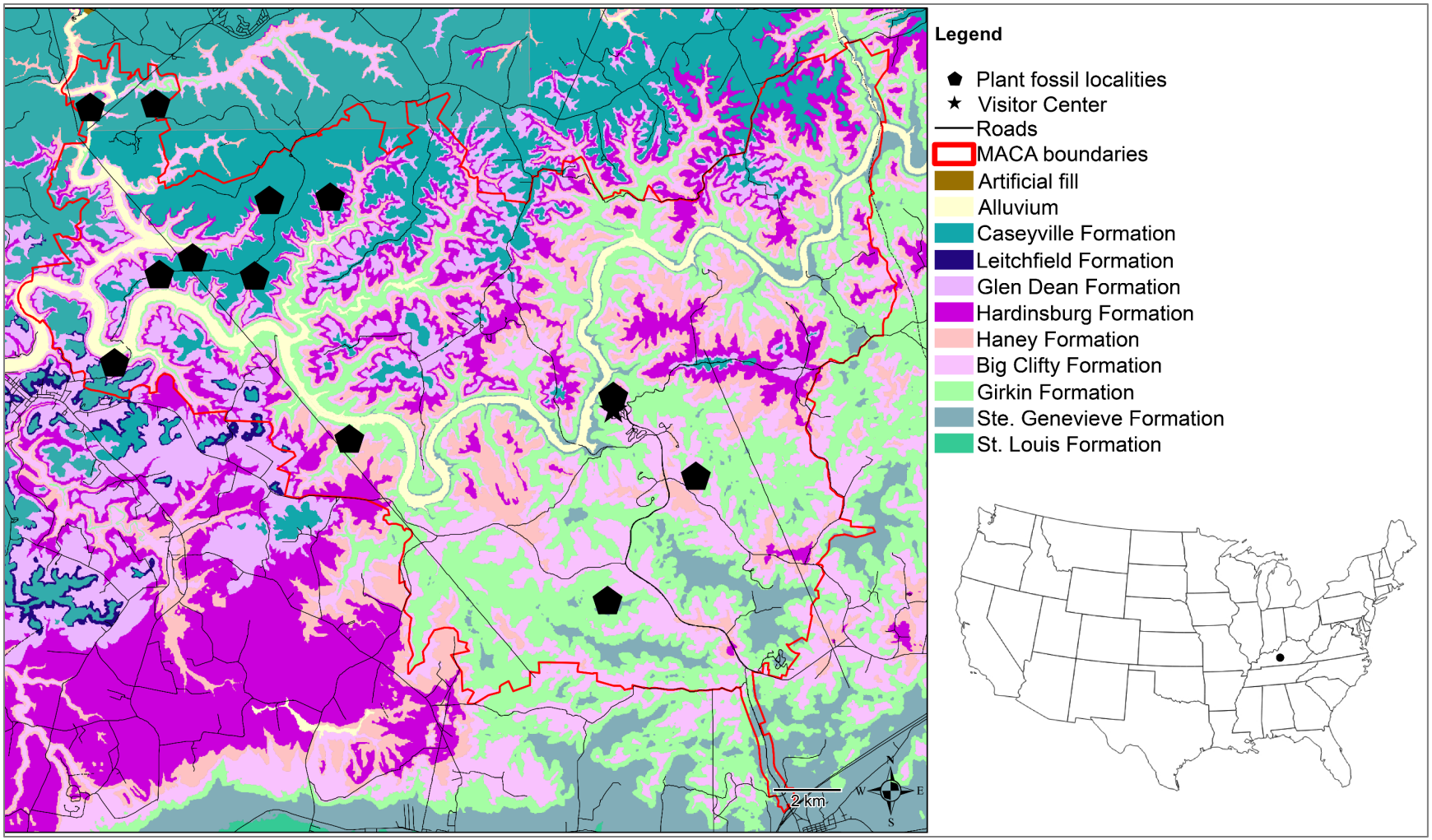


Figure 76. Geologic map of Mammoth Cave National Park with plant fossil localities. Geologic formations in the Legend are ordered stratigraphically (St. Louis Formation–Leitchfield Formation = Middle–Upper Mississippian, Caseyville Formation = Lower Pennsylvanian). The dot on the United States map indicates the location of the park. NPS GEOLOGIC MAP, LOCATIONS AFTER MICHAEL DONOVAN

History of the Paleobotanical Collection at MACA

Mammoth Cave National Park curates a small collection of Paleozoic fossil plant specimens collected as long ago as the mid-1800s (Appendix C). A large *Lepidodendron* impression, the trunk of an arborescent lycopsid, was collected around 1850 and originally displayed on the lawn outside the Mammoth Cave Hotel (Forwood 1870; Warrick 2017). Charles Waldack, a pioneering cave photographer, photographed the fossil in this location in 1866, and the specimen is now displayed in the Mammoth Cave Visitor Center (see Figures 5 and 6 in Chapter 2). In 1935–1936, geologist Erwin R. Pohl collected seven fossil plant specimens from the Upper Mississippian Big Clifty and Lower Pennsylvanian Caseyville formations. These specimens, now curated in the park's collection, include casts and impressions of arborescent lycopsid axes and rhizomorphs (the rooting structures of arborescent lycopsids consist of woody rhizomorphs that fork several times and bear spirally arranged rootlets) and axes of the sphenopsid *Calamites* (a member of the group containing extant horsetails). Pohl noted additional paleobotanical occurrences in his field notes. In his weekly report from September 21, 1935, Pohl found in situ plant fossils in the uppermost part of the Mississippian Big Clifty Formation (then called the Cypress Sandstone) at multiple localities on the south side of the Green River. Pohl noted in situ *Lepidodendron* and *Sigillaria* fossils, which had previously only been found in float. In the same report, he mentioned the discovery of a mix of marine invertebrates and plant fossils in sandstone at the transition between the Cypress Sandstone and Golconda (Haney) Formation. In Pohl's weekly report from September 28, 1935, he noted a *Lepidodendron* axis with leaves extending from the leaf cushions from the Cypress Sandstone (Big Clifty Formation). Occasionally, other Paleozoic plant fossils have been collected from Mississippian (Big Clifty Formation) and Pennsylvanian (Caseyville Formation) rocks during subsequent decades as a result of geologic surveys and chance encounters. Recently, park staff members have increasingly documented plant fossils during surveys of small caves intersecting the Big Clifty and Caseyville formations.

Paleozoic Plant Fossils from MACA

The rocks of MACA formed in both marine and terrestrial environments during the Mississippian and Pennsylvanian subperiods of the Carboniferous. Within the boundaries of MACA, Mississippian and Pennsylvanian plant fossils occur in fluvial rocks overlying the cave, including the Big Clifty Formation, Caseyville Formation, and possibly the Hardinsburg Formation. Below is an overview of the formations in which Paleozoic plant fossils occur, or may occur, in MACA. Locality information is available to qualified researchers upon request.

St. Louis Formation and Other Limestone Formations

The three limestones that form Mammoth Cave from oldest to youngest are the St. Louis Formation, Ste. Genevieve Formation, and Girkin Formation. They were deposited in a warm, shallow sea during the Middle–Late Mississippian. Although no plant fossils are known from these formations in MACA, plant fossils have been recorded from the St. Louis Formation elsewhere. Specimens of the lycopsid *Lepidodendron volkmannianum* Sternberg were recovered from a shale layer in the evaporite zone of the basal St. Louis Formation in Meade County, Kentucky (Browne and Bryant 1970). In west-central Kentucky, plant debris and marine fossils occur in carbonaceous shale in the St. Louis Formation (pers. comm. by R.C. Kepferle and E.G. Sable in Sable and Dever 1990). In

addition, fossil algae have been documented from the St. Louis Formation near St. Louis, Missouri, including *Koninckopora* and *Ortonella* (Myers 1980). *Ortonella* was also found in the St. Louis Formation in Putnam County, Indiana (Bieber 1965).

Big Clifty Formation

The Big Clifty Formation, a sandstone, siltstone, and shale unit overlying the Girkin Formation, was deposited in a river-delta system during the Late Mississippian (Chesterian). Exposures in MACA are 15–30 m (49–98 ft) thick and cap many of the ridges in the park, protecting passages in the Mammoth Cave System below and allowing some to grow to enormous sizes (Chapter 3). Locally outside of the park, coal beds in the Big Clifty Formation have been mined for private use (Thornberry-Ehrlich 2011), indicating that peat swamp forests prospered in the area during the Late Mississippian. Additionally, plant macrofossils from the basal Big Clifty Formation, including stigmarian rooting systems and unidentifiable impressions of axes, support the presence of nearby wetland and riparian ecosystems with arborescent lycopsids during the Late Mississippian.

Big Clifty fossil plants have typically been found as float; however, Edwin R. Pohl mentioned in situ *Lepidodendron* and *Sigillaria* fossils in his notes in 1935, and woody plant axes were recently discovered in Cave #267. Specimens from five localities are curated in the MACA collection, including rhizomorphs of *Stigmaria ficoides* (Sternberg) Brongniart (Figures 77A to 77G; specimens in Figure 77E and 77F possibly from the Hardinsburg Formation), and impressions of indeterminate plant axes from the Double Sinks area. Plant axes from Cave #267 occur in float on the cave floor and in situ in the cave wall but were not collected (Figures 77H and 77I). Most of the plant axes in Cave #267 appear woody, suggesting a possible cordaitalean affinity. Specimens exhibiting vertical ribs may be decorticated (outer covering removed) lycopsid axes (arrow in Figure 77I).

The Big Clifty flora of MACA is poorly preserved and low diversity, although the sample size is small (six curated specimens). *Stigmaria*, a form genus representing the rhizomorphs of arborescent lycopsids, is the most common fossil in the collection. Specimens are assigned to *Stigmaria ficoides* based on the spirally arranged rootlet scars, which are typically circular, raised above the rest of the rhizomorph surface, and marked with a central depression (Figures 77A to 77G). Only *Stigmaria* rhizomorphs and indeterminate plant axes, possibly cordaitalean and lycopsid, were available for study. However, Pohl noted arborescent lycopsid axes preserved in the Big Clifty Formation, including a *Lepidodendron* specimen with intact leaves. *Lepidodendron* axes with attached leaves are rarely encountered (e.g., Kosanke 1979; Leary and Thomas 1989; Opluštil 2010), suggesting the potential for future discoveries of more delicate plant organs. Together, the existence of arborescent lycopsid axes and rooting systems, possible cordaitalean axes, and local coal beds in the Big Clifty Formation indicate the presence of wetland plant communities growing in the ancient river delta. Mississippian floras are relatively rare in North America, so future prospecting for well-preserved fossil plants in the Big Clifty Formation is worthwhile.

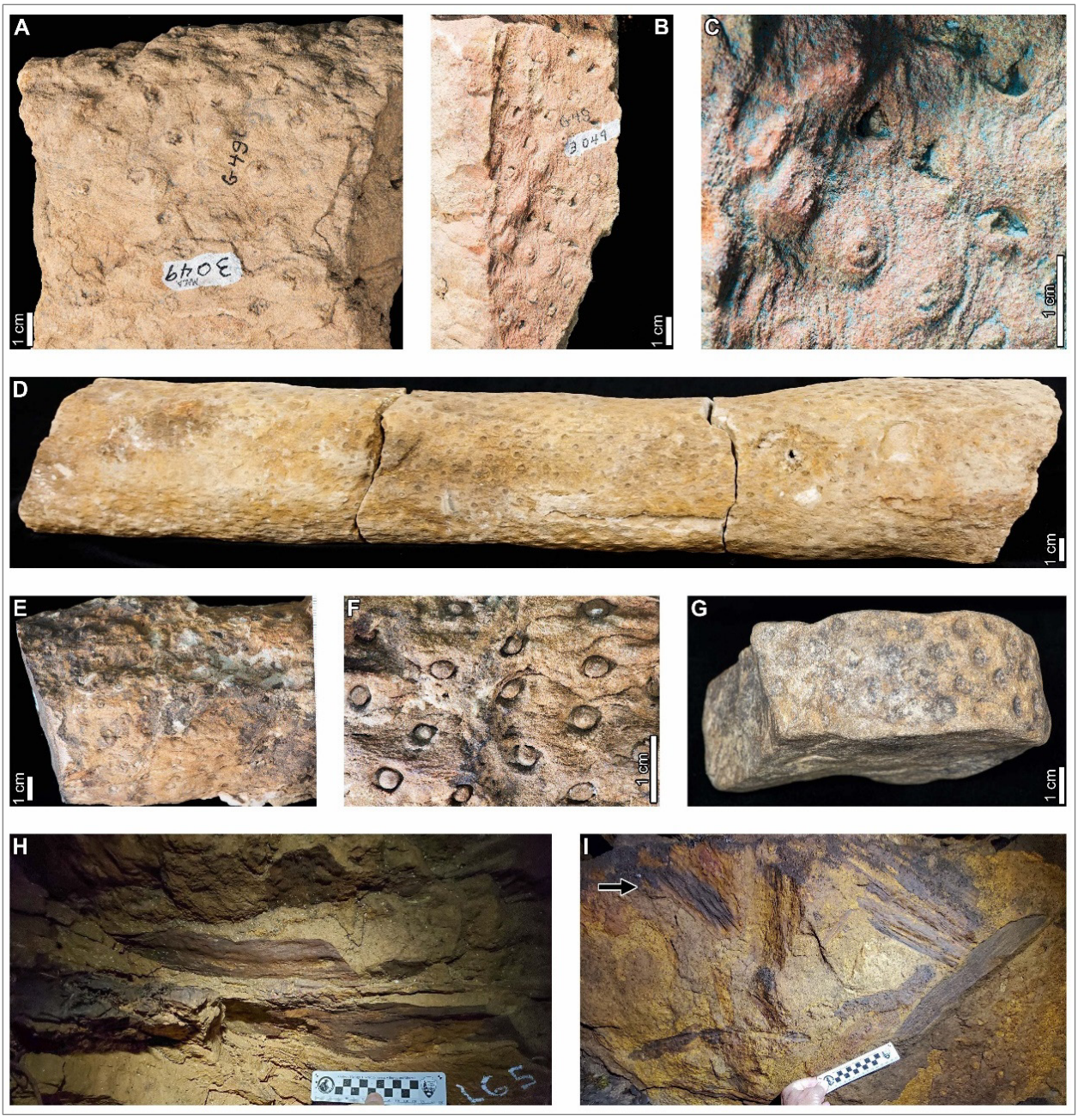


Figure 77. Plant fossils from the Big Clifty Formation (Upper Mississippian) in Mammoth Cave National Park. **A.** *Stigmaria ficoides* rhizomorph (MACA 3049). **B.** *Stigmaria ficoides* (same locality as **A**; MACA 3049) **C.** Close-up of rootlet "scars" in **B**. **D.** *Stigmaria ficoides* (Big Clifty Formation (?); MACA 1776). **E.** *Stigmaria ficoides* (Big Clifty or Hardinsburg Formations; MACA 2015). **F.** Close-up of rootlet "scars" in **E**. **G.** *Stigmaria ficoides* (float in stream; MACA 63197). **H.** In situ stem fragments, possibly cordaitalean, in Cave #267. **I.** Axis fragments in Cave #267, arrow points to possible decorticated lycopsid. **A–G:** © MICHAEL DONOVAN; **H, I:** NPS / RICK OLSON

Hardinsburg Formation

The Upper Mississippian Hardinsburg Formation is a resistant sandstone caprock overlying the Haney Formation and Big Clifty Formation. The Hardinsburg Formation may preserve fossil plants

within MACA, but currently there is no unequivocal evidence. A *Stigmaria* rhizomorph found as float may have originated from either the Big Clifty Formation or Hardinsburg Formation (Figures 77E and 77F), based on the presence of both units up-section near the locality. A second *Stigmaria* specimen, either from the Hardinsburg Formation or Caseyville Formation, was found as float at another site (Figure 78H). Plant fossils in shales associated with coal beds have been recognized in the Hardinsburg Formation in Illinois and western Kentucky (Sutton and Oesterling 1952; Swann 1963; Smith and Read 2001), including *Lepidodendron*, *Stigmaria*, and *Lepidophylloides* (Rogers and Trace 1976), and further prospecting in MACA may reveal in situ fossil plants.



Figure 78. Plant fossils from the Caseyville Formation (Lower Pennsylvanian) in Mammoth Cave National Park. **A.** Arborescent lycopsid axis with leaf cushions similar to "*Lepidodendron*" *worthenii* (MACA 3135). **B.** Close-up of leaf cushions in **A**. **C.** Lycopsid axis, possibly *Synchysidendron* or *Lepidodendron mannebachense* (MACA 3130). **D.** Decorticated lycopsid axis (MACA 3130). **E.** *Calamites* axis (MACA 36378). **F.** *Calamites* axis (MACA 3162). **G.** Arborescent lycopsid axis on cave wall in Cave #142. **H.** *Stigmaria ficoides* rhizomorph (float; Hardinsburg Formation or Caseyville Formation). **I.** Striated plant axis, possibly cordaitalean, on cliff face. **J.** Plant axis, possibly cordaitalean. **K.** Impression of crown branch of arborescent lycopsid on rock slab on floor of rock shelter. **A–F, I–K:**
© MICHAEL DONOVAN; **G, H:** NPS / KELLI TOLLESON

Caseyville Formation

The Lower Pennsylvanian Caseyville Formation consists of conglomerates, sandstones, siltstones, shales, and coals that cap the tallest hills in MACA (Sable and Dever 1990; Eble et al. 2001; Thornberry-Ehrlich 2011). Deposition of the Caseyville Formation began after an ancient river system cut through Upper Mississippian rocks creating paleovalleys (Pryor and Potter 1979). During the Early Pennsylvanian (Morrowan), clastic sediments from sources now located to the east filled the paleovalleys, transported by anastomosing and braided rivers followed by a meandering fluvial system (Pryor and Potter 1979; Greb et al. 1992; Eble et al. 2001). Quartz pebbles in the conglomeratic channel fills at the base of the Caseyville Formation may originate from schists in Virginia (Wanless 1975; Johnson and Schwalb 2010).

The Caseyville Formation in MACA preserves common Early Pennsylvanian wetland plant fossils, including arborescent lycopsid axes and rhizomorphs, calamitalean axes, and unidentifiable plant axes and fragments. Fossil plants in the Caseyville often occur along bedding planes, sometimes concentrated along scour surfaces (Pryor and Potter 1979), suggesting local subaerial exposure during the period of deposition (Williams et al. 2005). The fossil plants are typical of habitats with water-logged soils and were transported before fossilization, sometimes along with pebble-sized clasts. Therefore, the fossils are mostly poorly preserved stem casts and impressions (Haynes 1964). Delicate tissues, such as foliage and reproductive organs, were less likely to be preserved under these conditions and are currently unknown from Caseyville rocks in MACA.

During 1935–1936, Edwin R. Pohl collected paleobotanical specimens from the Caseyville Formation while conducting geologic surveys of MACA. Four specimens collected near the town of Cub Run, just north of the park in Hart County are now curated in the MACA collection, including a lycopsid impression characterized by wrinkled leaf cushions similar to those of "*Lepidodendron*" *worthenii* (Figures 78A and 78B). "*Lepidodendron" worthenii* may be related to *Paralycopodites* and its possible compression equivalent *Bergeria* (Álvarez-Vázquez et al. 2018; DiMichele and Bateman 2020), and the species was moved to *Bergeria worthenii* by Álvarez-Vázquez and Wagner (2014). However, the MACA specimen lacks fine leaf cushion features necessary for a definitive taxonomic assignment. The shape of the leaf cushions of a second lycopsid axis (Figure 78C) is similar to *Synchysidendron* (DiMichele and Bateman 1992) or *Lepidodendron mannebachense* (Opluštil 2010). *Lepidodendron mannebachense*, along with all *Lepidodendron* species, possesses infrafoliar parichnos (Bateman and DiMichele 2021). This feature is not visible on the MACA specimen, although the preservation is poor. Pohl also collected a decorticated lycopsid axis (Figure 78D) and a *Calamites* cast (Figure 78E) from the same area just west of Cub Run. In addition, Pohl found a *Calamites* cast (Figure 78F) along the west side of the Nolin River across from Cubby Cove.

More recent exploration by MACA staff has increased the number of Caseyville fossil plant localities (Appendix C). A piece of *Stigmaria* from the Hardinsburg or Caseyville was found as float (Figure 78H). A plant axis with striations, possibly a cordaitalean, occurs on a cliff face (Figure 78I). On the floor of a rock shelter, another possible cordaitalean woody axis (Figure 78J) is preserved next to an impression of the crown branch of an arborescent lycopsid (Figure 78K). The fossil lycopsid branch is weathered so confident taxonomic identification is not possible. One possibility is

Diaphorodendron based on the size, elongate shape, and tightness of packing of the leaf cushions, but other genera, including *Bergeria* and *Lepidodendron*, cannot be ruled out. At one locality, fossil plants are preserved both as float and in situ in fluvial beds on the cliff face and below rock shelters. Several unidentifiable plant axes, possibly decorticated lycopsid or woody axes (some striated) protrude from the cliff face (Figure 79A) or as float (Figure 79C). An arborescent lycopsid impression occurs in a conglomerate layer. The specimen cannot be assigned to a genus because of the poor preservation of the leaf cushions (Figure 79B). Possible log-jam deposits (Gastaldo and Degges 2007; Gibling et al. 2010) are characterized by multiple plant axes in different orientations stacked in overlying layers (Figure 79D). An indeterminate axis may be *Sigillaria* based on the parallel ribs; however, it is lacking leaf traces and parichnos scars (Figure 79E). Two arborescent lycopsid axes occurred in float below the rock shelter, including a *Lepidodendron* axis, possibly pertaining to *L. aculeatum* (Figures 79F and 79G). The shapes of the leaf cushions of the second arborescent lycopsid specimen (Figure 79H) are comparable to *Synchysidendron* and *Lepidodendron*, although poor preservation of leaf cushion features precludes assignment to a genus. At another locality, a three-dimensional cast of a lycopsid trunk protrudes from the cliff face and an impression of a 4.2-m (14-ft)-long unidentifiable trunk segment occurs in an overhang.

Recent surveys of small caves intersecting the Caseyville Formation have revealed new plant fossils exposed on cave walls, ceilings, and/or in float on the cave floor. Fossil plants are located by scanning the cave interior with headlamps. Cave #172 features a number of decorticated arborescent lycopsid axes, either parts of trunks or crown branches (Figure 79I). In Cave #057, woody debris occurs in a channel lag deposit on the ceiling and walls of the cave. A large tree trunk (28 cm [11 in] wide) with a striated texture extends from the wall across the ceiling (Figures 80A and 80B). On the cave wall, an arborescent lycopsid impression exhibits plump, nearly circular leaf cushions with large leaf scars (Figure 80C; photo is oriented to show the position of the fossil in the field), comparable to *Bergeria* and *Synchysidendron*. Plant debris is preserved on rocks in Cave #011 (Figure 80D). In addition, a large rock in the upper level of Cave #011 features a forked crown branch of an arborescent lycopsid with poorly preserved leaf scars (Figures 80E to 80G). The branch lacks lateral branch scars, typical of the Ulodendraceae, Diaphorodendraceae, and *Lepidophloios* (Lepidodendraceae), so it is unlikely that the specimen represents any of these groups. The leaf cushions are almost square instead of elongate, so *Lepidodendron* of the *L. mannebachense* type is a possible identification (Opluštil 2010). Nearby, a mold containing a partial cast of an arborescent lycopsid axis occurs in the wall (Figure 80H), but whether these two specimens came from the same tree is unclear. Unidentifiable wood axes and an eroded impression of an arborescent lycopsid axis occur on walls inside Cave #142 (Figure 78G) and Cave #250, respectively. A rock shelter locality preserves another log-jam type deposit, where several impressions of unidentifiable plant axes are visible in the ceiling.



Figure 79. Plant fossils from the Caseyville Formation (Lower Pennsylvanian) in Mammoth Cave National Park. Examples photographed in a rock shelter (**A–H**) and Cave #172 (**I**). **A.** Woody plant axis on cliff face. **B.** Arborescent lycopsid impression in conglomerate. **C.** Striated plant axes on float in rock shelter, possibly decorticated lycopsid. **D.** Layers of plant axes along bedding planes, similar to a log-jam deposit. **E.** Indeterminate axis impression, possibly *Sigillaria* sp. **F.** *Lepidodendron* sp., possibly *L. aculeatum*, float below rock shelter (photo oriented in field position, arrow indicates vertical direction of plant during life). **G.** Close-up of leaf cushions in **F** (photo oriented in field position, arrow indicates vertical direction of plant during life). **H.** Arborescent lycopsid, float below rock shelter near **F** (MACA 63198; photographed in laboratory). **I.** Decorticated lycopsid axis (MACA 63439). © MICHAEL DONOVAN



Figure 80. Plant fossils from the Caseyville Formation (Lower Pennsylvanian) in Mammoth Cave National Park. Examples photographed in Cave #057 (**A–C**) and Cave #011 (**D–H**). **A.** Woody debris on the roof of the cave. Fossil tree trunk extends into the cave wall. **B.** Detail of trunk in **A** showing striated texture. **C.** Arborescent lycopsid fossil on cave wall (photo oriented in field position, arrow indicates vertical direction of plant during life). **D.** Fossil plant debris. **E.** Forked crown branch of arborescent lycopsid, possibly *Lepidodendron*, on fallen rock in cave (photo oriented in field position, arrow indicates vertical direction of plant during life). **F.** Detail of left branch of possible *Lepidodendron* in **E**. **G.** Detail of right branch of possible *Lepidodendron* in **E**. **H.** Arborescent lycopsid trunk mold in cave wall. © MICHAEL DONOVAN

The MACA Caseyville flora is low diversity, composed of arborescent lycopsid axes *Stigmaria*, *Calamites*, and unidentifiable plant axes and organic hash. Most specimens are poorly preserved and are not identifiable to the species level. However, the genera present give clues about the local habitat, indicating the presence of wetland floras around the depositional environment. Arborescent lycopsids were dominant plants in equatorial wetland environments during the Pennsylvanian, growing in water-logged soils (DiMichele and Phillips 1985; Phillips and DiMichele 1992). Adaptations for living in wet conditions include their broad but typically shallow rooting systems, possible water-dispersed megasporangiate reproductive units, and a heterosporous life cycle (Phillips 1979; DiMichele and Phillips 1985; Phillips and DiMichele 1992; Bateman and DiMichele 1994). In addition to wetland environments, some *Sigillaria* species were capable of living in seasonally dry conditions, and parts of the root systems may have been able to access deeper water (Pfefferkorn and Wang 2009; Chen et al. 2022). Sigillarians were common components of plant communities in wetland margins and along streams and levees (Gastaldo 1987; Phillips and DiMichele 1992). The sphenopsid *Calamites* is a form genus representing axes of arborescent horsetails, relatives of the sole living horsetail genus, *Equisetum*. *Calamites* species lived in a variety of wet habitats, including peat swamps, clastic wetlands, and along river and lake margins (Reed 1926; Scott 1979; Gastaldo 1992; DiMichele et al. 2009; Tosal et al. 2022), and were able to survive in disturbed areas where they could be repeatedly buried by sediment (Gastaldo 1992; DiMichele et al. 2009). Many of the woody plant axes may be fragments of cordaitalean trunks and branches. Cordaitaleans, relatives of conifers, lived in wetland and seasonally dry habitats (Phillips et al. 1985; Falcon-Lang and Scott 2000; Raymond et al. 2010; Bashforth et al. 2014).

Although plant macrofossils from the Caseyville Formation in MACA have not previously been documented in detail prior to this report, a fossil flora from the Pounds Sandstone Member (the uppermost part of the Caseyville) in Illinois was described by Jennings (1974). The flora is composed of arborescent lycopsid axes (*Lepidodendron aculeatum*, *Lepidodendron rhodeanum*, *Lepidodendron* sp., *Lepidophloios* cf. *L. laricinus*, *Sigillaria tesselata*, *Sigillaria rugosa*, *Sigillaria brardii*, and *Syringodendron* sp.) and strobili (cones) (*Lepidostrobus* sp.); calamitalean axes (*Calamites cruciatus*, *C. cistii*, and *C. suckowii*); medullosan foliage (*Neuropteris* cf. *N. heterophylla*) and seeds (*Trigonocarpus parkinsonii*, *Hexagonocarpus crassus*, and *Holcospermum* sp.); and cordaitalean axes (*Cordaicladus* cf. *C. principalis*, *Artisia transversa*) and seeds (*Cordaicarpon major*). Cordaitalean fossils are the most abundant components of the flora. Like the Early Pennsylvanian plants collected in MACA, the Pounds Sandstone flora was transported before deposition and preserved in a medium to fine grained sandstone. Therefore, the Pounds Sandstone flora mostly consists of stem casts and impressions and seed casts and molds, and delicate foliage is rare. The MACA Caseyville fossils occur as float or exposed on rock surfaces, and weathering and coarse grain sizes limits the taxonomic resolution of the fossils. However, further exploration of the Caseyville Formation in MACA may reveal better-preserved plant fossils, enabling comparison with the Pounds Sandstone flora.

Coal beds in the Caseyville Formation are rare (Greb et al. 1992; Eble et al. 2001), and none are known within the boundaries of MACA. Outside the park, palynofloras from Caseyville coals in Illinois and Kentucky exhibit variable compositions (Willman et al. 1975; Eble et al. 2001). In

Kentucky, some coals are dominated by arborescent lycopsid spores (*Lycospora*), but others have higher proportions of small lycopsid, fern, and calamites spores and seed fern pollen mixed with *Lycospora* spores (Eble et al. 2001).

The Caseyville Formation was deposited during what was, arguably (see Cecil 1990), the wettest part of the Pennsylvanian across the Pangean tropics. Thus, conditions for peat formation should have been ideal, and were in certain areas, such as the Appalachian Basin. However, coal beds in the Caseyville Formation are thin, discontinuous, and rare. This rarity suggests that it was peat-bed preservation that was the limiting factor, not peat-bed formation. Subsidence in the Illinois Basin likely did not create enough accommodation space for peat accumulations to be buried prior to their destruction by microorganisms and erosion. In addition, the irregularity of the landscape in the basin, a consequence of the Mississippian–Pennsylvanian unconformity surface throughout the region (e.g., Siever 1951; Bristol and Howard 1971; Droste and Keller 1989), may have limited the physical area over which peat beds might have developed, resulting in discontinuity of the accumulations. Consequently, variation in palynofloral composition may be related to local environmental conditions and differences among plant communities in small, discontinuous swamps (Eble et al. 2001). The palynoflora of some Caseyville coals and the macroflora of the Caseyville in MACA are both dominated by arborescent lycopsids, although they did not live in the same environments (peat swamp vs. non-peat producing wetlands). However, the Caseyville macroflora in MACA is biased toward the preservation of plants with durable tissues that could survive transport, so the abundance of arborescent lycopsid axes is unsurprising.

One of the more unusual aspects of the MACA flora is the relatively abundant occurrence of the arborescent lycopsid rooting axis *Stigmaria*. Rhizomorphs are not a common component of most compression-impression assemblages, and the stigmarian axes found in the MACA sandstones have been stripped of their appendages, which were specialized organs, generally referred to as “rootlets”. Where these main root-system axes are found in place, such as in fossil soils beneath coal beds (underclays or seat-earths), or in coal balls (concretions that preserve the original fabric of the peat), the rootlets are almost always found attached (see examples in DiMichele et al. 2022), although *Stigmaria* casts do not typically preserve attached rootlets. The MACA stigmarian occurrences, in combination with the many large logs of lycopsids of various kinds, indicate growth of the plants in proximity to river systems. The travel distance of such large debris is limited by stream and river size (e.g., Braudrick and Grant 2001). Although stigmarian rhizomorphs may have grown subaerially away the trunk and underground distally (D’Antonio et al. 2023), the incorporation of large rhizomorphs in MACA deposits indicates some soil erosion. Given the dynamism of rivers, and the frequent accumulation of tree trunks within river channels (creating anabranching architectures—Nanson and Knighton 1996; Davies and Gibling 2013; Gibling et al. 2014—and log jams, as noted above), it is most likely that the large plant remains entered the channel bedload via growth of the plants on intrachannel bars within and/or bank collapse along the sides of the large rivers and streams in which the Mississippian and Pennsylvanian sandstones were deposited. Bank collapse and erosion of bars along and within active rivers, and the streams that feed them, is a common phenomenon (e.g., Langendoen and Simon 2008), and may explain both the unusual occurrence of large lycopsid

rhizomorphs, the absence of appendages on those axes, and their association with large logs of both lycopsids and woody plants, likely cordaitaleans.

Conclusions

The sandstone caprocks overlying Mammoth Cave preserve evidence of typical Late Mississippian and Early Pennsylvanian wetland plants that grew near ancient fluvial environments. Given the overall rarity of Mississippian floras, future prospecting in the Big Clifty Formation should focus on discovering in situ fossil plants. Edwin R. Pohl's notes on a *Lepidodendron* axis with attached leaves suggests that more delicate plant structures may be preserved in the Big Clifty Formation. The Hardinsburg Formation is another important target for future work, because although it may preserve fossil plants within the bounds of MACA, no in situ fossils have yet been found. Finally, preservation quality of Caseyville Formation fossil plants varies, so continued prospecting may eventually reveal better preserved fossils with higher potential for identification.

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Appendix C: Mississippian and Pennsylvanian Plant Fossils from MACA

Table 3 shows the Mississippian and Pennsylvanian plant fossils from MACA. Locality information is available to qualified researchers upon request.

Table 3. Mississippian and Pennsylvanian plant fossils from Mammoth Cave National Park. Fields with dashes indicate unknown data.

Catalog #	Identification	Geological Unit	Collection Date	Collector
MACA 1776	*Stigmaria ficoides*	Big Clifty(?)	10/20/60	Edmond J. Clancy
MACA 1795	*Stigmaria ficoides*	Big Clifty(?)	–	Edmond J. Clancy
MACA 2015	*Stigmaria ficoides*	Big Clifty or Hardinsburg(?)	6/1/57	Doc Ritter
MACA 2040	*Lepidodendron*	–	–	–
MACA 3049	*Stigmaria ficoides*	Big Clifty	9/19/35	Edwin R. Pohl
MACA 3130	Lycopsid axis, possibly *Synchysidendron* or *Lepidodendron mannebachense*; decorticated lycopsid	Caseyville	10/17/35	Edwin R. Pohl
MACA 3135	Lycopsid axis, similar to "*Lepidodendron*" *worthenii*	Caseyville	10/17/35	Edwin R. Pohl
MACA 3162	*Calamites*	Caseyville	10/30/36	Edwin R. Pohl
MACA 3216	*Mariopteris*	–	4/11/60	–
MACA 36103	*Stigmaria ficoides*	–	–	–
MACA 36361	*Lepidodendron*	–	–	–
MACA 36374	Plant fragments	–	–	–
MACA 36378	*Calamites*	Caseyville	10/17/35	Edwin R. Pohl
MACA 36379	*Stigmaria ficoides*	Caseyville	10/17/35	Edwin R. Pohl
MACA 63197	*Stigmaria ficoides*	Big Clifty	11/1/20	Maaz Fareedi
MACA 63198	Arborescent lycopsid	Caseyville	3/23/21	Rick Toomey and Larry Johnson
MACA 63438	*Stigmaria ficoides*	Caseyville	8/31/22	Rich Boldon, Michael Donovan, Rick Toomey, Larry Johnson, and Rheanna Kautzman
MACA 63439	Decorticated lycopsid axis	Caseyville	9/1/22	Michael Donovan, Rick Toomey, Kelli Tolleson, and Becca Dorsett

Table 3 (continued). Mississippian and Pennsylvanian plant fossils from Mammoth Cave National Park. Fields with dashes indicate unknown data.

Catalog #	Identification	Geological Unit	Collection Date	Collector
Field	Woody axes, arborescent lycopsid axes	Caseyville	not collected	Rich Boldon, Michael Donovan, Rick Toomey, Larry Johnson, and Rheanna Kautzman
Field	Woody axes, arborescent lycopsid axis	Caseyville	not collected	Photos by Rick Toomey and others
Field	Arborescent lycopsid axis	Caseyville	not collected	Photos by Kelli Tolleson
Field	Unidentifiable woody axes	Caseyville	not collected	Photos by Kristen Bobo
Field	Arborescent lycopsid crown branch impression, woody axes	Caseyville	not collected	Photos by Chelsea Ballard
Field	Forked crown branch of arborescent lycopsid, *Lepidodendron*; unidentifiable plant fragments	Caseyville	not collected	Photos by Amber Flowers
Field	Unidentifiable plant axes	Caseyville	not collected	Rick Olson and Kelli Tolleson
Field	Lycopsid trunk cast, unidentifiable trunk	Caseyville	not collected	Kelli Tolleson, Barbara Gawin, and Larry Johnson
Field	*Stigmaria*	Hardinsburg or Caseyville	not collected	Photos by Kelli Tolleson
Field	Unidentifiable plant axis	Big Clifty	not collected	Photos by Brice Leach
Field	Plant axes, possibly cordaitalean axes and a decorticated lycopsid axis	Big Clifty	not collected	Rick Olson, Garrett Pike

Chapter 5. Paleozoic Invertebrate Fossils (Exclusive of Echinodermata) and Ichnofossils of Mammoth Cave National Park

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Introduction

Paleozoic invertebrate fossils and ichnofossils are quite literally part of the fabric of the Mammoth Cave system (Figure 81) but a full documentation of these resources has never been made. Instead, they have generally been reported in passing, informally (e.g., abstracts or internal park reports), or both. A survey of the literature combined with detailed lithological studies (described in Chapter 3) and observations made during the Mammoth Cave National Park (MACA) paleontological inventory shows that five of the nine Paleozoic formations visible in the park preserve invertebrate fossils. These include numerous species of corals, bryozoans, brachiopods, mollusks, arthropods, and echinoderms. The echinoderms proved to be significant enough to warrant their own chapter in this volume (Chapter 6). In addition to macroscopic invertebrate body fossils, various trace fossils (including unusually large burrows) and microfossils traditionally classified with invertebrates are present and are documented here. These fossils are important for understanding the bedrock of the park and help to put the park in its proper geological, paleontological, and paleoecological context.

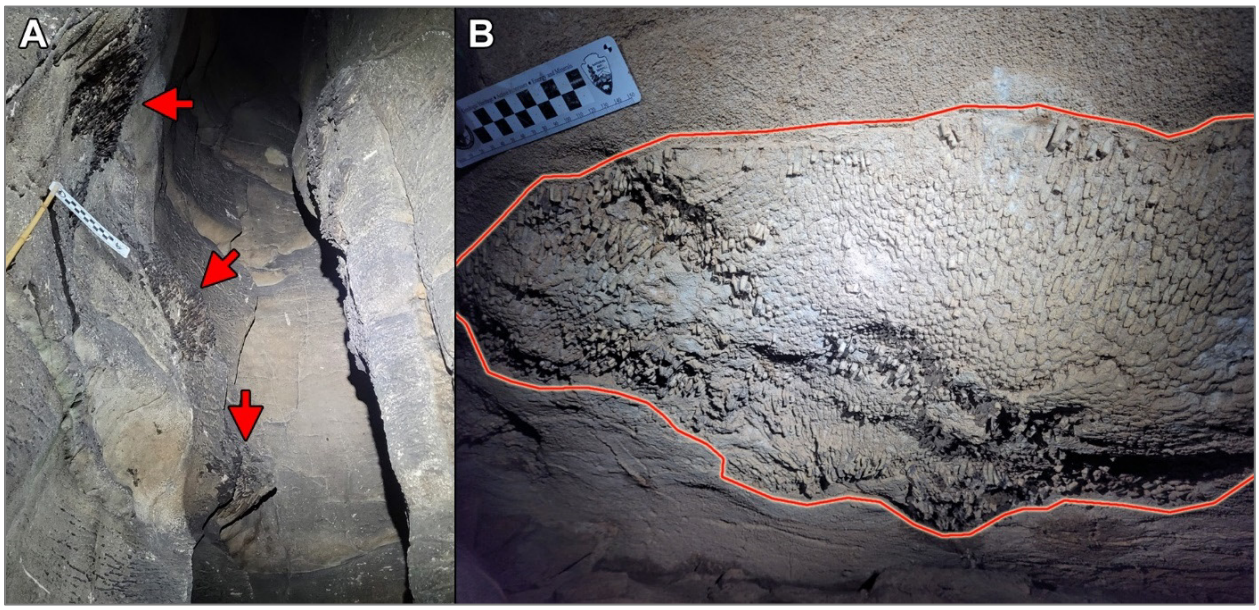


Figure 81. Fossils such as these colonial corals visible at the Ruins of Karnak (**A**; probably Fredonia Member, Ste. Genevieve Formation) and Cave #063 (**B**; possibly Levias Member, Ste. Genevieve Formation) are integral parts of the physical structure of the Mammoth Cave System. For this and other figures, the scale bar includes millimeter tick marks (poorly visible at this range) and 1 cm (0.4 in) black and white squares. NPS

General Descriptions of Groups

Most Paleozoic coral fossils belong to one of two extinct orders, both of which are represented at MACA: tabulate corals (Tabulata) and rugose corals (Rugosa). Tabulates and some rugose corals are colonial, but can usually be distinguished by the sizes of the living chambers of the colonies, also known as corallites (less than a few millimeters in diameter in tabulates [less than a tenth of an inch], substantially larger in rugose corals), and the structures in the chambers (simple or no vertical internal structures in tabulates, generally more complex in rugose corals). Rugose corals also include solitary forms known informally as horn corals, because these pointed conical fossils resemble animal horns.

Bryozoans are microscopic animals that build larger, macroscopic colonies and have a substantial fossil record. Individual animals are typically on the order of 0.5 mm (0.02 in) long and feed with a filter-feeding apparatus called a lophophore. Their colonies are sometimes mistaken for coral colonies, but the living chambers of bryozoans are much smaller than those of corals (sub-millimeter scale versus millimeter to centimeter scale). Bryozoan colonies may have a variety of shapes, such as stem- or branch-like (which can be mistaken for bones or plant fossils), domes, net-like, or irregular.

Brachiopods are shelled, sessile, filter-feeding marine invertebrates that resemble bivalve mollusks, but have very different soft anatomies and valve articulations. Like bryozoans, brachiopods feed using a tentacle-bearing organ called a lophophore, supported by a mineralized brachidium that is occasionally preserved in fossils. Brachiopods are often informally separated into articulate and inarticulate forms based on shell composition and how the shells are hinged; articulate brachiopod shells are usually made of calcium carbonate, whereas inarticulate brachiopod shells are usually phosphatic. The reported brachiopods of MACA all appear to be articulate forms. Articulate brachiopod shells can generally be distinguished from bivalve mollusks by symmetry. A single brachiopod shell (valve) usually has a line of symmetry showing the left and right sides as mirror images, but the two valves are usually different shapes and sizes and thus are not symmetric to each other. A single bivalve valve is usually clearly asymmetric (less obvious for some groups such as scallops), but the two valves are usually mirror images. Brachiopods also mineralize their shells using calcite, which has a higher preservation potential than the aragonitic shells of bivalves, so brachiopod fossils are often better preserved than bivalve fossils. During the Paleozoic, brachiopods were more abundant and diverse than bivalves, but now are much more restricted.

Mollusk groups represented by fossils at MACA include bivalves, cephalopods, and gastropods (snails and slugs). Bivalves are familiar aquatic invertebrates today, including clams, oysters, scallops, and others, but were much less abundant and diverse during the Paleozoic. As noted above, most bivalves can be distinguished from brachiopods by their symmetry (asymmetric single valves, valves symmetric to each other), although there are exceptions. Pectinids (scallops), for example, are visually more like brachiopods by having nearly symmetric single valves.

There are several subclasses of cephalopods, but only the Nautiloidea can be definitely reported from MACA, based on the presence of distinctive orthoconic (straight-shelled) forms. Orthoconic nautiloids, now extinct, grew elongate straight or gently curved conical shells, divided into numerous

internal chambers by walls called septa. Coiled cephalopod shells are also present at MACA, but to date have not been confidently classified. Both nautiloid cephalopods and their famous fossil cousins the ammonoids include coiled forms and may be represented at MACA. Coiled ammonoid shells generally have more complex septa compared to coiled nautiloids. Nautiloid septa also tend to be concave with respect to the opening of the shell, and the internal siphuncle may be centered in the whorl rather than near the outer curve as in ammonoids.

Arthropods (animals with jointed bodies and exoskeletons) are represented by fossils of two groups at MACA, trilobites and ostracods. Trilobites are one of the most familiar types of Paleozoic invertebrates. Because trilobites shed their exoskeletons to grow, most trilobite fossils are partial pieces of these shed exoskeletons, particularly the tail region (pygidium) and parts of the head region (the entire head shield is the cephalon; usually parts of the cheeks are missing, leaving what is called a cranidium). The central segments of the trilobite are rarely found intact, and the antennae and limbs are very rarely found at all. Fragments of trilobites may be biological "trash" in Paleozoic rocks, not identifiable except when observed microscopically. Ostracods, also known as "seed shrimp", are bivalved crustaceans, generally microscopic. Unlike trilobites, they continue to flourish today.

Echinoderms include living groups such as asteroids (sea stars), echinoids (sea urchins), and crinoids (sea lilies), and are noted for their radial five-fold symmetry, water vascular system, and exoskeleton of small mineralized ossicles. Upon death, an echinoderm's body usually disintegrates into its component ossicles, so complete specimens are rare but fragments are abundant. Crinoids, echinoids, and the extinct blastoids (sea buds, from the globular or nut-like body structure on a stalk) are the fossil echinoderm groups known from MACA; see Chapter 6 for more information.

Ichnofossils, also known as trace fossils, are fossilized evidence of the behavior or activity of living organisms, such as root traces, footprints, burrows, and coprolites (fossil feces). Stromatolites, finely laminated microbial mounds, are generally classified as trace fossils, but also overlap aspects of body fossils (because microscopic microbial body fossils may be present), sedimentary structures, and microbially induced sedimentary structures. MACA has large stromatolite-like fossils; because it is not clear if they are wholly microbial in origin, they are referred to in this chapter as stromatiforms and included under "Other Fossils" (see below).

Microfossils reported from MACA include conodonts and foraminifera. Conodonts are extinct eel-like chordates known almost exclusively from their microscopic jaw elements and noted for their biostratigraphic utility. Following the discovery of non-bony parts of conodont anatomy, it is apparent that conodonts are either basal true vertebrates or closely related non-vertebrate chordates. For convenience, they are briefly mentioned in this chapter. Foraminifera are the most paleontologically significant of these groups because they have a long fossil record and are frequently used for biostratigraphy and paleoecological assessments. They are single-celled organisms that can be described as "amoebas with shells"; the "shells" are known as "tests".

History of Research

Paleozoic invertebrate fossils and ichnofossils (trace fossils) have been reported sporadically from within the present (2024) boundaries of MACA for nearly two centuries, perhaps longer. In order not to repeat Chapter 2, an exhaustive chronological account will not be included here. Instead, a few reports have been selected for detailed discussion against the wider backdrop. Many of the earliest reports are ambiguous in one way or another, especially in terms of location.

Early in the 19th century, Samuel Brown, who was assessing caves in Kentucky for their potential as niter sources, sent fossils to Samuel Latham Mitchill. Mitchill in turn illustrated a fossil described as an "echinus" from Kentucky (Mitchill 1808, 1818), which was actually what would now be called a blastoid (then unknown). Mitchill's caption (1818: 431) described one as "Fig. 6. Petrified echinus from Kentucky. They are said to be frequent in the Great Cavern, near the Green River." More than a century later Fay (1961) revisited Kentucky seeking to establish a neotype for *Pentremites godoni*, the blastoid species Mitchill illustrated. He visited MACA and attempted to find blastoids with park naturalist "William" [sic; Willard] Dilley, but was unable to locate any of comparable preservation to the specimens Mitchill illustrated. Further research established that specimens of *Pentremites godoni* like the original type material are not found in the Mammoth Cave area, and the original illustrated material more likely came from the Bowling Green area (Fay 1961). However, it is still possible that what we would now recognize as blastoid fossils were known from Mammoth Cave in the early 19th century, as indicated by Mitchill's (second-hand or more distant) information. In fact, the species *Pentremites godoni* is now recognized from the cave (Chapter 6). It may be that rather than the species itself being absent, it was specimens with the particular preservational characteristics Fay was looking for that could not be found; either reading of the text is plausible.

The first substantiated report of MACA fossils was made by the brilliant but eccentric Constantine Samuel Rafinesque, who included the following passage in the Mammoth Cave section of his article "The Caves of Kentucky" (1832: 29): "They [mineral incrustations] cover the few fossils of the strata, yet I observed some Madrepores, a fine *Mastrema*, and a *Turbinolite*." Presumably his observations were made during his single visit to the cave in 1823 (Rafinesque 1836). The three names are obsolete in a paleontological context, and unfortunately there are no illustrations. "Madrepores" presumably refers to the modern *Madrepora*, a heavily branching scleractinian colonial coral. Scleractinian corals are not known from the Paleozoic, and in the context of Mammoth Cave there are several candidates for what Rafinesque might have been describing. They include: a branching or "bushy" tabulate coral (e.g., a partially exposed *Syringopora*, known to be present in the cave system); a rugose coral of similar form (e.g., *Schoenophyllum*, also present in the caves); a branching bryozoan; or a network of burrows. "*Mastrema*" is a name Rafinesque coined (Rafinesque 1819) that no one else has used scientifically, for a coral composed of several tubes; it may refer to a colonial coral that is less branching than a "madrepore" (*Acrocyathus* or *Lithodrumus*?). Finally, "*Turbinolite*" plausibly refers to the modern solitary coral *Turbinolia*, in which case the observed fossil may have been a horn coral. Tabulate corals, colonial rugose corals, and horn corals have all been observed by others in the surfaces of the Mammoth Cave system (e.g., Figure 81 and numerous figures below), so Rafinesque appears to have made accurate observations even if his taxonomy is difficult to interpret at this point in time.

Milne-Edwards and Haime (1851) published a new taxon of horn coral from Kentucky, *Zaphrentis cliffordana*. The locality information lists three locations (Button Mould Knob near Louisville, Mammoth Cave, and Grayson County). With hindsight, if the first-listed Button Mould Knob is considered the type locality (admittedly an anachronistic concern for an 1851 publication), it is not clear that "Mammoth Cave" specimens should belong to the same species. The strata of Button Mould Knob are older than any units exposed in MACA (Early Mississippian; McFarlan 1943), and this species has never been reported from the MACA area by any other author under its original name or numerous later revisions (e.g., *Triplophyllum cliffordana* Butts 1922; *Triplophyllum cliffordanum* Grove 1935; *Triplophyllites cliffordanus* Easton 1944a; *Zaphrentoides* Easton 1975; *Zaphrentites cliffordanum* Rodríguez and Kopaska-Merkel 2014). Therefore, it is here considered unlikely that whatever Milne-Edward and Haime (1851) reported from Mammoth Cave is actually their *Zaphrentis cliffordana*, but represents a different horn coral taxon.

The prolific fossil collector George K. Greene named a coral sourced either from MACA or just outside in the self-published series describing his collection. The new genus and species *Lithodrumus veryi* was based on a colony of compound horn corals (Figure 82) from "the St. Louis group, (sub-carboniferous) four miles south-east of Mammoth Cave, Kentucky" (Greene 1904: 169). This information is vague, but a few reasonable assumptions can be made. By "Mammoth Cave" Greene most likely meant the area of the Historic Entrance. "Four miles" suggests increments of one mile; on that basis, the site would most likely have been between 5.6 km (3.5 mi) and 7.2 km (4.5 mi) from the entrance. It is not known if this distance was along a road or a straight line. Tracing an arc with a radius of four miles from due east to due south shows that this distance is within MACA for slightly more than half the arc, from approximately where Cave City Road leaves the park to due south. Pohl (1970) reported that this species is abundant in the Beaver Bend Member of the Girkin Formation, and the Girkin Formation is indeed widely mapped on either side of the park boundary in this area. Therefore, the possibility that the fossil was collected within what is now southeastern MACA cannot be ruled out or confirmed. This statement holds true even if Greene erroneously swapped south for north or east for west.

During the pre-National Park Service cave tourism era, cave guides sometimes drew attention to invertebrate fossils in cave surfaces (e.g., Hovey and Call 1912). As the area transitioned to a park in the 1930s, park naturalist and future vertebrate paleontologist Claude Hibbard logged occurrences of invertebrate fossils during 1934–1935 (see Chapter 2 for a list of fossil reports). In autumn 1935, Erwin Pohl investigated the geology of the park area and made further observations of invertebrate fossils. Some of this information was incorporated into his later publications, although his stratigraphic nomenclature is not always clear due to later changes in stratigraphic terminology. There is little formal scholarly work from this era, but Weller (1927) documented invertebrate fossils from Bylew Creek (partially within MACA) and Great Onyx Cave. Following the establishment of the park, a few publications have documented invertebrate fossils within its boundaries, sometimes in the context of a field trip guide (McGrain and Walker 1954; Pohl and Cushman 1964). A number of fossils in subterranean localities were mentioned in passing in a master's thesis (BlackEagle 1989). Unusually large burrows have been reported from the cave system since the early 1990s, but to date

have only been published in abstracts (Eifert et al. 1995; Statler et al. 1996), newsletters (Holbrook 1991; Eifert 1995), and a senior thesis (Eifert 1996).

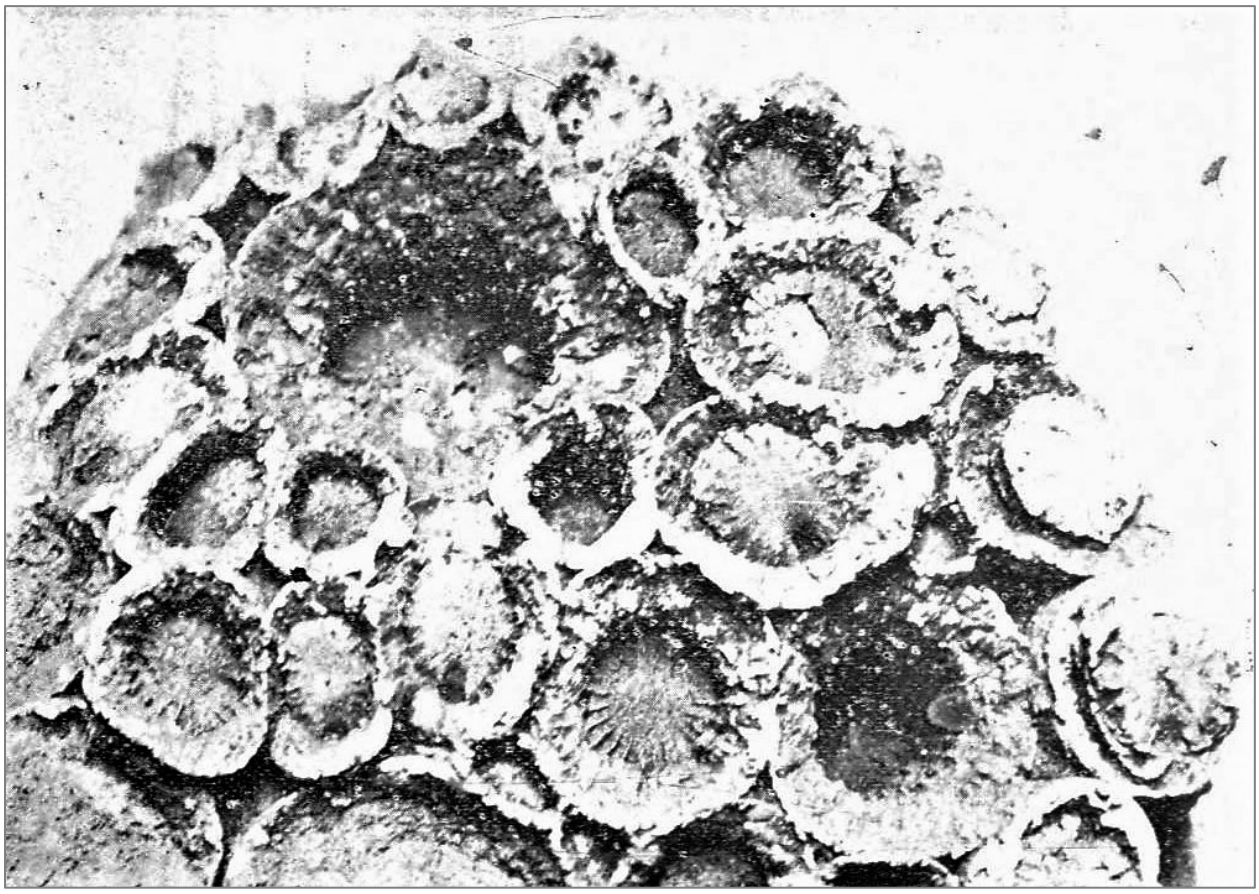


Figure 82. The missing holotype of *Lithodrumus veryi* Greene (1904), from within or near MACA. Cropped from Plate 49 (Greene 1904). PUBLIC DOMAIN

People working in the cave system have frequently noted invertebrate fossils in the various passages; approximately 90 Cave Research Foundation trip reports from 1963 to the present, documenting caves in and immediately adjacent to MACA, report invertebrate body and trace fossils. Most of these reports mention general groups, such as corals, brachiopods, and/or crinoids, rather than specific fossil genera or species. The MACA paleontological resource inventory encountered invertebrate fossils and ichnofossils in five stratigraphic units, as described in the following sections.

Stratigraphic Distribution of Paleozoic Invertebrate Fossils and Ichnofossils

Invertebrate fossils, ichnofossils, and microfossils from the various geologic units of MACA are discussed below in ascending order (oldest to youngest). See Chapter 3 for detailed descriptions of geological units, Appendix D for detailed taxonomic lists, and Table 4 for a brief summary. A geologic time scale is included as an appendix to this inventory (Appendix I). In addition to invertebrates, ichnofossils, and microfossils reported from MACA localities, reference is made to types of fossils and localities near the park, under separate subheadings. Because facies and

corresponding stratigraphic nomenclature vary for several formations, references to fossils found in the same geologic units outside of MACA are generally limited to nearby areas.

Table 4. Summary of MACA Paleozoic stratigraphy and invertebrate fossils, ichnofossils, and microfossils in descending order of age, youngest to oldest. Details and references can be found in the text. Note that "Early" and "Late" refer to age, whereas "Lower" and "Upper" refer to stratigraphic position.

Formation	Age	Invertebrate Fossils, Ichnofossils, and Microfossils at MACA
Caseyville Formation	Early Pennsylvanian	None to date
Leitchfield Formation	Late Mississippian	None to date
Glen Dean Formation	Late Mississippian	Rugose corals, bryozoans, brachiopods, gastropods, blastoids, and crinoids
Hardinsburg Formation	Late Mississippian	None to date
Haney Formation	Late Mississippian	Rugose corals, bryozoans, brachiopods, gastropods, blastoids, and crinoids
Big Clifty Formation	Late Mississippian	Potentially marine invertebrates
Girkin Formation	Middle–Late Mississippian	Rugose corals, bryozoans, brachiopods, bivalves, nautiloids, gastropods, trilobites, ostracods, blastoids, crinoids, echinoids, invertebrate burrows, fecal pellets, foraminifera, and conodonts
Ste. Genevieve Formation	Middle Mississippian	Tabulate and rugose corals, bryozoans, brachiopods, bivalves, ammonoids?, nautiloids, gastropods, trilobites, ostracods, blastoids, crinoids, echinoids, stromatiforms, invertebrate burrows, fecal pellets, foraminifera, and conodonts
St. Louis Formation	Middle Mississippian	Spicules, rugose corals, bryozoans, brachiopods, mollusks, ostracods, crinoids, echinoids, invertebrate burrows, fecal pellets, "algal" structures, and foraminifera

Stratigraphic nomenclature follows Chapter 3. Therefore, the Golconda Formation is not used: the Beech Creek Member is included in the Girkin Formation and the Big Clifty Sandstone and Haney Limestone Members are raised to formations. Significant differences with older literature describing geology in the Mammoth Cave area, e.g., the scheme used in Weller (1927), are mentioned where appropriate to facilitate translating between descriptions. Note that many of these units are referred to by lithological names in the literature, e.g., the Glen Dean Limestone or Hardinsburg Sandstone.

St. Louis Formation (Middle Mississippian)

Invertebrate, trace, and microfossils found within MACA: One of the most unusual types of fossils reported from MACA are large invertebrate burrows (Figure 83; additional photos under "Ichnofossils" below), to date only described in abstracts and other informal venues (Holbrook 1991; Eifert 1995, 1996; Eifert et al. 1995; Statler et al. 1996). These ichnofossils have been observed at Logsdon River at P. Strange Falls. Other fossils observed in the cave surfaces and thin sections include undetermined spicules, horn corals, bryozoans, brachiopods, nautiloids, undetermined mollusks, ostracods, crinoids, echinoids, fecal pellets, "algal" structures, and foraminifera (Chapter 3; inventory photos). Although the vast majority of St. Louis Formation fossils in MACA are in the

cave system, and park exposures are essentially limited to the cave, Pohl (written comm. for Mammoth Cave National Park Project, November 9, 1935) also observed fossils typical of the St. Louis Formation in gravel in a terrace deposit, including the colonial rugose coral *Lithostrotion canadensis* (now *Acrocyathus floriformis*).



Figure 83. Rick Olson and a floor laced with invertebrate burrow fossils (*Thalassinoides* isp.) in the St. Louis Formation. NPS

Invertebrate, trace, and microfossils found outside of MACA: Invertebrate fossils considered characteristic of the St. Louis Formation include the rugose corals *Acrocyathus floriformis* (=*Lithostrotionella castelnaui* and *Lithostrotion canadense* of older usage) and *Acrocyathus proliferum* (=*Lithostrotion proliferum*) (McGrain and Walker 1954; Sable and Dever 1990), and the brachiopod *Productus scitulus* (Jillson 1958).

In his description of the geology of Edmonson County, Weller (1927) noted that fossils are abundant in some layers of the St. Louis Formation but are difficult to extract from the rock, with the exception of fossils in residual cherts found in soils developed from weathering of the upper St. Louis Formation. He reported a fossil assemblage of tabulate and rugose corals, bryozoans, brachiopods, bivalves, gastropods, crinoids, and echinoids, as is commonly found elsewhere. Weller (1927) also

reported a small lower St. Louis Formation fauna from 2.82 km (1.75 mi) east of Rocky Hill, approximately 6 km (4 mi) south of MACA. This site included the bryozoan *Fenestella* (multiple species), brachiopods *Brachythyris altonenis*, *Dielasma* sp., *Eumetria verneuliana*, *Schellwienella* sp., and *Schuchertella* sp., gastropod *Bellerophon* sp., and echinoid *Archaeocidaris*.

Ste. Genevieve Formation (Middle Mississippian)

This unit is also known as the Ste. Genevieve Limestone (e.g., Haynes 1964). Geologists working at MACA have divided the Ste. Genevieve Formation into several members, in ascending order (oldest to youngest) the Fredonia, Spar Mountain, Karnak, Joppa, Aux Vases, and Levias Members. These divisions have been used in the Mammoth Cave area for decades (e.g., Pohl 1970). However, this scheme differs from stratigraphic nomenclature described from other locations and should be considered local only. In particular, the sandstone of the Spar Mountain unit is usually of limited extent and contained within the Fredonia Member, the Aux Vases corresponds to sandy tongues in the upper Ste. Genevieve and is either not used as a member or is raised to a formation where the Levias Member is not present, and the Levias Member is usually not included in the formation (Stephen Greb, Kentucky Geological Survey, pers. comm., August 2023; see also Greb 2017).

Invertebrate, trace, and microfossils found within MACA: Each member of the Ste. Genevieve Formation is fossiliferous within MACA, producing an overall assemblage of tabulate and rugose corals, bryozoans, brachiopods, cephalopods, gastropods, trilobites, ostracods, blastoids, crinoids, echinoids, stromatiforms, invertebrate burrows, fecal pellets, foraminifera, and conodonts. With the exception of colonial corals observed on a trail (Kelli Tolleson, MACA, pers. comm., January 2023), all fossils yet reported from this formation at specific locations in the park occur within the cave system. However, the Mammoth Cave 7.5-minute geological quadrangle (Haynes 1964) lists the distinctive plates of the crinoid *Platycrinites* throughout the unit and *Schoenophyllum aggregatum* (*Lithostrotion* (*Siphonodella*) *genevievensis* of Haynes's usage) near the top. Many fossil hash zones are exposed in cave passages, such as Fossil Avenue, Katherine's Domes, Marion Avenue, New Discovery, and Rodgers Avenue (Rick Toomey, MACA, pers. comm. in Hunt-Foster et al. 2009).

Fredonia Member—This member has one of the more diverse assemblages of the Ste. Genevieve Formation members. BlackEagle (1989) observed rugose corals and brachiopods. Other types of fossils observed in the surfaces or in thin sections include the tabulate coral *Syringopora*, bryozoans, mollusks, ostracods, crinoids, echinoids, possible burrows, and foraminifera (Chapter 3). Horn corals (solitary rugose corals; usage of "rugose coral" here refers to Rugosa as a whole, or examples that are not specified as colonial or solitary), brachiopods, and crinoids can be seen in Jessup Avenue, colonial corals in Bird Avenue, bivalves and coiled nautiloids in Briggs Avenue, large bellerophont gastropods in Bird Avenue and Emily's Avenue, and stromatiforms are present at Robertson Avenue (inventory photos).

Spar Mountain Member—Bryozoans, large brachiopods, gastropods, crinoids, echinoids, and possible invertebrate burrows have been observed in rock surfaces or thin sections (small slices of rock cut thin so they can be viewed through a microscope) (Chapter 3).

Karnak Member—BlackEagle (1989) observed rugose corals, brachiopods, and probable invertebrate burrows. In addition, thin sections show the presence of crinoids and echinoids (Chapter 3). Stromatiforms are present in this member in the Pass of El Ghor (R. Toomey, pers. comm., February 2023), and photos from a Felicia's Dome crawl show horn corals (Figure 84) and various brachiopods.



Figure 84. A large, well-preserved horn coral (solitary rugose coral) from the crawl to Felicia's Dome, Ste. Genevieve Formation (Karnak Member). NPS / RICK OLSON

Joppa Member—This member also has a diverse assemblage. BlackEagle (1989) reported tabulate corals, bryozoans, brachiopods, crinoids, and other unspecified fossils. Several taxa of blastoids, crinoids, and echinoids are identifiable from cave surfaces (Chapter 6). Other types of fossils observed in surfaces and thin sections include horn corals, the colonial rugose coral *Schoenophyllum aggregatum*, gastropods, trilobites, ostracods, and foraminifera (Chapter 3). Photos (see under "Types of Fossils" for examples) from Colossal Cave, Cox Avenue, Croghan Hall, Fossil Avenue, Jeanne's Avenue, Long Cave (Echo Passage), Serena's Arbor, and Specimen Avenue (Figure 85) show a variety of tabulate corals, horn corals, colonial rugose corals, bryozoans, brachiopods, cephalopods, gastropods, blastoids, crinoids, echinoids, and possible invertebrate burrows.

Conodonts are also present (JP Hodnett, Maryland National Capital Parks and Planning Commission, pers. comm., June 2023). References to J1 and J2 refer to the lower and upper divisions of the member, respectively (see Chapter 3 for more information).

Aux Vases Member—Macroscopic fossils have not been reported, but thin sections show the presence of brachiopods, ostracods, crinoids, and echinoids in the matrix rock (Chapter 3).

Levias Member—BlackEagle (1989) reported rugose corals, possible bryozoans, and unspecified fossils. Horn corals are preserved on exposed surfaces, and thin sections show the presence of bryozoans, crinoids, echinoids, and pellets (Chapter 3).

Invertebrate, trace, and microfossils found outside of MACA: Invertebrate fossils considered characteristic of the Ste. Genevieve Formation include the colonial rugose coral *Schoenophyllum aggregatum* (formerly *Lithostrotion* (*Siphonodendron*) *genevievensis*, *Lithostrotion harmodites*, and *Siphonodendron genevievensis*), the crinoid *Platycrinites penicillus* (formerly *Platycrinus penicillus*) (McGrain and Walker 1954; Sable and Dever 1990), and the brachiopods *Orthotetes kaskaskiensis*, *Pugnoides ottumwa*, and *Anthracospirifer pellaensis* (formerly *Spirifer pellaensis*) (Jillson 1958). In the area, the top of the unit was often picked at the uppermost limestone containing *Platycrinites penicillus* (Haynes 1962, 1966; Klemic 1963). Both *Pugnoides ottumwa* and *Platycrinites penicillus* can also be found in the underlying St. Louis Formation (Pohl 1970). Fossils of significance reported by Weller (1927) include the tabulate *Syringopora* in the lower portion of the formation, abundant "*Lithostrotion harmodites*" (now *Schoenophyllum aggregatum*) in a "fairly well defined zone near the top of the formation" (Weller 1927: 102), and the distinctive oval columnals of the crinoid *Platycrinites penicillus*, regarded as present at any extensive exposures of the formation. The *Schoenophyllum* horizon has also been reported in the neighboring Horse Cave quadrangle (Haynes 1966).



Figure 85. An assortment of fossils (scale not available). Specimen Avenue, Ste. Genevieve Formation (Joppa Member). **Abbreviations: BR**, preserved brachidium; **CL**, *Cleiothyridina sublamellosa*; **CO**, *Composita*; **FB**, fenestellid bryozoans. © AMBER FLOWERS

Girkin Formation (Middle–Upper Mississippian)

The Girkin Formation is a thick limestone on the southeastern margin of the Illinois Basin. It represents the stratigraphic interval from the Renault Limestone to the Cypress Sandstone to the west in the basin. Being on the margin of the basin, most of the sandstone and shale units found to the west pinch out, leaving a dominantly limestone interval that can be difficult to subdivide. At MACA, the Girkin name is used in conjunction with the western member identifications, and the formation is subdivided, in ascending order, into the Paoli, Bethel, Beaver Bend, Sample, Reelsville, Elwren, and Beech Creek Members. As with the Ste. Genevieve Formation, this scheme differs from other nomenclature in Kentucky and may be considered local and informal, and the reader is referred to Chapter 3 and previous Mammoth Cave area literature (e.g., McGrain and Walker 1954; Pohl et al. 1964; Pohl 1970) for further details. For reference, Kentucky Geological Survey usage (Greb 2017) attributes no members to the Girkin, and to the west the members used here are distributed as follows: the Bethel Sandstone is a formation in its own right; the Beaver Bend, Sample, and Reelsville Members are assigned to the Paint Creek Limestone; the Elwren interval is instead called the Cypress Sandstone and is a formation in its own right; and the Beech Creek Limestone is included as a member of the Golconda Formation with the Big Clifty Sandstone and Haney Limestone. The Paoli interval may also be identified as the Renault Limestone (Greb 2017). The Reelsville Member is also notable as including the Middle–Late Mississippian boundary (S. Greb, pers. comm., August 2023). Sandberg and Bowles (1965), in their geologic map of the Cub Run Quadrangle, used an intermediate scheme. They divided the Girkin Limestone into three informal members: lower, middle, and upper. The lower member was considered equivalent in part to the Paoli (=Renault of their usage) Limestone, the middle member was considered equivalent in part to the Beaver Bend Limestone, and the upper member was considered equivalent to the Sample, Reelsville, Elwren, and Beech Creek Members.

One of the more significant references for the MACA area, Weller (1927), does not use members, instead describing the interval as the Renault-Paint Creek Limestone. In the literature of the Mammoth Cave area, the Renault has been described as approximately equivalent to the lower three members and the Paint Creek to the upper three members (McGrain and Walker 1954: Figure 14), which differs from the modern Kentucky Geological Survey usage as explained above. The only significant subdivision used by Weller (1927) is the *Productus* zone near the top of the formation; this is likely part of the Beech Creek Member, as a *Productus*-producing interval (*Productus inflatus*, or *Inflatia inflata* of more recent usage) is noted in this unit (e.g., McGrain and Walker 1954; Haynes 1964), and this species is considered characteristic (Sable and Dever 1990). Therefore, references to the "*Productus* zone" in Weller (1927) are here tentatively attributed to the Beech Creek Member. (*Inflatia inflata* is now known to extend down into the Ste. Genevieve Formation [Pohl 1970], but Weller's intent is clear.)

Invertebrate, trace, and microfossils found within MACA: Each member of the Girkin Formation is fossiliferous within MACA, producing an overall assemblage of rugose corals (especially horn corals), bryozoans, brachiopods, bivalves, nautiloids, gastropods, trilobites, ostracods, blastoids, crinoids, echinoids, possible sponge spicules, invertebrate burrows, foraminifera, and conodonts.

Paoli Member—Weller (1927) documented a small assemblage of rugose corals, brachiopods, bivalves, and crinoids from just above the Ste. Genevieve Formation at Great Onyx Cave, here attributed to the Paoli Member. In addition, thin sections show the presence of bryozoans and echinoids in this member (Chapter 3), and photos show examples of *Lithodrumus veryi*.

Bethel Member—Thin sections show the presence of crinoids and foraminifera in the matrix rock (Chapter 3).

Beaver Bend Member—Thin sections show the presence of bryozoans, brachiopods, ostracods, crinoids, and echinoids (Chapter 3). If Greene's *Lithodrumus veryi* was indeed collected from MACA, the Beaver Bend Member would be the most likely source based on stratigraphic distribution (e.g., Pohl 1970).

Sample Member—Pohl and Cushman (1964) reported the presence of fenestellid bryozoans in partings and the brachiopods *Diaphragmus* cf. *montesanae*, *Girtyella* sp., *Productus* (now *Linoproductus*) *ovatus*, and *Spiriferina* sp. at a locality in MACA. In addition, thin sections show the presence of possible trilobites, ostracods, crinoids, and foraminifera (Chapter 3).

Reelsville Member—Pohl and Cushman (1964) reported that this member was "highly fossiliferous in part" at the above locality, with the brachiopods *Composita subquadrata*, *Composita trinuclea*, and *Spiriferina* (now *Reticulariina*) *spinosa*, and large crinoid stems. In addition, thin sections show the presence of horn corals (Chapter 3), and a trilobite, a blastoid, and crinoid fragments were observed at Salts Cave.

Elwren Member—Pohl and Cushman (1964) reported fossil hash in this member at the above locality, with fenestellid bryozoans, brachiopods, and gastropods. They also observed fossil hash at another locality in MACA. In addition, thin sections show the presence of trilobites, ostracods, crinoids, and echinoids (Chapter 3).

Beech Creek Member—Weller (1927) reported a number of brachiopod species from outcrops including the "*Productus* zone" on the lower part of Bylew Creek, likely at least partially within MACA. The large productid brachiopod *Inflatia inflata* and a large crinoid stem have been documented in MACA (McGrain and Walker 1954). Conodonts were collected from locality 8 of Rexroad and Jarrell (1961), also in MACA, but taxa were not identified. Pohl and Cushman (1964) observed the brachiopods *Inflatia inflata*, *Anthracospirifer pellaensis*, and *Spiriferina spinosa*, and crinoids *Agassizocrinus* spp. and unidentified "very large" stems at a MACA locality. In addition, thin sections show the presence of bryozoans, ostracods, pellets (presumably invertebrate feces), and foraminifera (Chapter 3). Photos from Cave #197 show brachiopods and large bellerophont gastropods, and a mudstone in this member at Salts Cave has been observed to include lacy bryozoans, abundant productid brachiopods, bivalves, possible orthoconic nautiloids, gastropods including bellerophonts, trilobites, and crinoids.

During his 1935 field investigations, Pohl observed an "excellent fossil horizon" about 10 cm (4 in) thick in the upper "Gaspar" [Girkin], 6 m (20 ft) below the "Cypress Sandstone" [Big Clifty

Formation] in MACA. He described it as “practically a coquina of brachiopod shells,” pinching out to either side in less than 12 m (40 ft) (written comm. for Mammoth Cave National Park Project, July 20, 1935). Invertebrate fossils were documented at several localities during the inventory; for the most part, the member has not been determined, the exceptions being a branching colonial coral in the Paoli Member at Grand Avenue in Long Cave and colonial rugose corals comparable to *Lithodrumus veryi* in Houchins Narrows/the Rotunda and Rafinesque Hall, and the Reelsville Member and Beech Creek Member finds at Salts Cave. Examples of horn corals, bryozoans (fenestellids and *Archimedes*), brachiopods, nautiloids, gastropods, and blastoids were observed at Crystal Cave. A gastropod shell was photographed at Great Onyx Cave. A limestone outcrop containing large horn corals has been observed in an area mapped as the Girkin Formation (Figure 86). Invertebrate burrows were observed at the Top of the Corkscrew.



Figure 86. Large horn corals exposed in relief on a limestone slab. They may be the typical large lower Girkin (“Renault”) horn coral *Amplexus geniculatus*. NPS / KELLI TOLLESON

Invertebrate, trace, and microfossils found outside of MACA: The lower Girkin (=Renault Formation deeper in the Illinois Basin) is characterized by the appearance of the crinoid *Talarocrinus* (McGrain and Walker 1954). *Talarocrinus* was reported from the lower, middle, and upper part of the Girkin (Paoli through Sample) in the neighboring Cub Run Quadrangle (Sandberg and Bowles 1965). The lower and upper Girkin faunas (Renault and Paint Creek of Weller) in Kentucky are generally similar. Taxa characteristic of the “Renault” include the horn coral *Amplexus geniculatus*, brachiopod *Spirifer subspinosa*, and crinoids *Talarocrinus buttsi* and *Globocrinus unionensis*. *Pentremites* blastoids with elongated bases appear in the lower Girkin and bases of the bryozoan *Lyropora* are

abundant, while the screw-shaped bryozoan *Archimedes* is present but rare in comparison to overlying rocks (Weller 1931). The middle Girkin "Paint Creek"-equivalent strata (including the Beaver Bend, Sample, and Reelsville equivalents) often include *Pentremites* and *Archimedes*, and the brachiopod *Chonetes chesterensis* is characteristic (Weller 1931). The compound rugose coral *Lithodrumus veryi* (=*Campophyllum gasperense* of many reports) is characteristic of the Paoli and Beaver Bend Members (McFarlan et al. 1955), and was reported from the middle Girkin (Beaver Bend) in the Cub Run Quadrangle (Sandberg and Bowles 1965). *L. veryi* is used here in preference to *C. gasperense* (e.g., Easton 1944b, Pohl 1970) because it has priority; the major reason it has often been overlooked in the literature is the apparent loss of the type specimen. Jillson (1958) regarded the brachiopods *Chonetes chesterensis* and *Productus* (now *Linoproductus*) *ovatus* and the crinoid *Talarocrinus patei* as index fossils for the formation in Barren County. The middle Paint Creek (Sample Sandstone and younger) interval is commonly characterized by the appearance of the crinoid *Agassizocrinus* (McGrain and Walker 1954). *Agassizocrinus* was reported from the upper Girkin (Sample and Beech Creek equivalents) in the Cub Run Quadrangle (Sandberg and Bowles 1965). Horn corals and spiriferid and productid brachiopods are also described from the Beech Creek interval in that quadrangle. Rexroad and Liebe (1962) reported conodonts from the Paoli Member at Wootens Knob, about 16 km (10 mi) east of MACA, one of several assemblages of early Chesterian age in the article.

Big Clifty Formation (Upper Mississippian)

The Big Clifty Formation or Sandstone of the MACA area has been variously treated as a member of the Golconda Formation (e.g., Haynes 1964; Sandberg and Bowles 1965) or as a formation in its own right (e.g., Pohl and Cushman 1964). Pohl and Cushman (1964) and Pohl (1970) also used another name in conjunction with the Big Clifty: the Fraileys Shale, which they applied to finer-grained rocks in the same stratigraphic interval.

The Cypress Sandstone name seen in some literature for the MACA area is used inconsistently. It is considered to refer to the same rocks as the Elwren Sandstone Member of the Girkin Formation, and has been used with or in place of that name in some MACA literature (e.g., Pohl and Cushman 1964; Pohl 1970). However, Weller (1927) appears to have had a different interpretation, applying the Cypress name to rocks between the Renault-Paint Creek Limestone (=Girkin Formation, in part or entirely) and Golconda Limestone (=Haney Formation). This interval would later be identified using the Big Clifty name (McGrain and Walker 1954; compare Weller's Figure 39 with McGrain and Walker's Figure 6).

Invertebrate, trace, and microfossils found within MACA: Invertebrate fossils have not yet been reported unequivocally from the Big Clifty Formation within MACA. There is one potential record from Pohl's 1935 field investigations (written comm. for Mammoth Cave National Park Project, September 21, 1935): he reported collecting fossils from a dense medium-grained red-weathering sandstone in the transition zone from the Cypress [Big Clifty?] to the Golconda [Haney], including marine fossils as well as plant fossils. Frustratingly, he did not specify the fossils or the location(s) from among 13 locations generally but not exclusively within the modern boundaries of the park. Nor did he ever publish details on this seemingly significant record of the "most prolific fauna"

found in either unit, although it may be referred to in the Big Clifty and Fraileys description of Pohl (1970: 4 ["Marine fauna occasionally present in sandstone and shale facies, sometimes mixed with land plants."]). With the lack of clarity for faunal content, stratigraphic assignment, and location, this report can only be treated as a potential note for future exploration at present. A reference to the Big Clifty Formation being fossiliferous on Cane Run within MACA in Hunt-Foster et al. (2009), based on Sandberg and Bowles (1965), appears to be erroneous; Cane Run does not enter MACA.

Invertebrate, trace, and microfossils found outside of MACA: If the Cypress Sandstone of Weller (1927) is indeed the Big Clifty Formation, brachiopods, bivalves, gastropods, and trilobites have been found in this unit in the MACA area. They are described as restricted to a few horizons, only one yielding recognizable internal casts. Jillson (1958) described the brachiopods *Camarophoria explanata*, *Composita trinuclea*, *Productus* (now *Linoproductus*) *ovatus*, and *Spiriferina spinosa* as index fossils for the Cypress Sandstone of Barren County. Browne and Pohl (1973) described a foraminifera assemblage from the Fraileys Shale facies of the unit, recovered from the Broad Ford area about 13 km (8 mi) north of MACA.

Haney Formation (Upper Mississippian)

As with the Big Clifty Formation, the Haney Formation or Limestone of the MACA area has been variously treated as a member of the Golconda Formation (e.g., Haynes 1964; Sandberg and Bowles 1965) or as a formation in its own right (e.g., Pohl and Cushman 1964).

Invertebrate, trace, and microfossils found within MACA: White residual chert of the Haney Formation found in southern MACA yielded fossils of horn corals (*Zaphrentites spinulosum*), blastoids (*Pentremites abruptus*, *P. pyriformis*, and *P. welleri* [=*P. pyriformis*]), and crinoids (*Agassizocrinus conicus*, *A. ovalis*, and *Eupachycrinus* sp.) (Pohl and Cushman 1964). The MACA paleontological inventory recorded the bryozoan *Archimedes*, a probable bellerophont gastropod, and crinoid fragments at Cave #293; and *Archimedes*, brachiopods, gastropods, and an obliquely conical fossil (*Platyceras*?) at Cave #203 (Figure 87).

Invertebrate, trace, and microfossils found outside of MACA: Fossils are noted as a component of the Haney Formation in lithological descriptions found on many geologic maps; for example, 16 of 17 quadrangle maps used to produce the MACA–ABLI (Abraham Lincoln Birthplace National Historical Park) geologic resources inventory bedrock map that include the unit describe it as fossiliferous (National Park Service 2022). The most extensive such description mentions horn corals, bryozoans, brachiopods, mollusks, and crinoids (Shawe 1963). This contrasts with Weller (1927), which described the Golconda Limestone (usage approximately equivalent to the Haney Formation) as "rather unfossiliferous." Apart from the fossils known from MACA, other types of fossils found in some abundance in the region include bryozoans (*Archimedes* sp.) (Shawe 1963). Per Weller (1931), the Haney (Golconda) fauna of Kentucky is more recognizable for its combination of taxa rather than particular index forms.

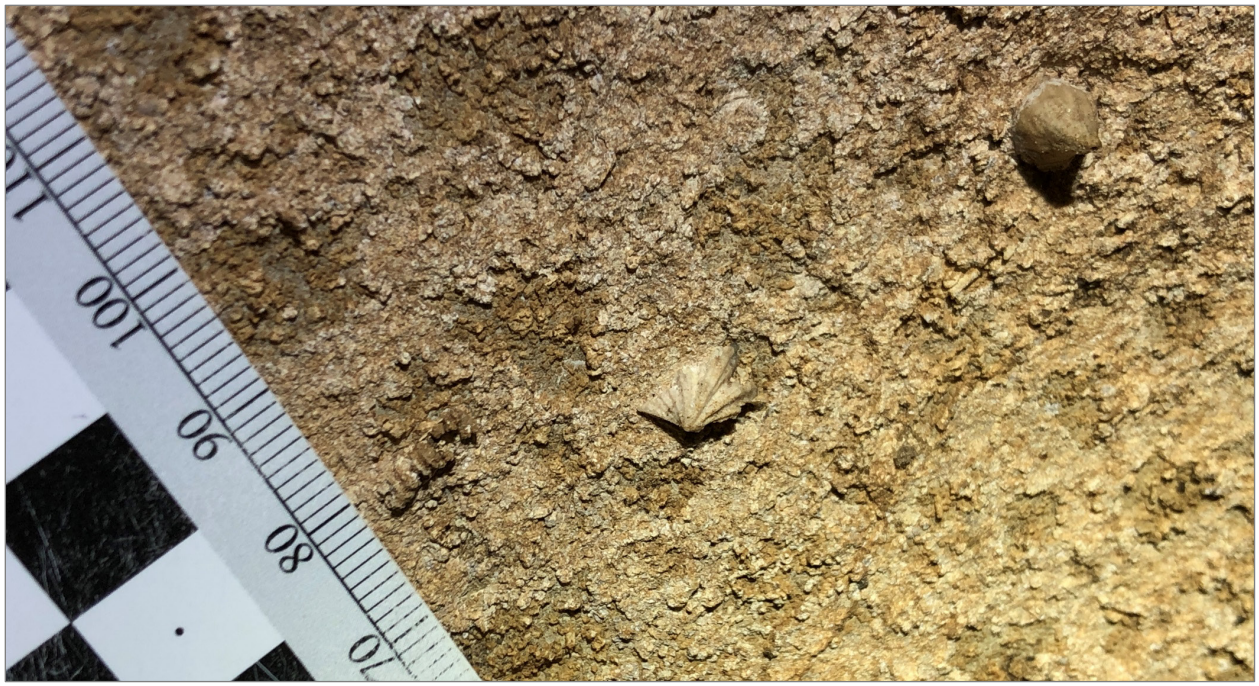


Figure 87. Crinoids, a spiriferid brachiopod (center), and a conical fossil, probably the gastropod *Platyceras* (upper right), in the Haney Formation, Cave #203. NPS / JP HODNETT

Hardinsburg Formation (Upper Mississippian)

This unit is also known as the Hardinsburg Sandstone (e.g., Haynes 1964).

Invertebrate, trace, and microfossils found within MACA: Fossils have not yet been reported from the Hardinsburg Formation within MACA.

Invertebrate, trace, and microfossils found outside of MACA: Fossils are uncommon in the Hardinsburg Formation in much of the Illinois Basin. Haynes (1964) reported the presence of silicified fossil fragments in red clay filling cracks in the formation. Weller (1927) observed that casts and impressions of invertebrate fossils had been found in residual Hardinsburg Formation blocks at several localities in Warren County, but not in situ. As a side note, these casts and impressions would be of interest because of the paucity of invertebrate fossils in this formation, which is otherwise more paleontologically notable for plant spores (Hoffmeister et al. 1955, 1961).

Glen Dean Formation (Upper Mississippian)

This unit is also known as the Glen Dean Limestone (e.g., Haynes 1964).

Invertebrate, trace, and microfossils found within MACA: Marine fossils are abundant in the Glen Dean Formation. For example, all 14 of the quadrangle maps used to produce the MACA–ABLI geologic resources inventory bedrock map that include the Glen Dean Formation mention the presence of fossils (National Park Service 2022). The paleontological inventory encountered horn corals and crinoids (Figure 88), *Archimedes*, and a high-spired gastropod in this unit. However, there appear to be no publications reporting Glen Dean Formation fossils from specific, unambiguous

MACA locations. Livesay (1953; Figure 1 in 1962 revision) includes a photograph of a Glen Dean Formation block with abundant fossils, among them the bryozoan *Archimedes*, the brachiopod *Spiriferina*, and crinoids, but no location is specified. The block greatly resembles a specimen formerly in the collections of the University of Minnesota but now at the Cincinnati Museum Center as CMC IP80689 (Figure 89). A note with this specimen observed by the author while it was still held by the University of Minnesota indicates the specimen is from the Glen Dean Formation from "near Mammoth Cave"; what is meant by "near" is not specified. The fossiliferous block was collected circa 1964, well after MACA was established; one would hope that the collection was authorized if it came from within the park. It is also not known whether a promise in the note to give further information if desired was fulfilled. This block includes a number of examples of *Archimedes* sp. and the crinoids *Phanocrinus* sp. and *Platycrinites* sp.



Figure 88. A horn coral (center) and crinoid columnal in oblique cross-section (horseshoe-shaped fossil right of center) in the Glen Dean Formation. NPS



Figure 89. A block of fossiliferous Glen Dean Formation collected within or near MACA, reposited at the Cincinnati Museum Center. NPS / VINCENT SANTUCCI

Invertebrate, trace, and microfossils found outside of MACA: The Glen Dean Formation is one of the most fossiliferous units in the Illinois Basin. Weller (1927) described several collections from the Glen Dean Formation in Edmonson County and nearby counties, including one from rocks found on the road at the back of the Brownsville jail near MACA. Invertebrates from the Brownsville collection included horn corals (*Amplexus* and *Triplophyllum spinulosa* [now *Zaphrentites*]), bryozoans (*Anisotrypa symmetrica*, *Archimedes swallovanus*, *Archimedes proutanus*, *Archimedes terebriformis*, *Eridopora punctifera*, *Fenestella tenax*, *Fenestella serratula*, *Fistulipora montifera*, *Glyptopora* sp., *Lyropora* sp., *Polypora cestriensis*, *Prismopora serrulata*, *Reteporina flexuosa*, *Septopora subquadranus*, *Septopora cestriensis*, *Streblotrypa nicklesi*, and *Tabulopora* [sic; *Tabulipora*] *tuberculata*), brachiopods (*Cleiothyridina sublamellosa*, *Composita trinuclea*, *Diaphragmus elegans*, *Productus ovatus* [now *Linoproductus*], *Spirifer leidyi* [now *Anthracospirifer*], and *Spiriferina spinosa*), gastropods (*Bellerophon* sp. and *Platyceras chesterensis*), trilobites (*Phillipsia* sp.), blastoids (*Pentremites brevis* and *P. okawensis*), and crinoids (*Pterotocrinus* sp.). Microconchids ("*Spirorbis*") have also been reported from the area (Weller 1927). Conodonts (Rexroad and Clarke 1960) have also been collected from the formation in Kentucky, and ostracods and foraminifera have been found in Illinois (Coryell and Rozanski 1942). Fossils are reportedly more abundant near the top of the formation (Weller 1927). Characteristic taxa include the bryozoans *Archimedes laxus* and *Prismopora serrulata* and the blastoid *Pentremites*

spicatus (Weller 1931). In a study on preserved blastoid color patterns that may have some interest for MACA due to the number of blastoid specimens found there, Beaver and Fabian (1998) include a group of *Pentremites tulipaformis* from the Glen Dean Formation of Leitchfield, about 11 km (7 mi) north of MACA.

Leitchfield Formation (Upper Mississippian)

Invertebrate, trace, and microfossils found within MACA: Invertebrate fossils have not been reported from the Leitchfield Formation within MACA; within the park the formation is only mapped in a small area near the southwestern border, reducing the likelihood of finding fossils.

Invertebrate, trace, and microfossils found outside of MACA: Invertebrate fossils have been found in this formation near MACA and in other parts of western Kentucky. The formation includes the stratigraphic interval from the Tar Springs Sandstone to the top of the Mississippian, including several commonly fossiliferous limestones. The Leitchfield Formation, however, is locally truncated by overlying Pennsylvanian sandstones, so some of the fossiliferous strata may not be present at all localities. Weller (1927) identified two productive localities southwest of MACA: one 8.6 km (5.3 mi) southwest of the park at the mouth of Little Beaverdam Creek with bryozoans, brachiopods, bivalves, trilobites, blastoids, and crinoids; the other more than 19 km (12 mi) southwest of the park, 5 km (3 mi) north of Richfield, with bryozoans and brachiopods. Gildersleeve (1965) reported that bryozoan and brachiopod fragments had been found 2.1 km (1.3 mi) northwest of Wingfield School, on the order of 12 km (7 mi) southwest of MACA. Irham et al. (2010) described a crustacean from a limestone conglomerate in the formation approximately 19 km (12 mi) north of MACA, south of Leitchfield. Also present were fossils of corals, brachiopods, bryozoans, gastropods, ostracods, stalked echinoderms, and foraminifera (Irham et al. 2010). Fossils are absent from shale beds, but may be abundant in thin limestone beds, especially near the base of the formation (Weller 1927).

Caseyville Formation (Lower Pennsylvanian)

Invertebrate, trace, and microfossils found within MACA: No invertebrate fossils have been reported from the Caseyville Formation within MACA.

Invertebrate, trace, and microfossils found outside of MACA: Invertebrate fossils are not known from the Caseyville Formation nearby (Weller 1927; Jillson 1958), but small assemblages have been reported from farther west in Kentucky (Whaley et al. 1979) and southern Illinois (Rexroad and Merrill 1985; Jennings and Fraunfelter 1986; Devera et al. 1987; Weibel and Norby 1992). Much of the Caseyville is dominated by fluvial sandstones, which is why invertebrate fossils are relatively rare. In areas where estuarine and marine facies are preserved, such fossils include horn corals (Jennings and Fraunfelter 1986), brachiopods (Whaley et al. 1979; Jennings and Fraunfelter 1986; Devera et al. 1987), bivalves (Jennings and Fraunfelter 1986), cephalopods (Whaley et al. 1979; Devera et al. 1987), gastropods (Whaley et al. 1979; Jennings and Fraunfelter 1986), ostracods (Whaley et al. 1979), conodonts (Rexroad and Merrill 1985; Devera et al. 1987; Weibel and Norby 1992), and invertebrate trails and other trace fossils (Whaley et al. 1979).

Types of Fossils

Photos of many of the characteristic Mississippian invertebrate fossils of Kentucky can be seen in Weller (1931; note that some of the genus and species names are outdated).

Invertebrates

The majority of macroscopic invertebrate fossils observed at MACA can be attributed to corals, bryozoans, brachiopods, cephalopods, gastropods, and various echinoderms, especially crinoids. Because of the abundance and outstanding preservation of the park's echinoderm fossils, they have been documented in a separate chapter of this report (Chapter 6).

Phylum Cnidaria: Class Anthozoa (corals)

Tabulate corals are known from the St. Genevieve Formation at MACA, where the "pipe-organ"-like *Syringopora* has been reported from the Fredonia Member (Chapter 3) and is also present in Colossal Cave in the Joppa Member (Figure 90).



Figure 90. A tabulate coral (*Syringopora*) from the Joppa Member of the Ste. Genevieve Formation in Colossal Cave. It is partially darkened by mineral impurities. NPS / KELLI TOLLESON

Most of the rugose corals reported from MACA are solitary forms (horn corals), but colonial forms are also present, and may be more easily seen because of their larger size. The colonial rugosans *Acrocyathus floriformis* and *A. proliferum* are considered characteristic of the St. Louis Formation (e.g., McGrain and Walker 1954). Pohl observed loose *Acrocyathus floriformis* (as *Lithostrotion*

canadensis) in stream terrace deposits (written comm. for Mammoth Cave National Park Project, November 9, 1935). *A. floriformis* has tightly packed corallites with polygonal boundaries while *A. proliferum* resembles a mass of cylindrical horn corals. *Schoenophyllum aggregatum* is known from the Ste. Genevieve Formation (Figures 91 and 92) (Chapter 3; inventory photos). This coral may be confused with the tabulate *Syringopora*, but the corallites are larger (on the order of a half-centimeter or a quarter of an inch in diameter) and the apertures of the corallites resemble miniature horn corals with a radial pattern of structural features (Figure 92). A branching colonial coral photographed in the Paoli Member of the Girkin Formation at Grand Avenue in Long Cave may be something similar, but this is not clear from the photos (Figure 93A). *S. aggregatum* is considered to be diagnostic of a specific stratigraphic interval in the upper Ste. Genevieve Formation in western Kentucky (Dever and McGrain 2015), but the presence of this species or something very similar in multiple horizons at Mammoth Cave indicates greater stratigraphic range. This possibility had already been noted in Dever and McGrain (2015): a written communication from A. Palmer identified two horizons in the cave system.

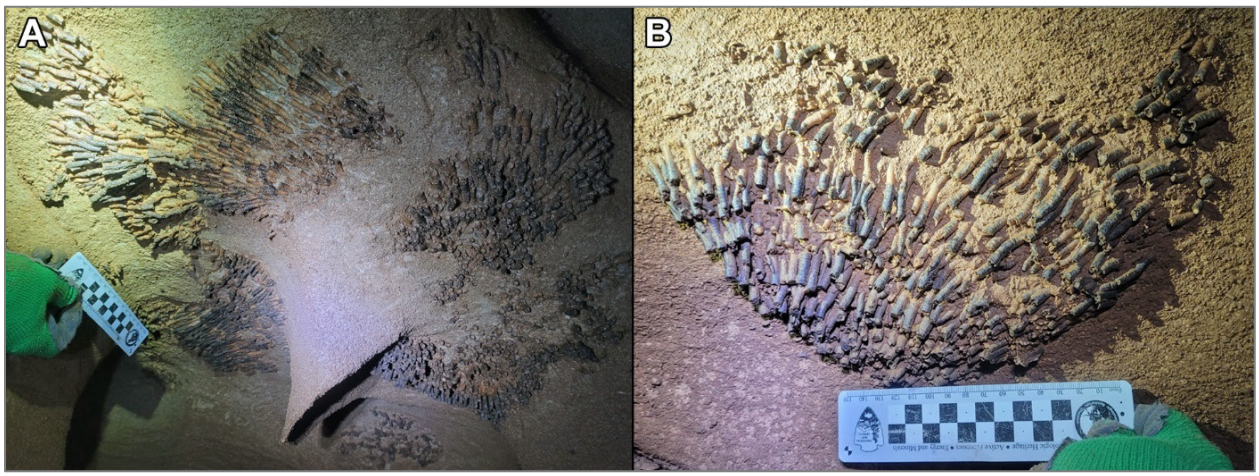


Figure 91. Large *Schoenophyllum aggregatum* colonies at Cave #063, near the Ste. Genevieve–Girkin contact (potentially the Levias Member of the Ste. Genevieve Formation). NPS

Lithodrumus veryi of the lower Girkin Formation is similar to *Acrocyathus proliferum* but more exaggerated, resembling a bouquet of flaring, overlapping horn corals (Figure 82). Probable examples of this species have been photographed in the Paoli Member at Houchins Narrows/the Rotunda and Rafinesque Hall (Figure 94). A colonial rugose coral observed as float in a pancake room in the upper part of the Colossal section (Megan Harder, Cave Research Foundation, pers. comm., July 2023 via R. Toomey) is attributed to the Girkin Formation (Figures 93B and C). It does not closely resemble *Lithodrumus*, instead appearing more like the older *Acrocyathus floriformis* and species of *Palaeosmilia*/*Palastraea* from younger rocks. A similar fossil has been observed in the Joppa Member of the Ste. Genevieve Formation at New Discovery (Ljubomir Risteski, MACA, pers. comm., June 2024).



Figure 92. Details of *Schoenophyllum aggregatum*. **A.** A colony in the Ste. Genevieve Formation (Joppa Member) on Cox Avenue. Note the larger diameters of the corallites, their central peaks, and crenulated internal margins compared to the tabulate *Syringopora* in Figure 90. **B.** Detail of the lateral surfaces of corallites; Ruins of Karnak, Ste. Genevieve Formation (Fredonia Member). **C.** Detail of corallite apertures; Cox Avenue, Ste. Genevieve Formation (Joppa Member). **A:** NPS / RICK OLSON; **B, C:** NPS

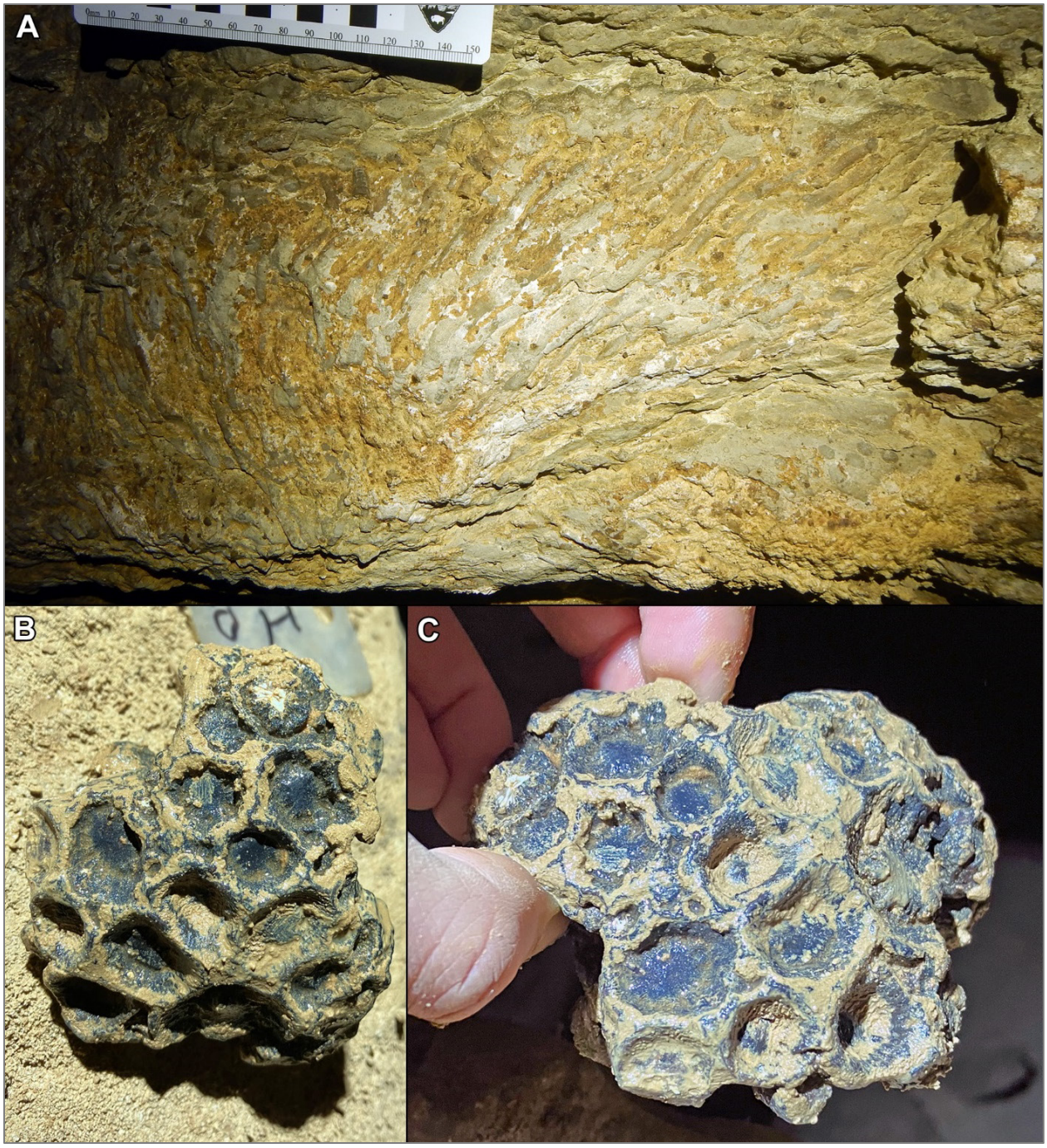


Figure 93. Colonial rugose corals from the Girkin Formation. **A.** The corallites in this colonial coral are closer in diameter to *Schoenophyllum* than *Syringopora*; Long Cave (Grand Avenue), Paoli Member. **B, C.** A weathered colonial coral resembling *Acrocyathus floriformis* and species of *Palaeosmilia*/*Palastraea*; scale not available. **A:** NPS; **B, C:** © MEGAN HARDER



Figure 94. Aspects of *Lithodrumus veryi* at Rafinesque Hall, Ste. Genevieve Formation (Paoli Member). **A.** Flattened apertures. **B, C.** Masses of corallites in longitudinal and oblique longitudinal section. NPS

Horn corals are the most frequently reported coral fossils from MACA to date. At MACA, horn corals frequently have fairly dark external surfaces, sometimes with a corduroy-like texture due to the internal anatomy. They may be seen intact or weathered in apertural view (showing a radiating starburst of internal structures) (Figures 95 and 96), side view (Figures 95 and 97), any angle between, in section at any angle (Figures 98 and 99), or weathered and crushed (Figure 99). They are present in the St. Louis (inventory photos), Ste. Genevieve (BlackEagle 1989; Chapter 3; inventory photos), Girkin (Weller 1927; Pohl 1970; Chapter 3; inventory photos), Haney (Pohl and Cushman 1964), and Glen Dean Formations (inventory photos) at MACA. Several morphologies are evident, some of which may be of taxonomic value. Many are conical, potentially with a curved tip (Figures 95 [left] and 99C show this tip). Others resemble cattails (Figure 95 right), are flared at the aperture (Figure 97A), are short and squat (Figure 97B), or are elongate (Figure 97C). Horn corals are an occasional feature of cave surfaces, and there is an interesting bedrock "panel" with several examples visible aboveground (Figure 86).



Figure 95. Three horn corals showing various views; Serena's Arbor, Ste. Genevieve Formation (Joppa Member). Left: Side view. Center: Apertural view (with corn-kernel-like mineralizations). Right: Oblique apical view (apex missing; more bulbous than tapering form on left). NPS / RICK TOOMEY

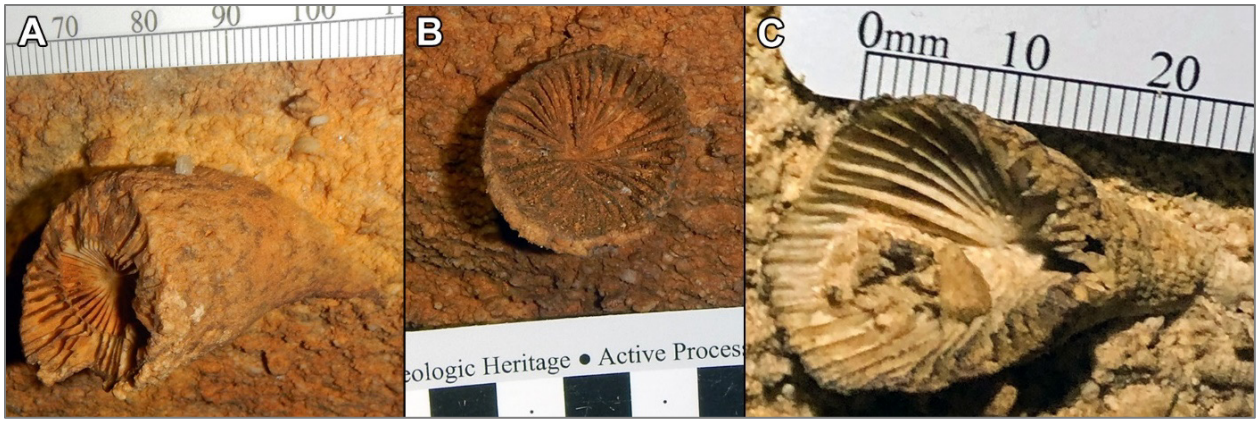


Figure 96. Aspects of horn coral apertures. **A.** A coral with a weathered aperture, with the aperture surface exposed in conjunction with damaged walls; Cox Avenue, Ste. Genevieve Formation (Joppa Member). **B.** Typical apertural view; same provenance as **A**. **C.** Obliquely weathered aperture of a deep cup showing vertical structures, likely *Menophyllum princetonensis*; Specimen Avenue, Ste. Genevieve Formation (Joppa Member). **A, B:** NPS; **C:** © AMBER FLOWERS

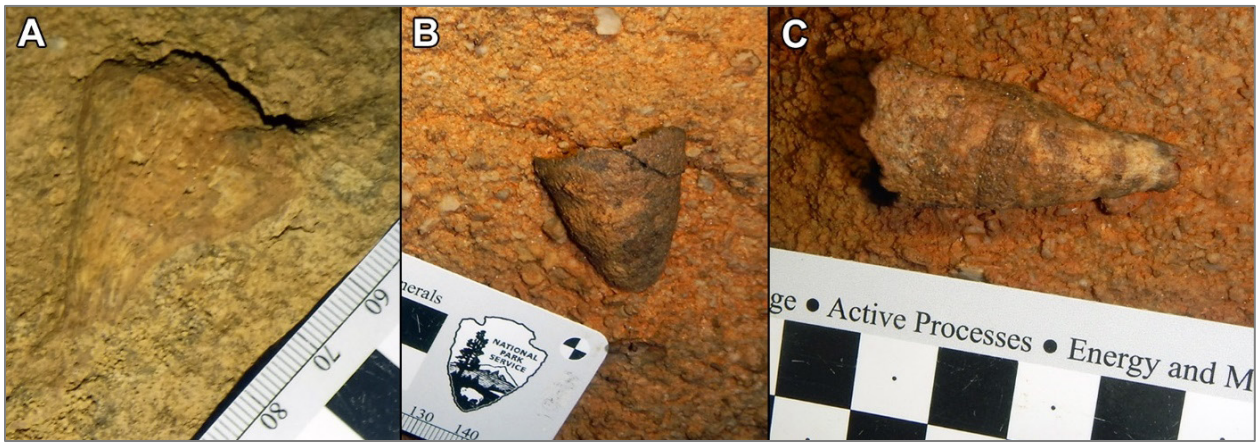


Figure 97. Different horn coral shapes. **A.** Upwardly flaring; Crystal Cave (Helictite Route), Girkin Formation. **B.** Squat, cup-shaped; Cox Avenue, Ste. Genevieve Formation (Joppa Member). **C.** Elongate, cone- or horn-shaped; same provenance as **B**. **A:** NPS / RICK TOOMEY; **B, C:** NPS



Figure 98. Preservational aspects of horn corals. **A** is from Crystal Cave (Helictite Route), Girkin Formation. **A.** This coral cross-section may be mistaken for a cephalopod with preserved tentacles. **B** and **C** are from Long Cave (Echo Passage), Ste. Genevieve Formation (Joppa Member). **B.** Horn corals with dark exteriors may be confused with fossil teeth by inexperienced observers. **C.** These two horn corals, one in cross-sectional view, have been partially replaced by a form of chalcedony known as beekite, giving them bumpy surficial textures. **A:** NPS / RICK TOOMEY; **B, C:** NPS



Figure 99. Examples of horn corals with suboptimal preservation or orientation of exposure. **A, B.** Two views of a weathered horn coral in section, showing the walls of the cup of the aperture; Long Cave (Echo Passage), Ste. Genevieve Formation (Joppa Member). **C.** Two flattened and weathered horn corals, resembling discarded banana peels; Crystal Cave (Helictite Route), Girkin Formation. **D.** A weathered section showing some of the internal anatomy; smaller sections may be confused with fragments of strongly ribbed shells; Cox Avenue, Ste. Genevieve Formation (Joppa Member). **A, B, D:** NPS; **C:** NPS / RICK TOOMEY

Phylum Bryozoa (moss animals)

Bryozoans have been reported from several formations at MACA, but little is known of their taxonomy because bryozoans are difficult to classify to genus or species without making detailed study of microscopic structures using thin section (specimens that have been cut and polished so thinly that light passes through). Therefore, observers often only report either the general presence of bryozoans, or classify them by general shapes or characteristics. One distinctive taxon found at MACA is *Archimedes*, which appears as a screw-like form when weathered in relief, and may be mistaken by non-specialists for a vertebral column when seen in section (Figure 100). The "screw" is the axial support of the colony, which grew as a spiraling mesh. Bryozoans with mesh- or net-like

colonies are commonly called fenestrate or fenestellid bryozoans, and most of the MACA bryozoans for which an identification or a description have been supplied are fenestellids (Figure 85). Overall, bryozoans are infrequently reported in MACA literature, with macroscopic examples previously reported only from the Ste. Genevieve Formation within the cave (BlackEagle 1989) and in the Girkin Formation outside of the cave (Pohl and Cushman 1964). One reason for this may be that fenestrate bryozoans are most commonly seen on bedding surfaces, but are difficult to impossible to see in vertical sections, such as predominate in the caves. Bryozoans have been reported in thin sections taken from the St. Louis Formation, several members of the Ste. Genevieve Formation, and several members of the Girkin Formation (Chapter 3). Inventory photos show *Archimedes* in the Girkin, Haney, and Glen Dean Formations (Figure 100), lyre-shaped bryozoans in the Girkin Formation (either *Lyropora* or *Lyroporidra*) (Figure 101) and net-like and sheet-like bryozoans in the Ste. Genevieve and Girkin Formations (Figure 102). Bryozoans are more widely reported in Upper Mississippian units outside of the park, but are rarely identified to genus or species. For example, fenestellids are very common in the Glen Dean Formation.

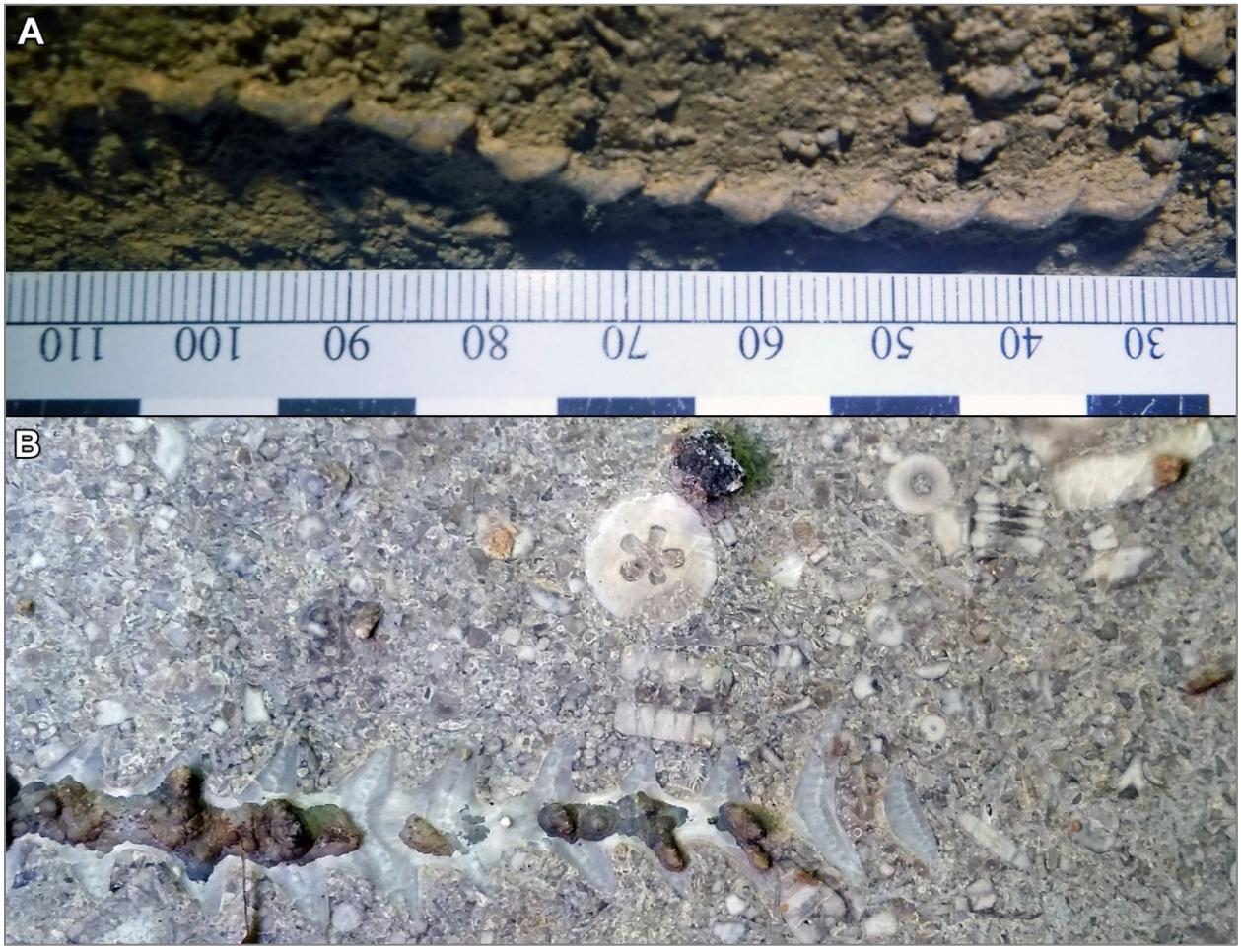


Figure 100. *Archimedes*. **A.** A central axis exposed in relief; Crystal Cave (Helictite Route), Girkin Formation. **B.** A central axis partially in relief and partially in section; Glen Dean Formation (scale not available). Note also the crinoid ossicles in cross and longitudinal section. **A:** NPS / RICK TOOMEY; **B:** NPS



Figure 101. Lyre-shaped bryozoans at a site near MACA, in the Girkin Formation. Similar fossils are visible within the park at Cave #048 and Houchins Narrows. **A.** The base of a lyre-shaped bryozoan, which may resemble a checkmark. **B.** A lyre-shaped support with the filtering “mesh” preserved between the lyre struts. These U-shaped or lyre-shaped bryozoans are either *Lyropora* or *Lyroporella*. NPS

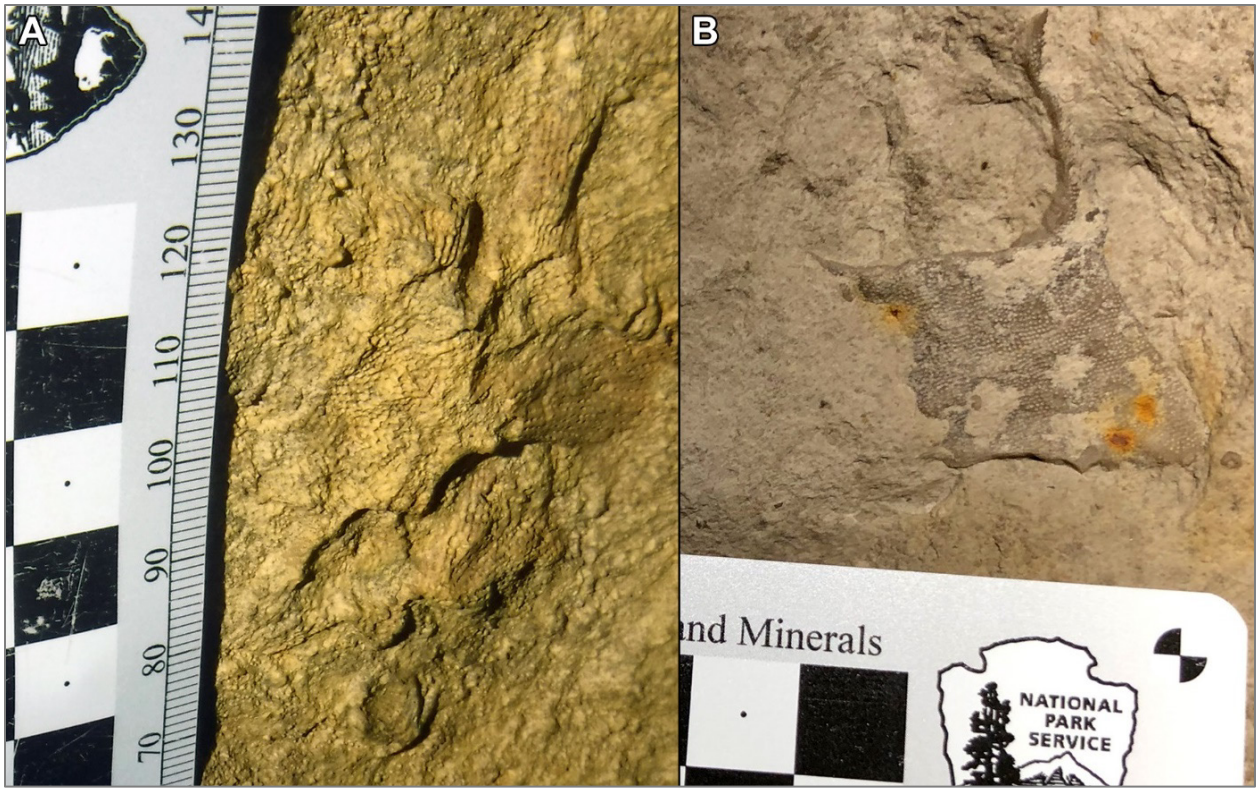


Figure 102. Sheet-like bryozoans. **A.** A net-like bryozoan; Crystal Cave (Helictite Route), Girkin Formation. **B.** A sheet-like bryozoan (the light-colored dots on the gray fragment are the individual bryozoan living chambers); Jeanne's Avenue at the Forks of the Cave, Ste. Genevieve Formation (Joppa Member). **A:** NPS / RICK TOOMEY; **B:** NPS

Phylum Brachiopoda (lamp shells)

At MACA, brachiopods are to date most abundant and diverse in the Ste. Genevieve and Girkin Formations, with isolated reports from the St. Louis Formation (Chapter 3), the Haney Formation (inventory photos), and potentially the Glen Dean Formation (park collections). Preservation in the park's limestone beds is sometimes good enough to include the internal brachidium (Figures 85 and 103). The brachiopod fauna of the Ste. Genevieve members in the park has not been rigorously determined to genus or species level to date, although at least eight or nine taxa are evident in inventory photos (e.g., Figure 104). For the Girkin Formation, Weller (1927) and Pohl and Cushman (1964) identified 17 forms to the species level from aboveground and cave sites in MACA, representing most of the formation's members.



Figure 103. A brachiopod with the brachidium silicified and partially exposed. Cox Avenue, Ste. Genevieve Formation (Joppa Member) (scale not available). NPS

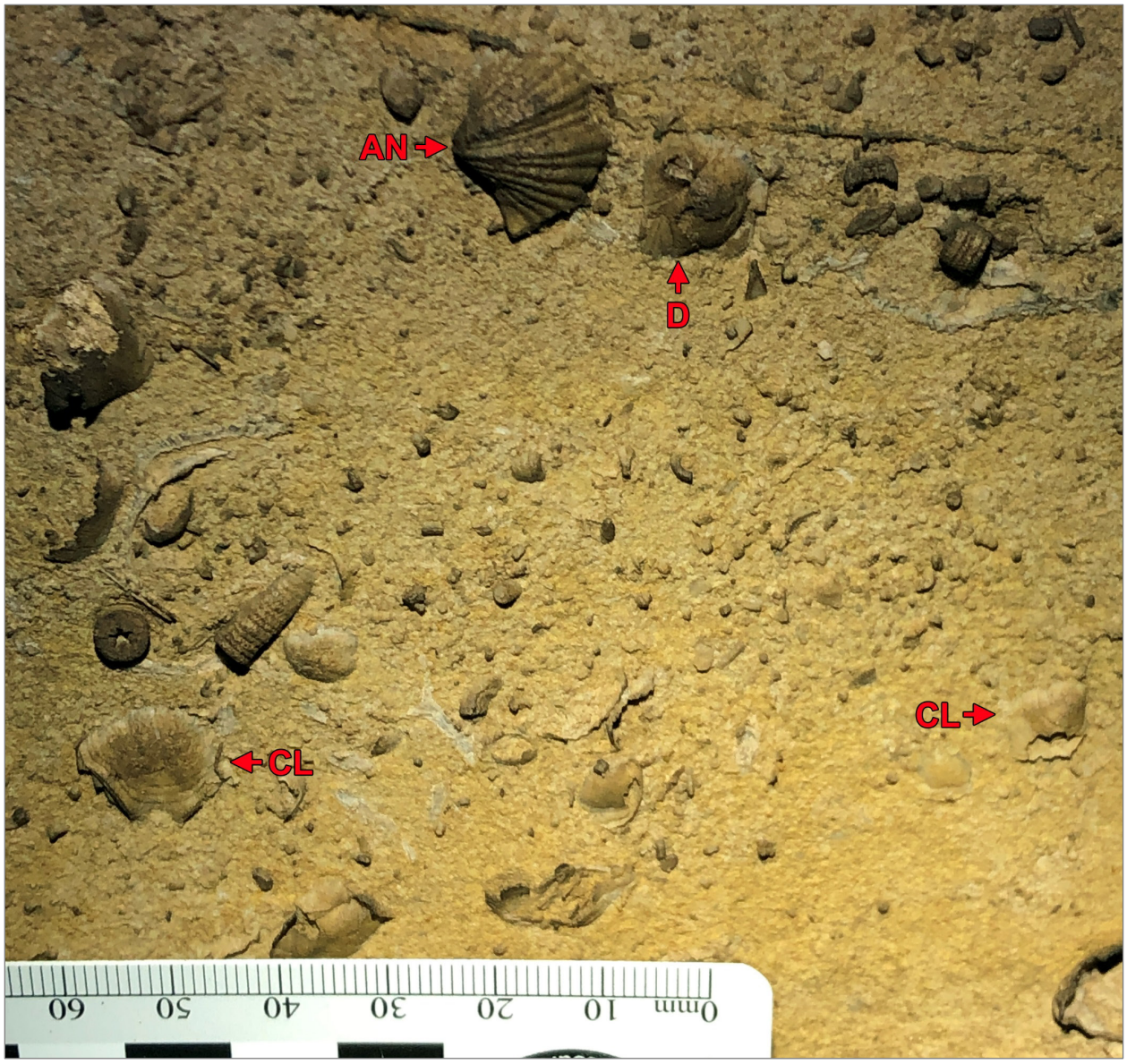


Figure 104. Brachiopods at Specimen Avenue, Ste. Genevieve Formation (Joppa Member).
Abbreviations: AN, *Anthracospirifer leidyi*; **CL**, *Cleiothyridina sublamellosa*; **D**, smooth D-shaped shell.
NPS / JP HODNETT

Many of the brachiopods seen in the cave system are strongly ribbed and can be attributed to Order Spiriferida, such as *Anthracospirifer* (assigned to *Spirifer* in older references) (Figures 104 to 106). Another common type of MACA brachiopods are the bulbous productids (Figure 107). Other types of brachiopods encountered in the Joppa Member include: *Cleiothyridina sublamellosa*, with concentric growth lines and a flaring margin (Figures 85 and 104); *Composita*, generally smooth or with fine growth lines and a slightly "warped" appearance, often appearing slightly bilobed (Figure 108); and several unidentified forms (Figure 109), including a smooth D-shaped shell (Figures 104 and 105A), a finely ribbed shell (Figure 109A), and microscopic shells. Similar brachiopods are

present in the Karnak Member, including *Cleiothyridina*, *Composita*, and spiriferids (Figure 110). These brachiopods are all common in these units outside of park boundaries.

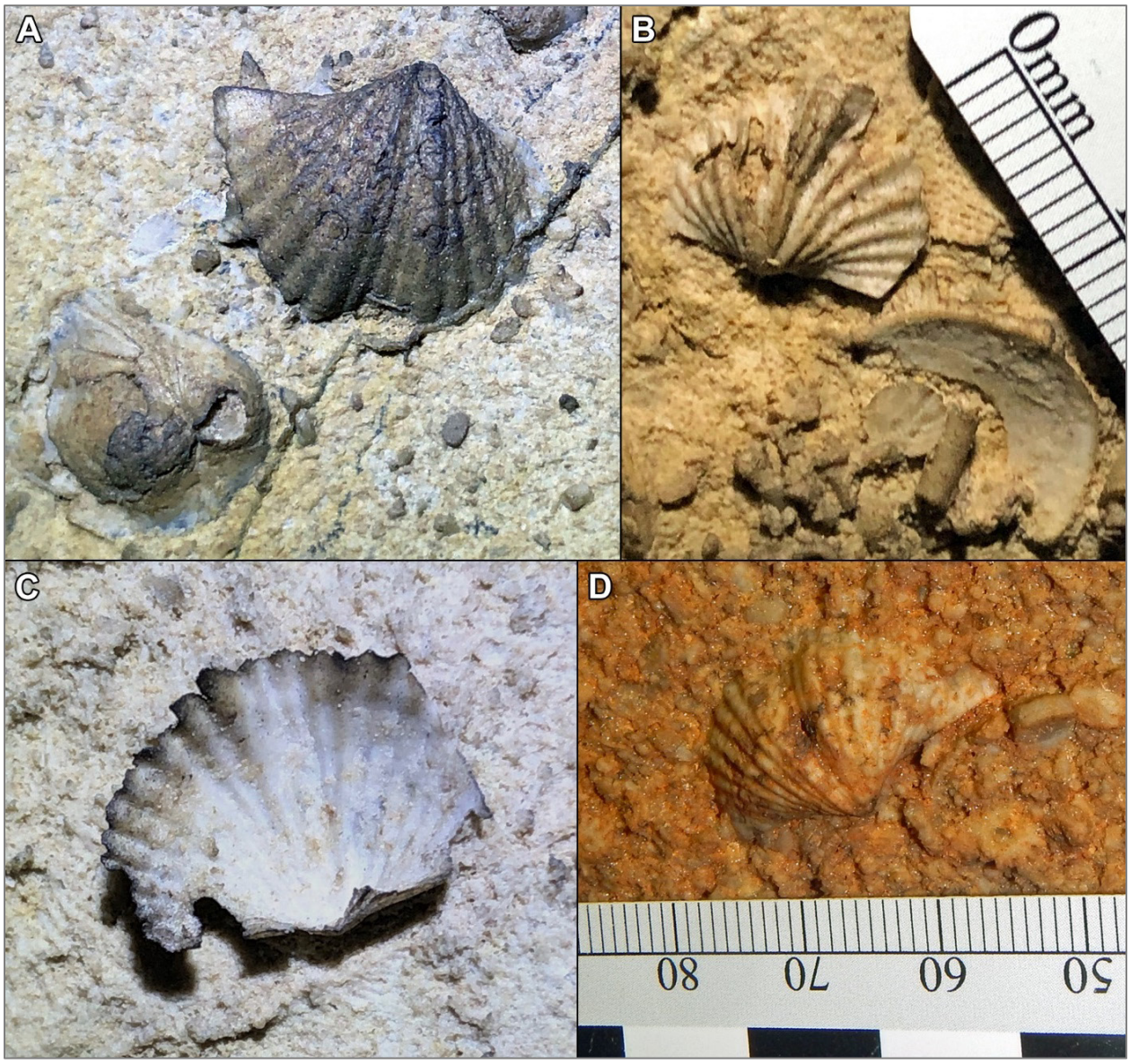


Figure 105. Spiriferids from the Joppa Member of the Ste. Genevieve Formation. **A–C** are from Specimen Avenue; **D** is from Cox Avenue; scale not available for **A** and **C**. **A.** A closer view of the *Anthracospirifer leidyi* and smooth shell from Figure 104. **B.** A spiriferid with five or six widely spaced ribs on either side of the obscured central fold (*Reticulariina spinosa*?). Note also the fenestellid bryozoan fragment beneath it. **C.** Inner view of a spiriferid shell. **D.** A spiriferid with wing-like corners (*Anthracospirifer pellaensis*). **A–C:** © AMBER FLOWERS; **D:** NPS

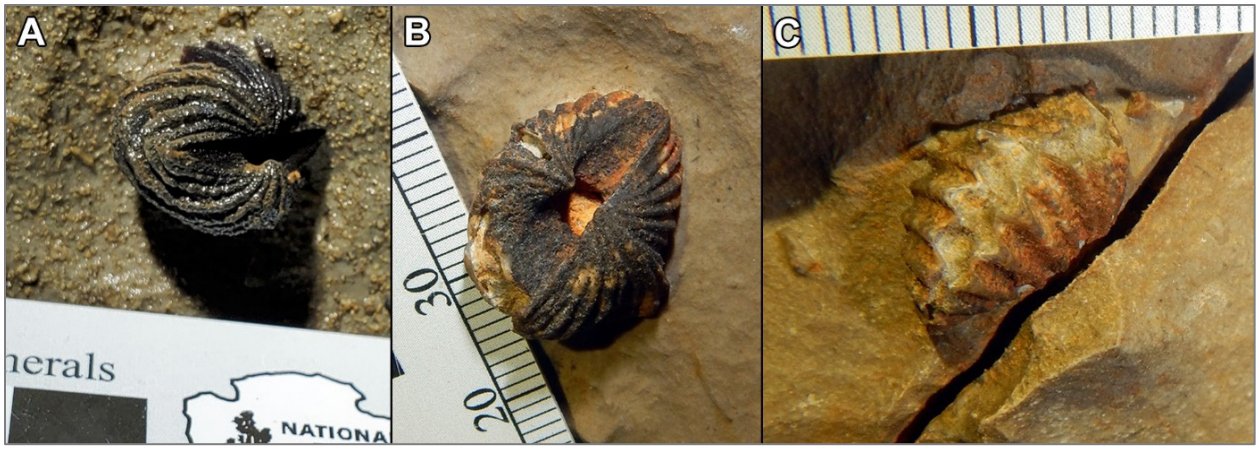


Figure 106. Various other views of spiriferids. **A.** Side view; Discovery 70, Ste. Genevieve Formation? **B.** Hinge (posterior) view; Jeanne's Avenue, Ste. Genevieve Formation (Joppa Member). **C.** Anterior view; Jeanne's Avenue, Ste. Genevieve Formation (Joppa Member). **A:** NPS / RICK OLSON; **B, C:** NPS



Figure 107. Productids. **A.** A productid from Roaring River, St. Louis Formation. **B–D** are from the Joppa Member of the Ste. Genevieve Formation; **B** and **C** are from Cox Avenue, and **D** is from Specimen Avenue. **A–C:** NPS; **D:** © AMBER FLOWERS



Figure 108. Examples of *Composita* from Jeanne's Avenue, Ste. Genevieve Formation (Joppa Member). The dark or rusty color is due to mineral staining. NPS

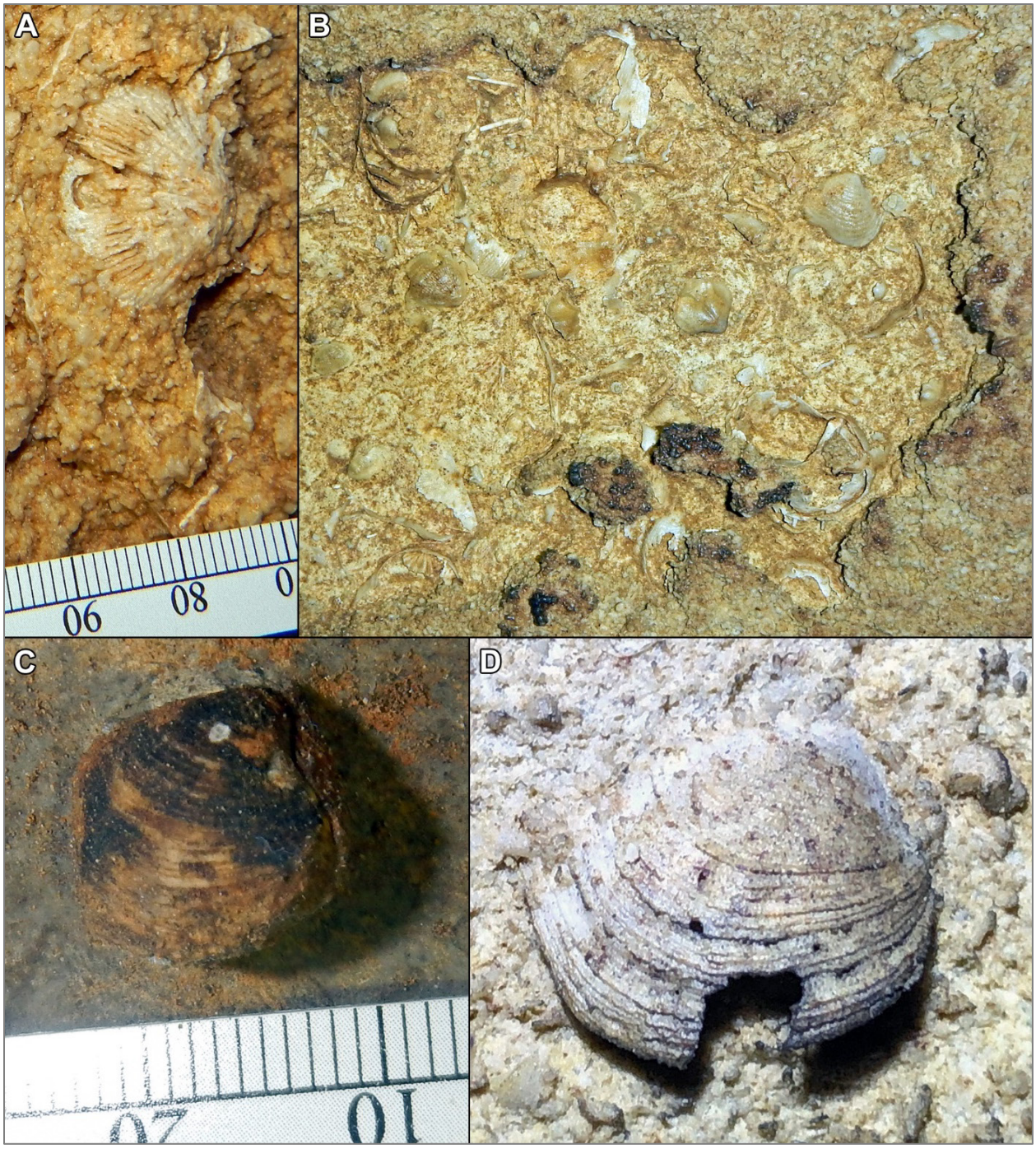


Figure 109. Brachiopods from the Joppa Member of the Ste. Genevieve Formation. **A.** A poorly preserved finely ribbed form, Long Cave (Echo Passage). **B.** A shell hash with several poorly preserved or poorly exposed taxa, Long Cave (Echo Passage) (scale not available). **C.** A shell with strong growth lines, Jeanne's Avenue. **D.** A damaged shell with strong growth lines, Specimen Avenue (scale not available). **C** and **D** are potentially *Cleiothyridina*. **A–C:** NPS; **D:** © AMBER FLOWERS



Figure 110. Brachiopods from the Karnak Member of the Ste. Genevieve Formation, all from the crawl to Felicia's Dome. **A.** *Composita trinuclea*. **B.** Spiriferid. **C.** *Cleiothyridina sublamellosa*. **D.** *Composita* sp. **E.** An unknown smooth-shelled form, perhaps *Dielasma* (or a mollusk). NPS / RICK OLSON

Phylum Mollusca (bivalves, cephalopods, gastropods, etc.)

Three or four of the major mollusk classes are known from MACA as accessory elements of the invertebrate assemblages. Until this inventory, the published fossil mollusk record of MACA consisted of two bivalve genera identified by Weller (1927) from the Girkin Formation of Great Onyx Cave, and an undetermined gastropod from the same formation reported by Pohl and Cushman (1964). Gastropods are now known also from the Haney Formation and particularly the Ste. Genevieve Formation (Chapter 3; inventory photos), and cephalopods have been observed in the St. Louis Formation, the Fredonia and Joppa Members of the St. Genevieve Formation, and the Girkin Formation (inventory photos). A tapering tubular fossil observed in the Joppa Member may pertain to a scaphopod ("tusk shell") (inventory photos), as scaphopods have been reported in the Ste.

Genevieve Formation of Illinois (Weller 1916; identity questioned in Godefroid et al. 2006), or represent an undetermined but outwardly similar animal.

The only bivalves yet reported from MACA are *Aviculopecten* and *Leiopteria* from the Paoli Member of the Girkin Formation at Great Onyx Cave (Weller 1927), and undetermined taxa reported from the Fredonia Member of the Ste. Genevieve Formation at Briggs Avenue and Beech Creek Member of the Girkin Formation at Salts Cave (Figure 111; inventory photos).

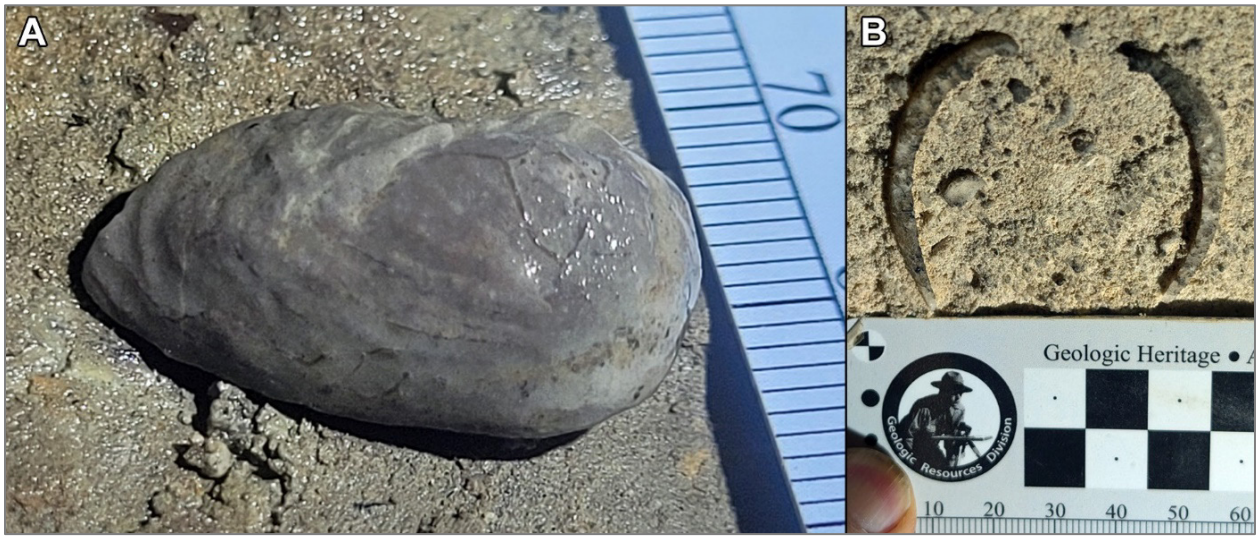


Figure 111. Bivalves. **A.** A bivalve observed at Salts Cave, from the Beech Creek Member of the Girkin Formation. **B.** Cross-sections of bivalve shells observed in Briggs Avenue, Ste. Genevieve Formation (Fredonia Member). **A:** NPS / K. TOLLESON; **B:** NPS

Cephalopods are a minor but distinctive constituent of the fossil invertebrate assemblages within MACA. The inventory team has recorded orthoconic nautiloids in the St. Louis Formation, Fredonia and Joppa Members of the Ste. Genevieve Formation (Figure 112A), and the Girkin Formation at MACA (Figure 112B; see also Figure 11 in Chapter 2).

Coiled cephalopods have been photographed in the Joppa Member (Figure 113). The fossils are frequently incompletely preserved, incompletely exposed, or both, making it difficult to determine whether individual specimens are coiled ammonoid or nautiloid cephalopods. There are at least two distinct taxa present at MACA, one with a kink in the septa, which are convex (Figures 113A and 113B), and another with concave septa and a centrally located siphuncle (Figure 113C). The former may be a goniatite ammonoid and the latter is interpreted as a nautiloid. Another coiled nautiloid is present in Briggs Avenue (Ste. Genevieve Formation, Fredonia Member) (Figure 114).



Figure 112. Orthoconic nautiloids. **A.** A small example from near Wellpipe Hill, Ste. Genevieve Formation (Joppa Member). **B.** A larger example; Crystal Cave (Helictite Route), Girkin Formation. Septa are apparent on both. **A:** NPS; **B:** NPS / RICK TOOMEY

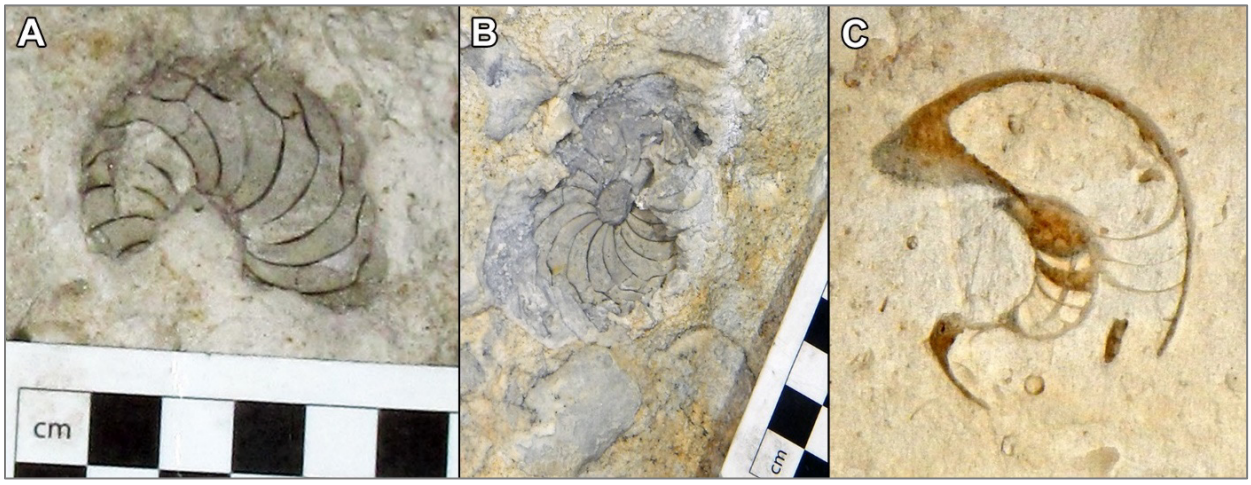


Figure 113. Coiled cephalopods of the Ste. Genevieve Formation (Joppa Member) at MACA. **A.** A shell exposed at Serena's Arbor. **B.** A shell at Croghan Hall. **A** and **B** represent the same taxon, as shown by the kink in the septa. It may be a goniatite ammonoid. **C.** A cross-section exposed at Long Cave (Echo Passage) (scale not available). Parts of two whorls are visible; the central position of the siphuncle in the inner whorl and the concave shape of the septa indicate a nautiloid. **A:** NPS / RICK TOOMEY; **B, C:** NPS

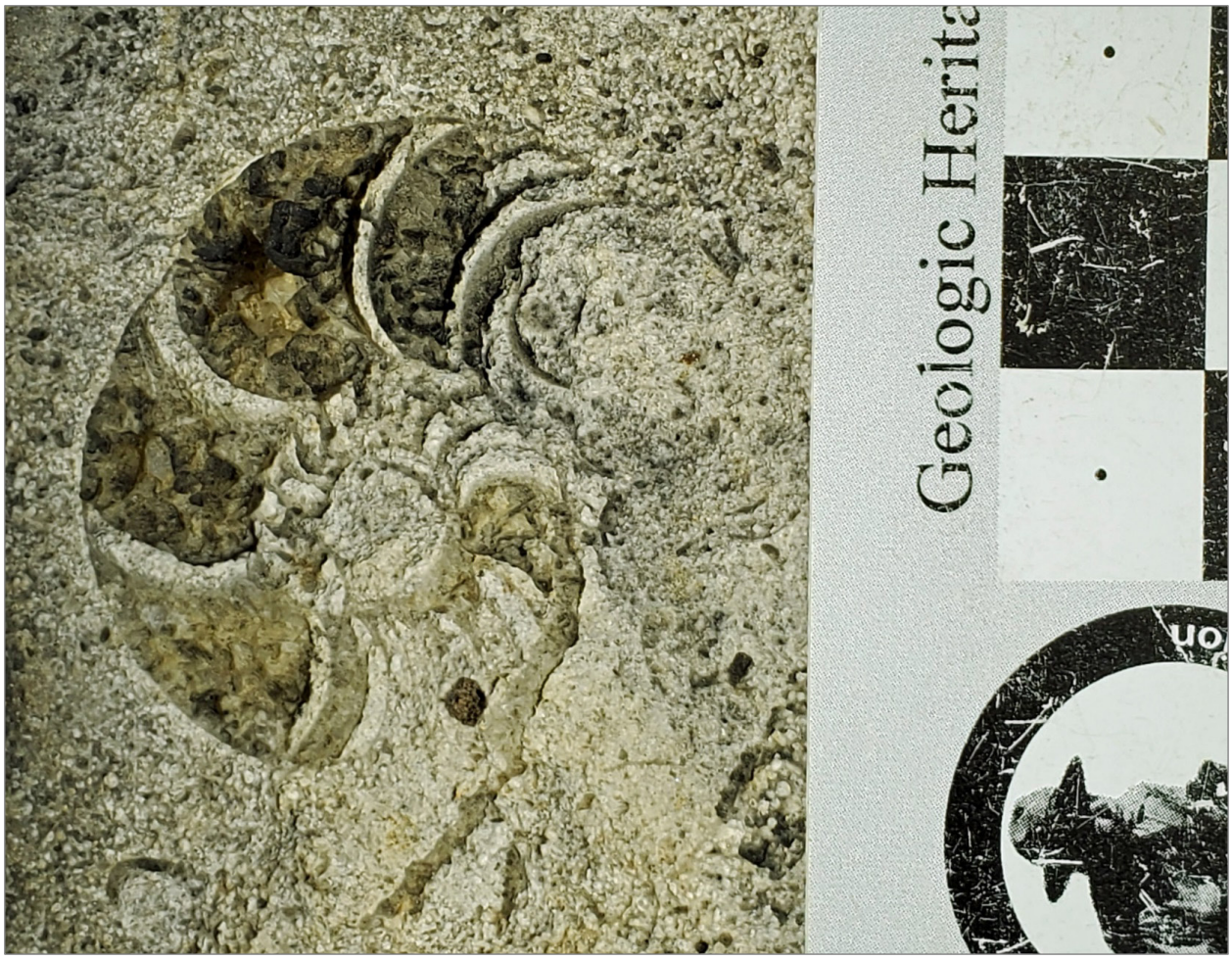


Figure 114. A coiled nautiloid photographed in Briggs Avenue, Ste. Genevieve Formation (Fredonia Member), with mineralization filling the chambers. NPS

Gastropods, represented today by snails and slugs, are the most frequently reported fossil mollusks at MACA. Many Paleozoic snails had shells that resemble modern forms. The majority of snail shells are coiled. Diverse coiling shapes are known from fossil and modern snails, and the shape of coiling can be used to identify some fossil genera and species. Many of the snail shells at MACA can be placed in one of two basic configurations: cap-like forms with minimal coiling at the "tip" of the "cap", represented by *Platyceras* (Figure 115); and planispiral shells (coiling in a flat plane) or near-planispiral shells (Figures 116 and 117). Other morphologies are seen less frequently (Figures 118 and 119). *Platyceras* is elsewhere noted for its propensity to infest crinoids (Rollins and Brezinski 2007; Syverson et al. 2018), so it is not surprising that this genus would be found in the same rocks as abundant crinoid fossils. These shells may be confused with small horn corals (compare to Figure 95 [left] or Figure 99C [right], for example).

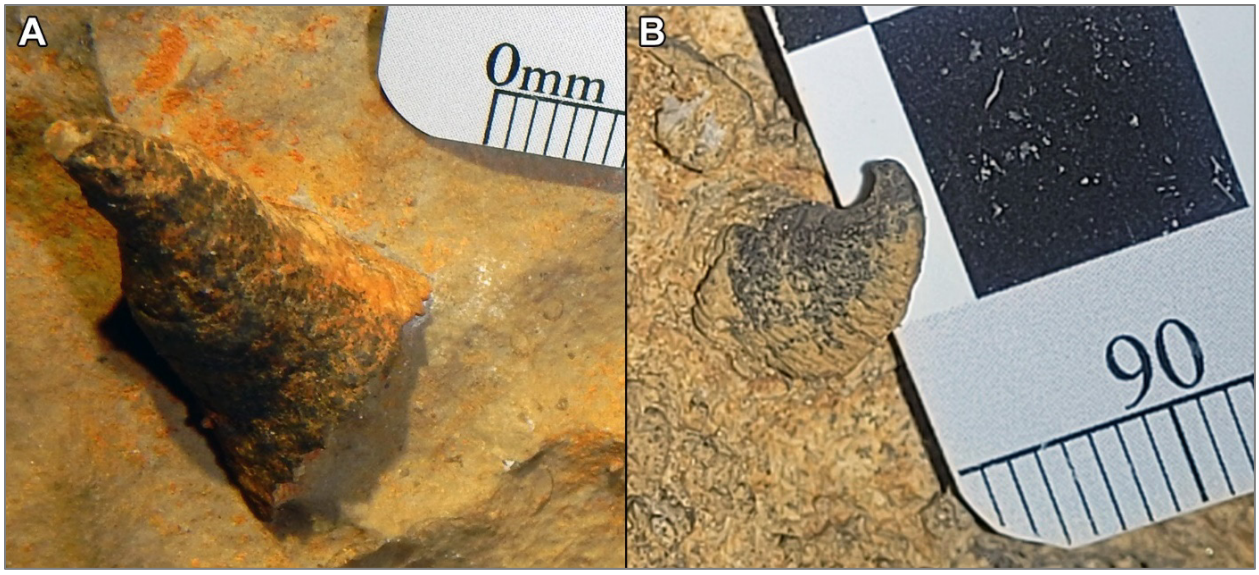


Figure 115. *Platyceras*. **A.** Dorsal view of a *Platyceras*, Jeanne's Avenue, St. Genevieve Formation (Joppa Member) (note the orange mineralization staining the surface). **B.** A small shell, more complete than **A** and in oblique lateral view, Colossal Cave, Ste. Genevieve Formation (Joppa Member). **A:** NPS; **B:** NPS / KELLI TOLLESON



Figure 116. Various views of planispiral or low-coiled snails. Scales are unavailable for most; these are included for visual reference. **A.** A cross-section showing a spiral coil, Cave #203, Haney Formation. **B.** A shell section, possibly of a bellerophont, replaced by coarse crystals, Cave #293, Haney Formation. **C.** Partially exposed shells, uncertain provenance. **D.** Cross-section, Long Cave (Echo Passage), Ste. Genevieve Formation (Joppa Member). **A–C:** NPS / JP HODNETT; **D:** NPS

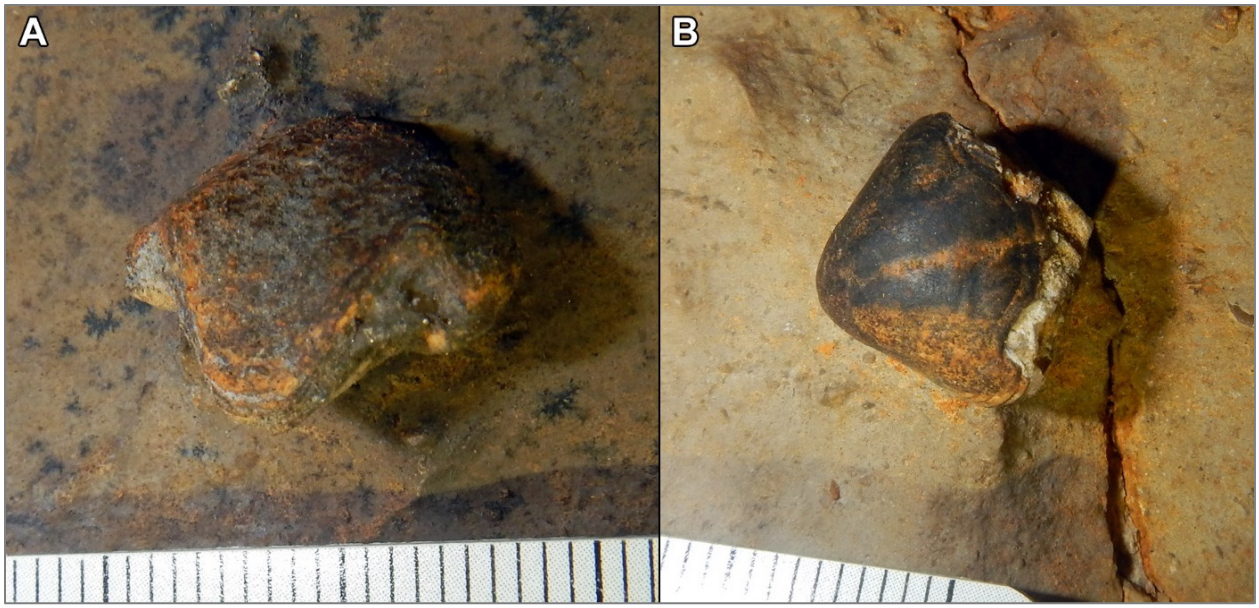


Figure 117. Views of bulbous bellerophonts. Specimens are seen from (**A**) behind and (**B**) the front (comparable to *Retispira ornatus*), from Jeanne's Avenue, Ste. Genevieve Formation (Joppa Member). The dark or rusty color is due to mineral staining. NPS

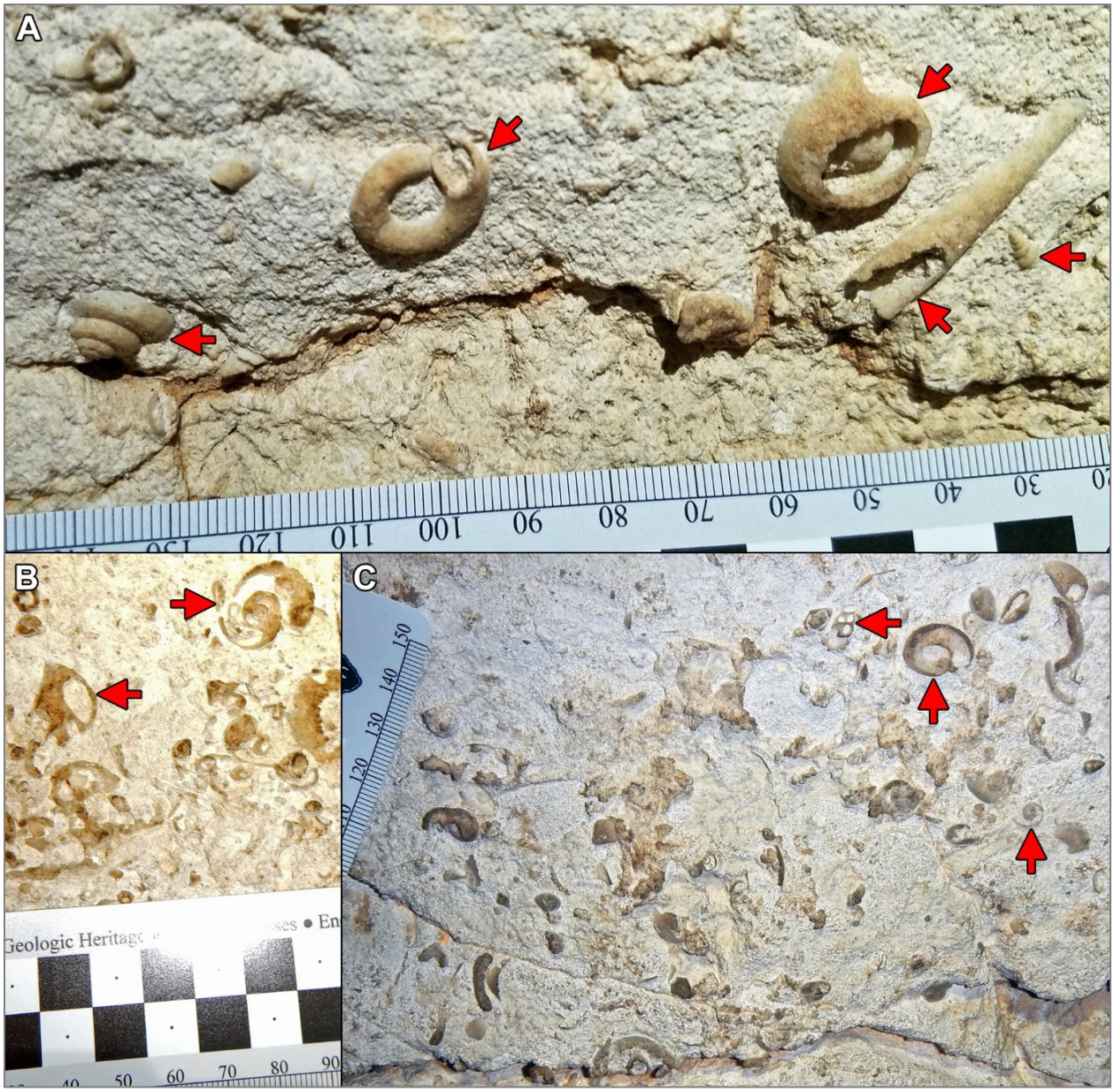


Figure 118. Other gastropods. **A.** Several taxa are visible here, including a stepped coiling form ("ziggurat"; left and potentially left-center), a bulbous planispiral form (upper right), and a small high-coiling form (center of right margin, uncertain provenance (Fossil Avenue?, Ste. Genevieve Formation [Joppa Member]?). The elongate tapering hollow form near the right margin resembles an orthoconic nautiloid but appears to lack chambers; it may be a scaphopod or an outwardly similar tubular fossil of different origin. **B.** A tall, rounded form (similar to the modern *Olivella*) is present on the left, and a crushed planispiral section is present in the upper right, Long Cave (Echo Passage), Ste. Genevieve Formation (Joppa Member). **C.** Among the shell types visible here are a small high-coiling form (right of upper center), a potential "ziggurat" (near the upper right corner), and a planispiral form (near center right margin), Long Cave (Echo Passage), Ste. Genevieve Formation (Joppa Member). NPS



Figure 119. Other gastropods. **A.** A high-coiling form among several bulbous bellerophonts, Marion Avenue, Ste. Genevieve Formation (Joppa Member). **B.** A “ziggurat”, so-called informally for its stepped profile (in contrast to a rare, smoother “pyramid” snail), Fossil Avenue, Ste. Genevieve Formation (Joppa Member). **C.** A high-coiling form with a “snowman”-like cross-section, Cave #321, Glen Dean Formation. NPS

Many of the planispiral shells probably represent bellerophont snails, which are often bulbous and have a rapidly expanding coil. The outer whorl may look like it is devouring the previous whorls. Bellerophont shells may be relatively large and are often preserved in various cross-sections, including spirals that may resemble coiled nautiloids. They can be distinguished by looking at their insides: bellerophont shells are not chambered but have open whorls. Some bellerophonts may also resemble smooth brachiopods, depending on orientation or preservation (Figure 117).

Many fossils of gastropods and other mollusks are the mineralized shells of the original animal, but often shells dissolved during burial, leaving behind natural internal molds and casts of the interior spaces. Internal casts are known as steinkerns. Lithological studies (Chapter 3) and inventory photos show the presence of gastropods in the Ste. Genevieve, Girkin, Haney, and Glen Dean Formations at MACA. Upper Mississippian gastropods of western Kentucky and neighboring states are documented in Thein and Nitecki (1974).

Other Invertebrates

The following groups are to date recognized primarily as microfossils at MACA. Except for trilobites, which are well-represented by macroscopic fossils worldwide, fossils of these groups are unlikely to be observed with the naked eye except at very close range.

Phylum Porifera (sponges): Spicules, potentially representing sponges, have been observed in thin sections taken from the St. Louis Formation at MACA (Chapter 3).

Phylum Arthropoda: Two groups of arthropods have been observed, mostly in thin sections: trilobites and ostracods (Chapter 3). Trilobite remains are present in the Joppa Member of the Ste. Genevieve Formation, the Sample (potentially) and Elwren Members of the Girkin Formation (Chapter 3), and the Reelsville and Beech Creek Members of the Girkin Formation at Salts Cave (Figure 120). Trilobite tail sections (pygidia) and whole enrolled trilobites (Figure 120) have been found at this site and are consistent with the common Late Mississippian *Kaskia chesterensis*, but this identification should be considered tentative. Ostracod fossils have been identified from the St. Louis Formation and most of the members of the Ste. Genevieve and Girkin Formations (Chapter 3).



Figure 120. An enrolled trilobite found at Salts Cave in a loose stone sourced from the upper Girkin Formation. NPS / KELLI TOLLESON

Inevitably, not all fossils can be identified in the field. Lemon-shaped structures a few millimeters (less than half an inch) across with crystallized interiors are seen in some places (Figures 101A and 121) and appear to represent some kind of small shelled animal, perhaps large ostracods.



Figure 121. A lemon-shaped cross-section with internal mineralization, Cave #069, Girkin Formation (probably upper; ostracod?). NPS / RICK OLSON

Ichnofossils

MACA's Paleozoic trace fossils are fairly typical in terms of categories, but include some unusually large examples. A variety of invertebrate ichnofossils have been observed in MACA rocks, but almost none of them have been documented in any detail. Lithological studies (Chapter 3) and inventory photos show a variety of burrows and potential burrows, presumably invertebrate, in the St. Louis Formation (Figures 83 and 122), most of the members of the Ste. Genevieve Formation (Figure 123, most likely upper Ste. Genevieve), and the Girkin Formation (Figure 124). These are mainly typical of bioturbated shallow marine environments. The most unusual of these burrows is a series of relatively enormous examples found in the St. Louis Formation (Figures 83 and 122), to date documented only in internal reports and abstracts. They are 3.8–6.4 cm (1.5–2.5 in) in diameter and chertified (Holbrook 1991; Statler et al. 1996) and are attributable to *Thalassinoides* isp. Other ichnofossils reported from the cave system include pellets (presumably invertebrate fecal pellets) in the St. Louis Formation, Levias Member of the Ste. Genevieve Formation, and Beech Creek Member of the Girkin Formation (Chapter 3).

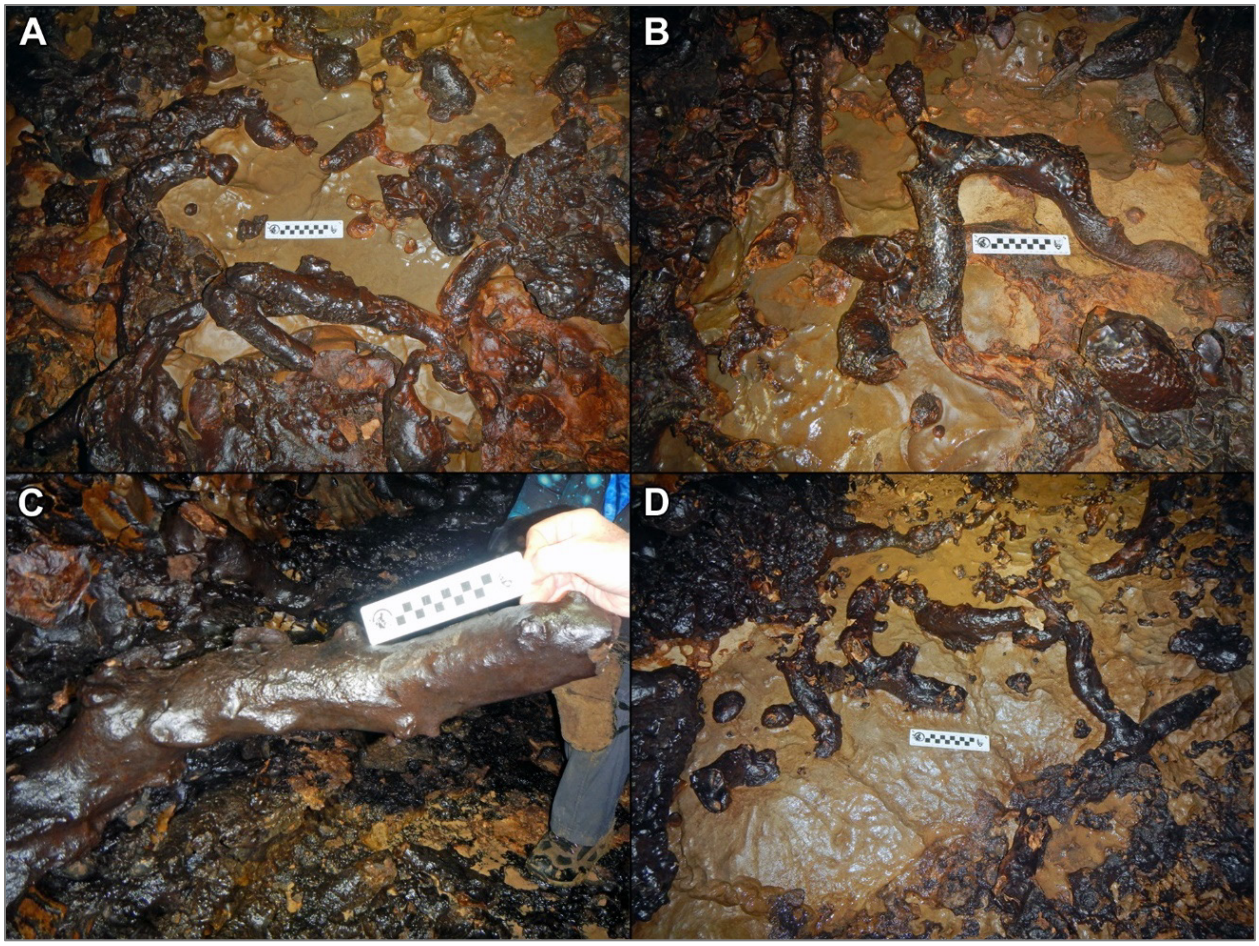


Figure 122. Several views of the unusually large invertebrate burrows (*Thalassinoides* isp.) in the St. Louis Formation at Logsdon River at P. Strange Falls. NPS



Figure 123. Burrow casts (*Chondrites* isp.?) weathering out of cave surfaces in Watson Trace, most likely upper Ste. Genevieve Formation. Burrow diameter approximately 1 cm (0.4 in). NPS / RICK OLSON

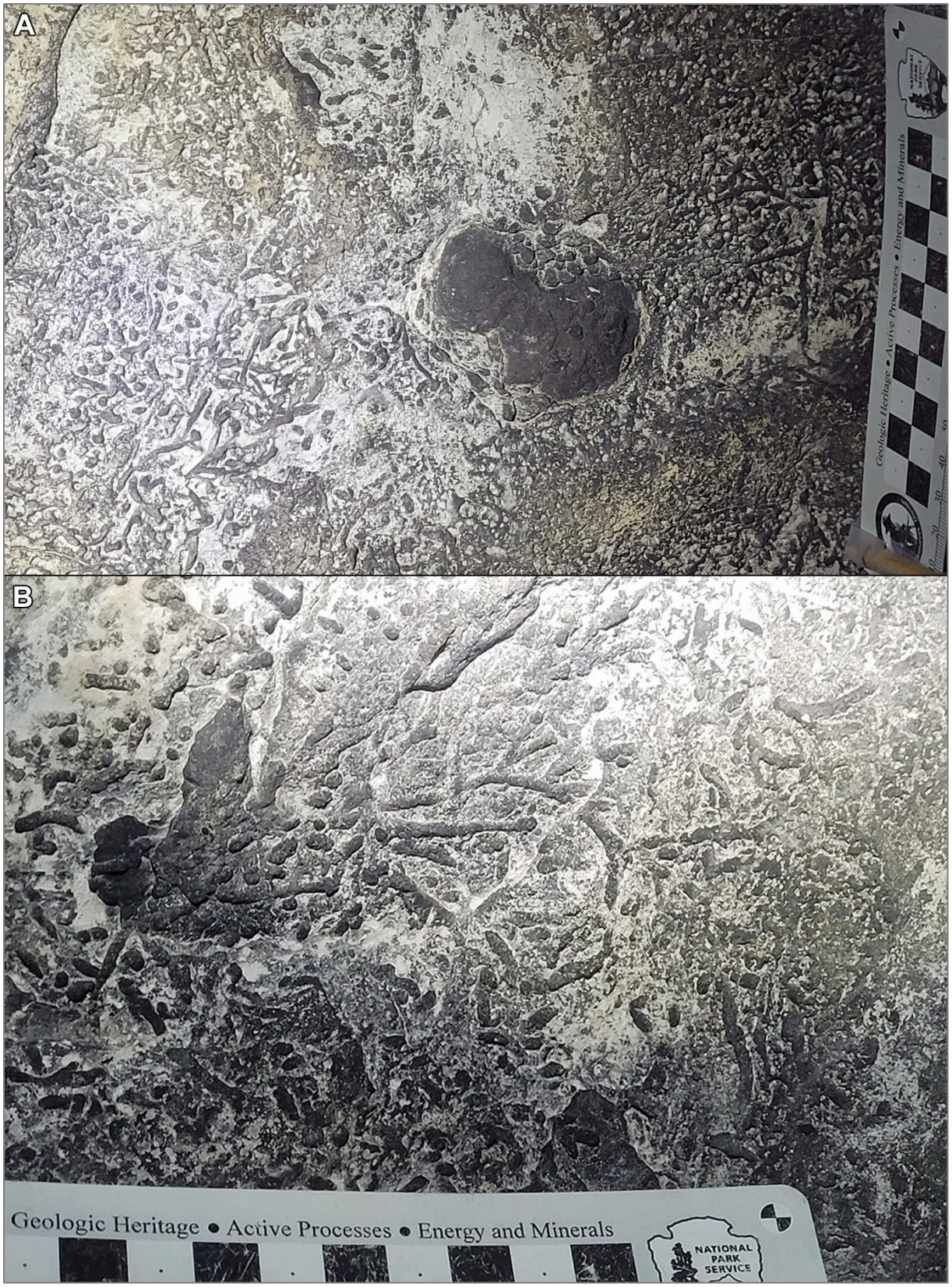


Figure 124. Invertebrate burrows (*Chondrites* isp.) at Top of the Corkscrew, Girkin Formation. They are figured here at medium (**A**) and close range (**B**). NPS / KELLI TOLLESON

Other Fossils

Finally, apart from unidentified invertebrates (it can be difficult to determine whether a poorly preserved shell fragment came from a brachiopod, bivalve, or gastropod, for example), there are a few types of fossils reported from MACA's bedrock that do not belong to the categories covered above or in other chapters.

The inventory team observed structures interpreted as large stromatiforms at Robertson Avenue (Ste. Genevieve Formation, Fredonia Member), Rhoda's Arcade (Ste. Genevieve Formation, Fredonia Member), and El Ghor (Ste. Genevieve Formation, Karnak Member) (Figure 125); these have apparently never been documented in the literature. These structures appear to be essentially stromatolitic but at a large scale. They strongly resemble spongiostromate stromatolites of similar age (Robert Blodgett, pers. comm., February 2024). A polished section from the margin of one section shows clotted, "cloudy" layering, consistent with this identification. Because the original spongiostromate stromatolite, *Spongiostromata*, may be a demosponge (Lee and Riding 2023, but see Neuweiler et al. 2023), the MACA features are tentatively described as stromatiforms rather than definite stromatolites pending more detailed analysis. Interestingly, separate from this assessment one of the reviewers noted that the photographed examples resemble stromatoporoid sponges, otherwise not known to have existed in this timeframe.

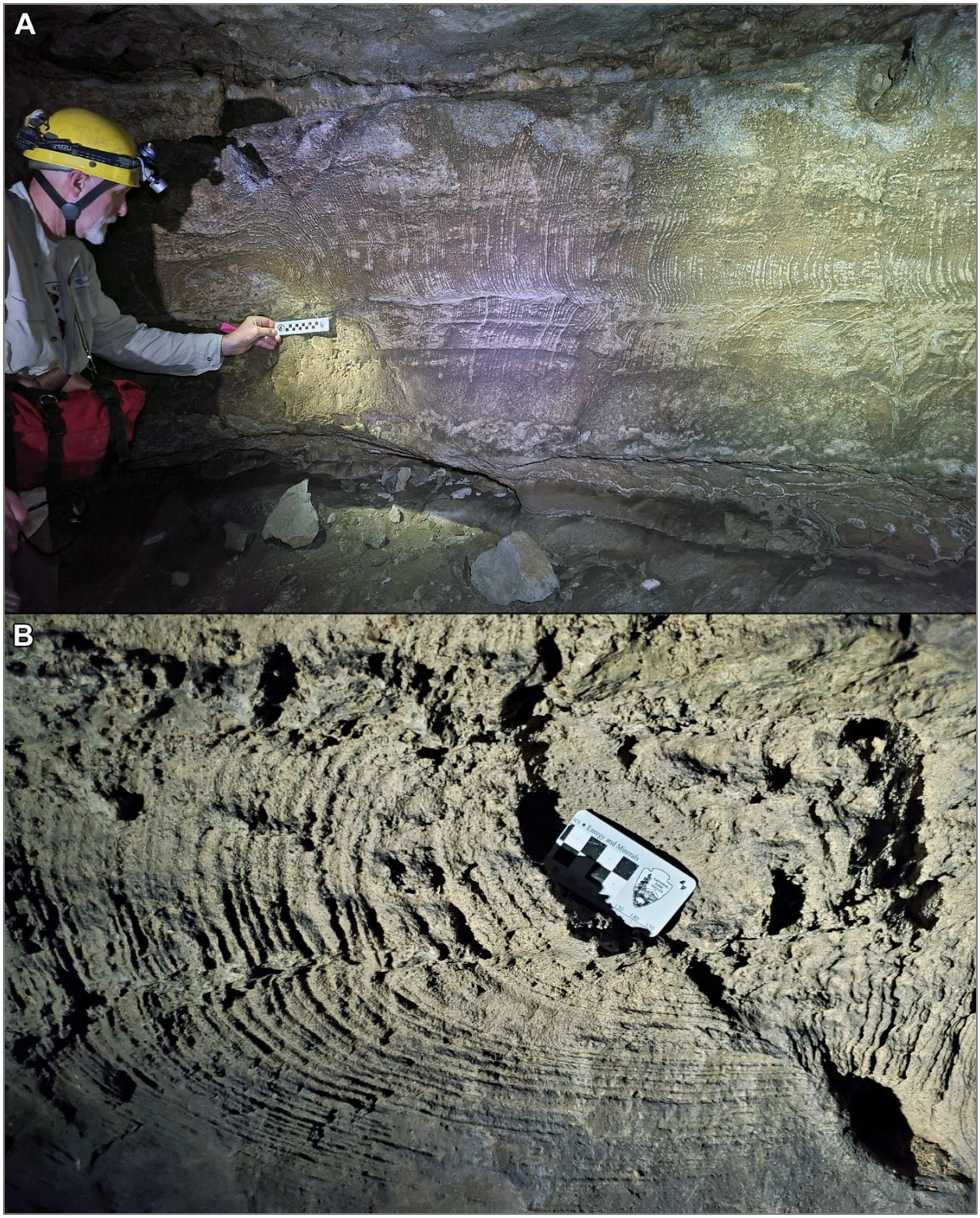


Figure 125. Large stromatiform structures in the Ste. Genevieve Formation. **A.** Rick Olson providing scale to an example in Robertson Avenue, Fredonia Member. **B.** An example in El Ghor, Karnak Member. **A:** NPS / KELLI TOLLESON; **B:** NPS / RICK OLSON

Conodonts were collected from sediments under the *Saivodus* in Specimen Avenue, in the J2 unit of the Joppa Member of the Ste. Genevieve Formation (Figure 126) (JP Hodnett, pers. comm., June 2023), but taxa were only identified to genus. Rexroad and Jarrell (1961) reported the presence of conodonts at a Girkin Formation (Beech Creek Member) site in MACA but did not provide any taxonomic identifications. Further collection and study of conodonts from MACA may provide useful biostratigraphic information.

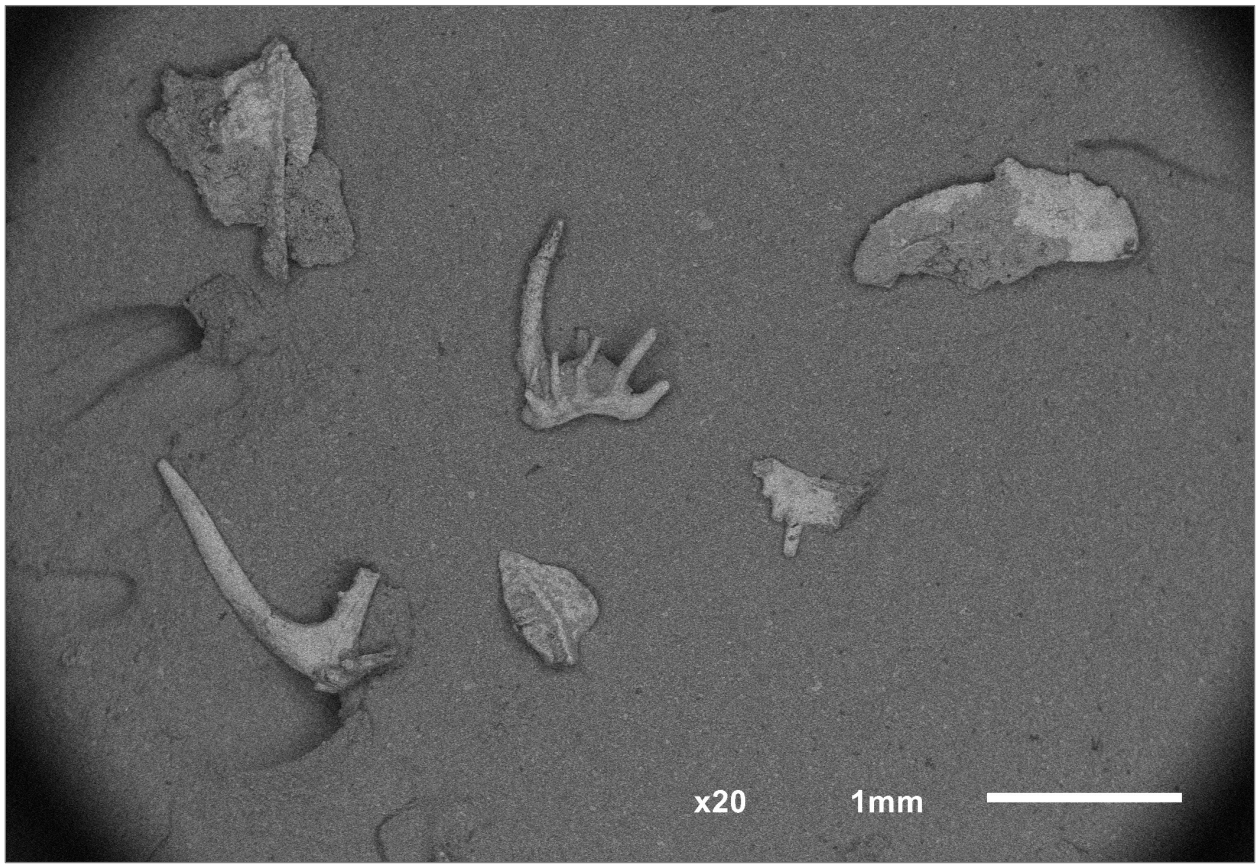


Figure 126. Conodont elements from the Ste. Genevieve Formation (Joppa Member, J2 unit), Specimen Avenue. Upper row, left to right: *Gnathodus*, *Prioniodus*, *Gnathodus*. Lower row: *Prioniodus*, *Gnathodus*, undetermined ramiform element (identifications by Lance Lambert, University of Texas at San Antonio, pers. comm. to JP Hodnett, June 2023). NPS / JP HODNETT

Algal (or microbial) structures including potential balls and filaments have been observed in thin sections of the St. Louis Formation (Chapter 3). Finally, foraminifera have been observed in thin sections from several geologic units, including the St. Louis Formation, Fredonia and Joppa Members of the Ste. Genevieve Formation, and the Bethel, Sample, and Beech Creek Members of the Girkin Formation (Chapter 3).

Conclusions

Paleozoic invertebrate fossils, ichnofossils, and microfossils represent diverse and important parts of the ancient ecosystems preserved in the strata of MACA. These fossils are the most common fossils

in Mammoth Cave. The invertebrate fossils reported in rock units in the cave system are typical of these units outside of it. Some of the fossils are typical of certain units and help to identify those units (biostratigraphy), and some are useful for interpreting the original environments in which the units were formed, long before the cave began to form in the units. Study of these fossils contributes an important key to the understanding of the natural history of the park.

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I would like to thank a number of paleontologists, geologists, and MACA staff for their comments and assistance on this chapter. First is the core team, JP Hodnett, Rick Olson, Vincent Santucci, Kelli Tolleson, and Rick Toomey. Other authors in this volume, Bill Ausich and Art and Peggy Palmer, contributed paleontological and geological information. Rich Boldon, Warren Briggs, Amber Flowers, Louise Hansson, Megan Harder, Edward Jakaitis, Lance Lambert, Terry Langford, Ljubomir Risteski, and others spotted and photographed notable fossils in the caves. Stephen Thomas, Cumberland Piedmont Inventory & Monitoring Network program manager, facilitated the review process. Norman Warnell provided historical information pertaining to sites. Jeff Thole (Macalester College) assisted with preparation of the stromatiform polished piece, and Robert Blodgett offered comments on the stromatiform's identity. Finally, reviewers Stephen Greb (Kentucky Geological Survey) and Alycia Stigall (University of Tennessee, Knoxville) greatly improved the final chapter with their thoughtful comments and suggestions.

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Appendix D: Paleozoic Invertebrate Taxa and Ichnotaxa

Table 5 below documents the fossil invertebrate taxa and ichnotaxa found at MACA in stratigraphic context, as reported in the literature, in museum collections, and through personal observations. Rows are organized systematically, placing taxa of the same broad groups together (first column), with summary rows for particularly diverse groups. The columns are organized by formation, which are presented in ascending order (oldest to youngest) left to right. Formations without relevant fossils are omitted. The columns also include the taxon (second column) and references (last column; included in “Literature Cited” above).

Table 5. Invertebrate taxa and ichnotaxa from MACA (see text that follows table for definitions of acronyms and codes).

Group	Taxon	Msl	Msg	Mg	Mgh	Mgd	References
Phylum Cnidaria: Class Anthozoa	**Anthozoa overall**	**Y**	**Y**	**Y**	**Y**	**Y**	**–**
	Anthozoa undetermined	–	1, 4	6	–	–	Chapter 3; inventory photos
Phylum Cnidaria: Class Anthozoa: Order Tabulata	*Syringopora* sp.	–	1, 4	–	–	–	Chapter 3; inventory photos
	Tabulata undetermined	–	4	–	–	–	BlackEagle 1989
Phylum Cnidaria: Class Anthozoa: Order Rugosa	*Acrocyathus floriformis*	Y	–	–	–	–	Pohl, written comm. 1935
	Amplexus geniculatus?	–	–	Y	–	–	Inventory photos
	Lithodrumus veryi	–	–	1, 3	–	–	Weller 1927; Pohl 1970; inventory photos
	Menophyllum princetonensis	–	4	–	–	–	Inventory photos
	Schoenophyllum aggregatum	–	1, 4, 6?	–	–	–	Chapter 3; inventory photos
	Zaphrentites spinulosum	–	–	–	Y	–	Pohl and Cushman 1964
	"*Triplophyllum* sp."	–	–	Yc	Yc	–	MACA collections
	Undetermined horn corals	Y	3, 4, 6	5, 0	–	Y	BlackEagle 1989; Chapter 3; inventory photos
	Branching colonial coral	–	–	1	–	–	Inventory photos
	Acrocyathus floriformis- or *Palaeosmilia*-like colonial rugose coral	–	4	1, Y	–	–	Inventory photos
	Rugosa undetermined	–	1, 3, 6	–	–	–	BlackEagle 1989
Phylum Bryozoa (moss animals)	**Bryozoan overall**	**Y**	**Y**	**Y**	**Y**	**Y**	**–**
	Archimedes sp.	–	–	Y	Y	Y	Inventory photos
	"*Batostomella* sp."	–	–	Yc	–	–	MACA collections
	Lyropora or *Lyroporidra*	–	1	Y	–	–	Inventory photos
	Encrusting bryozoan	–	–	Yc	–	–	MACA collections
	Fenestrida undetermined	–	4	4, 6, 0	Yc	–	Pohl and Cushman 1964; BlackEagle 1989; inventory photos, MACA collections

Table 5 (continued). Invertebrate taxa and ichnotaxa from MACA (see text that follows table for definitions of acronyms and codes).

Group	Taxon	Msl	Msg	Mg	Mgh	Mgd	References
Phylum Bryozoa (moss animals) (continued)	Lacy bryozoan	–	–	7	–	–	Inventory observations
	Stony bryozoan (Treptostomata)	–	–	Yc	–	Yc	MACA collections
	Sheet-like bryozoan	–	4	–	–	–	Inventory photos
	Bryozoa undetermined	Y	1, 2, 4, 6	1, 3, 4, 7	Yc	–	Chapter 3; MACA collections
	Bryozoa undetermined?	–	6?	–	–	–	BlackEagle 1989
Phylum Brachiopoda (lamp shells)	**Brachiopoda overall**	**Y**	**Y**	**Y**	**Y**	**Yc**	**–**
	Unspecified articulate brachiopods	–	1, 3, 4	Yc	–	–	BlackEagle 1989; MACA collections
	Brachiopoda undetermined 1 (D-shaped and smooth)	–	4	–	–	–	Inventory photos
	Brachiopoda undetermined 2 (finely ribbed)	–	4	–	–	–	Inventory photos
	Brachiopoda undetermined 3 (smooth shell)	–	3	–	–	–	Inventory photos
	Brachiopoda undetermined	Y	1, 2, 3, 4, 5	1, 3, 4, 6, 7	Y	–	Pohl and Cushman 1964; Chapter 3; inventory photos
Phylum Brachiopoda: Class Rhynchonellata	*Anthracospirifer leidyi*	–	4	7	–	–	Inventory photos; MACA collections
	Anthracospirifer pellaensis	–	4	1, 7	–	–	Weller 1927; Pohl and Cushman 1964; inventory photos
	Camarotoechia purduei	–	–	7	–	–	Weller 1927
	Cleiothyridina sublamellosa	–	3, 4	7	–	–	Weller 1927; inventory photos
	Cleiothyridina sp.	–	4	1	–	–	Weller 1927; inventory photos
	Composita subquadrata	–	–	5	–	–	Pohl and Cushman 1964
	"*Composita subtilita*"	–	–	Yc	–	–	MACA collections
	Composita trinuclea	–	3	1, 5, 7	Yc	–	Weller 1927; Pohl and Cushman 1964; MACA collections
	Composita sp.	–	1, 3, 4	Yc	–	–	Inventory photos; MACA collections

Table 5 (continued). Invertebrate taxa and ichnotaxa from MACA (see text that follows table for definitions of acronyms and codes).

Group	Taxon	Msl	Msg	Mg	Mgh	Mgd	References
Phylum Brachiopoda: Class Rhynchonellata (continued)	*Dielasma arkansanum*	–	–	1	–	–	Weller 1927
	Dielasma illinoisensis	–	–	7	–	–	Weller 1927
	Eumetria vera	–	–	7	–	–	MACA collections
	Girtyella indianensis	–	–	1, 7	Yc	–	Weller 1927; MACA collections
	Girtyella sp.	–	–	4	–	–	Pohl and Cushman 1964
	Martinia contracta	–	–	7	–	–	Weller 1927
	Punctospirifer sp.	–	–	Yc	–	–	MACA collections
	Reticulariina spinosa	–	4	5, 7	–	–	Pohl and Cushman 1964; inventory photos
	Spirifer increbescens	–	–	7	–	–	Weller 1927
	Spirifer sp.	–	3	Yc	–	–	BlackEagle 1989; MACA collections
	"*Spiriferina* sp."	–	–	4	–	–	Pohl and Cushman 1964
	Spiriferida undetermined	–	1, 3, 4	Yc	Yc	Yc	Inventory photos; MACA collections
Phylum Brachiopoda: Class Strophomenata	*Diaphragmus elegans*	–	–	7	Yc	–	Weller 1927; MACA collections
	Diaphragmus cf. *D. montesanae*	–	–	4	–	–	Pohl and Cushman 1964
	Diaphragmus sp.	–	–	Yc	–	–	MACA collections
	Inflatia inflata	–	–	7	Yc	–	Weller 1927; McGrain and Walker 1954; Pohl and Cushman 1964; MACA collections
	Linoproductus ovatus	–	–	1, 4, 7	–	–	Weller 1927; Pohl and Cushman 1964
	Orthotetes kaskaskiensis	–	–	7	–	–	Weller 1927
	"*Productus* sp."	–	–	1, 7	–	–	Weller 1927
	Schuchertella costatula	–	–	7	Yc	–	Weller 1927; MACA collections
	Productida undetermined	Y	4	7	Yc	–	Inventory photos and observations; MACA collections
	Strophomenida undetermined	–	–	–	Yc	–	MACA collections

Table 5 (continued). Invertebrate taxa and ichnotaxa from MACA (see text that follows table for definitions of acronyms and codes).

Group	Taxon	Msl	Msg	Mg	Mgh	Mgd	References
Phylum Mollusca	**Mollusca overall**	**Y**	**Y**	**Y**	**Y**	**Y**	**–**
	Mollusca undetermined	Y	1	–	–	–	Chapter 3
Phylum Mollusca: Class Bivalvia	*Aviculopecten* sp.	–	–	1	–	–	Weller 1927
	Leiopteria sp.	–	–	1	–	–	Weller 1927
	Bivalvia undetermined	–	1	7	–	–	Inventory photos
Phylum Mollusca: Class Cephalopoda	Coiled nautiloids	–	1, 4	–	–	–	Inventory photos
	Orthoconic nautiloids	Y	1, 4	Y	–	–	Inventory photos
	Orthoconic nautiloids?	–	–	7	–	–	Inventory observations
	Ammonoidea?	–	4	–	–	–	Inventory photos
Phylum Mollusca: Class Gastropoda	*Platyceras* sp.	–	4	Y*	–	–	Chapter 6; inventory photos
	Platyceras sp.?	–	4	–	–	–	Inventory photos
	Retispira ornatus?	–	4	–	–	–	Inventory photos
	Gastropoda undetermined 1 (bellerophont)	–	1, 4	1, 7	Y	–	Inventory photos and observations
	Gastropoda undetermined 2 (“ziggurat”)	–	4	Y	–	–	Inventory photos
	Gastropoda undetermined 3 (small, stacked high-coiling)	–	1, 4	–	–	–	Inventory photos
	Gastropoda undetermined 4 (large, stacked high-coiling)	–	–	–	–	Y	Inventory photos
	Gastropoda undetermined 5 (broad *Olivella* shape)	–	4	–	–	–	Inventory photos
	Gastropoda undetermined 6 (pyramidal)	–	1	–	–	–	Inventory photos
	Gastropoda undetermined 7 (planispiral or near-planispiral)	–	1, 4	–	Y	–	Inventory photos
	Gastropoda undetermined	–	2, 4, 0	6, 0	Y	Y	Pohl and Cushman 1964; Chapter 3; inventory photos

Table 5 (continued). Invertebrate taxa and ichnotaxa from MACA (see text that follows table for definitions of acronyms and codes).

Group	Taxon	Msl	Msg	Mg	Mgh	Mgd	References
Phylum Arthropoda	Trilobita: cf. *Kaskia chesterensis*	–	–	7	–	–	Inventory photos
	Trilobita undetermined	–	4	5, 6	–	–	Chapter 3; inventory photos
	Trilobita undetermined?	–	–	4	–	–	Chapter 3
	Ostracoda undetermined	Y	1, 4, 5	3, 4, 6, 7	–	–	Chapter 3
Phylum Echinodermata	**Echinodermata overall**	**Y**	**Y**	**Y**	**Y**	**Y**	**–**
	Echinodermata undetermined	Y	1, 4	2	–	–	Chapter 3; Chapter 6
Phylum Echinodermata: Class Blastoidea (sea buds)	*Pentremites abruptus*	–	–	–	Y	–	Pohl and Cushman 1964
	Pentremites godoni	–	4	Y	–	–	Chapter 6
	Pentremites pyriformis	–	4	Y	Y	–	Pohl and Cushman 1964; Chapter 6
	Pentremites tulipaformis	–	–	Y*	–	–	Chapter 6
	Pentremites sp.	–	–	Y*	Y*	–	Chapter 6; specimens in CMC and YPM collections
	Blastoidea undetermined	–	4	7, Y	–	Y	Inventory photos
Phylum Echinodermata: Class Crinoidea	*Agassizocrinus conicus*	–	–	–	Y	–	Pohl and Cushman 1964
	Agassizocrinus occidentalis	–	–	Y*	Y*	–	Chapter 6
	Agassizocrinus ovalis	–	–	–	Y	–	Pohl and Cushman 1964
	Agassizocrinus spp.	–	–	7	–	–	Pohl and Cushman 1964
	Culmicrinus missouriensis	–	4	–	–	–	Chapter 6
	Dinotocrinus huntsvillae	–	4	–	–	–	Chapter 6
	Eupachycrinus sp.	–	–	–	Y	–	Pohl and Cushman 1964
	Globocrinus unionensis	–	4	–	–	–	Chapter 6
	Onychocrinus magnus	–	4	–	–	–	Chapter 6
	Phanocrinus maniformis	–	–	Y*	Y*	Y*	Chapter 6
	Phanocrinus? *unusualis*	–	4	–	–	–	Chapter 6
	Platycrinites s.l. *penicillus*	–	4	?	–	–	Chapter 6

Table 5 (continued). Invertebrate taxa and ichnotaxa from MACA (see text that follows table for definitions of acronyms and codes).

Group	Taxon	Msl	Msg	Mg	Mgh	Mgd	References
Phylum Echinodermata: Class Crinoidea (continued)	*Pterotocrinus serratus*?	–	–	Y*	–	–	Chapter 6
	Talarocrinus cornigerus	–	–	1, Y*	–	–	Weller 1927; Chapter 6
	Talarocrinus sexlobatus	–	–	Y	–	–	Chapter 6
	?*Taxocrinus*	–	4	–	–	–	BlackEagle 1989
	Zeacrinites magnoliaeformis	–	–	Y*	–	–	Chapter 6
	Crinoidea undetermined	Y	1, 2, 3, 4, 5, 6	1, 2, 3, 4, 5, 6, 7	Y	Y	McGrain and Walker 1954; Pohl and Cushman 1964; BlackEagle 1989; Chapter 3; inventory photos and observations
Phylum Echinodermata: Class Echinoidea	*Melonechinus indianensis*	?	?	?	?	?	Chapter 6; USNM specimen (stratigraphy not known)
	Proterocidaridae undetermined	–	4	–	–	–	Chapter 6
	Echinoidea undetermined	Y	1, 2, 3, 4, 5, 6	1, 3, 6	–	–	Chapter 3; inventory photos
Undetermined invertebrates	Horn coral or *Platyceras*	–	–	–	Y	–	Inventory photos
	Lemon-shaped cross-sections (ostracods?)	–	–	Y	–	–	Inventory photos
	Spicules	Y	–	–	–	–	Chapter 3
	Tubular and tapering	–	4	–	–	–	Inventory photos
	Undetermined shells	–	4	–	–	–	BlackEagle 1989; inventory photos
Ichnofossils	Invertebrate burrows and likely invertebrate burrows	Y	1, 2, 3, 4	–	–	–	BlackEagle 1989; Chapter 3
	Chondrites isp.	–	4+?	Y	–	–	Inventory photos
	Thalassinoides isp.	Y	–	–	–	–	Statler et al. 1996; inventory photos
	Pellets	Y	6	7	–	–	Chapter 3
Other fossils: Phylum Chordata: Class Conodonta	*Gnathodus* sp.	–	4	–	–	–	L. Lambert, pers. comm. 06/2023 via JP Hodnett

Table 5 (continued). Invertebrate taxa and ichnotaxa from MACA (see text that follows table for definitions of acronyms and codes).

Group	Taxon	Msl	Msg	Mg	Mgh	Mgd	References
Other fossils: Phylum Chordata: Class Conodonta (continued)	*Prioniodus* sp.	–	4	–	–	–	L. Lambert, pers. comm. 06/2023 via JP Hodnett
	Conodonta undetermined	–	4	7	–	–	Rexroad and Jarrell 1961; L. Lambert, pers. comm. 06/2023 via JP Hodnett
Other fossils: Miscellaneous	"Algal" structures	Y	–	–	–	–	Chapter 3
	Foraminifera undetermined	Y	1, 4	2, 4, 7	–	–	Chapter 3
	Stromatiforms	–	1, 3	–	–	–	Inventory photos
	Unspecified fossils	–	4?, 6	5, 6	–	–	Pohl and Cushman 1964; BlackEagle 1989

The taxonomy should not be considered authoritative. It is likely that some of the genera and species cited here are duplicates due to different authors identifying the same forms using different names. In addition, genera and species are frequently synonymized or transferred to other taxa. This publication is not intended to settle usage, and comprehensive accounting of usage is beyond its scope; the rule of thumb is that the usage in the most recent publication is preferred, and any older usages in park literature are listed in the notes section following the tables. Exceptions to this "hands-off" policy include corrections of typographical errors. In some cases, a source included a non-standard, obsolete, or otherwise unconventional taxonomic usage that cannot be evaluated without further information; therefore, these records have been reproduced as originally presented. Similarly, some outdated names have been retained because it is not possible to determine a modern equivalent (for example, use of [*Genus*] sp. where [*Genus*] is historically species-rich and/or has a complex taxonomic history); examples have been marked with quotation marks. In addition, in the absence of photos or specimens, it is not possible to evaluate identifications made in publications, for example locality faunal lists, so names that may no longer be stratigraphically appropriate are retained. Identifications from photos have been primarily after Weller et al. (1920), Weller (1931), and Weller et al. (1952). Unidentifiable debris is omitted, as it will be present at a background level in any fossiliferous unit. The unique "Sloan's Valley" taxa in park collections have been omitted (see Appendix E in Chapter 6 for more information on this site).

Acronyms and Symbols

If a taxon is present in a given formation at a locality that can be placed within MACA, that cell is marked "Y" or with a number if a specific member is known (see below).

Occurrences of non-echinoderm taxa only attested in park collections are marked as "Yc"; this has been done because the taxonomic and stratigraphic identifications of these specimens are frequently provisional and informal. Echinoderms from MACA collections do not require this because they have been reidentified (Chapter 6).

If there is some question about the stratigraphic identification, the cell is marked "?".

If a taxon is not present in a given formation, the cell is marked "–".

Asterisks (*) in formation column cells denote specimens originating from MACA collections with inexact provenance information, requiring educated inference of the geologic unit; it is possible that some of the collections in question are stratigraphic composites.

Taxa in quotation marks are considered to be obsolete or stratigraphically unlikely, but have not been or cannot be evaluated.

Unit acronyms (after National Park Service 2022; "M" refers to "Mississippian", and the other letters indicate specific formations):

- Mgd = Glen Dean Formation
- Mgh = Haney Formation

- Mg = Girkin Formation
- Msg = Ste. Genevieve Formation
- Msl = St. Louis Formation

Both the Ste. Genevieve and Girkin Formations have several fossiliferous members at MACA. They are identified in the cells by number (ascending stratigraphic order, oldest to youngest) as follows:

Ste. Genevieve:

1. Fredonia
2. Spar Mountain
3. Karnak
4. Joppa
5. Aux Vases
6. Levias

Girkin:

1. Paoli
2. Bethel
3. Beaver Bend
4. Sample
5. Reelsville
6. Elwren
7. Beech Creek

For both, a record without a member from a reference that includes member-level stratigraphy for other records is marked with "0".

Taxonomic Notes

(old name → name used in table)

- *Bucanopsis ornatus* = *Retispira ornatus*
- Cryptostomata: records of cryptostome bryozoans (BlackEagle 1989) and lacy cryptostomates (MACA collections) are included as undetermined fenestellids because Fenestellida (also known as Fenestrida or Fenestrata) was formerly included in Cryptostomata.
- *Campophyllum gasperense* = *Lithodrumus veryi*; synonymization of this species (as *C. gasperense*) with *Lublinophyllum flaccidum* per Rodríguez and Kopaska-Merkel (2014) may

be correct, but both *C. gasperense* and *L. veryi* have priority over *L. flaccidum*, and *Lithodrumus* has priority over *Lublinophyllum*.

- *Lithostrotion canadensis = Acrocyathus floriformis*
- *Martinia sulcata = Martinia contracta*
- *Pentremites welleri = Pentremites pyriformis*
- *Platycrinus penicillus = Platycrinites penicillus*
- *Productus inflatus = Inflatia inflata*
- *Productus ovatus = Linoproductus ovatus*
- *Siphonodendron genevievensis = Schoenophyllum aggregatum*
- *Spirifer leidyi = Anthracospirifer leidyi*
- *Spirifer pellaensis = Anthracospirifer pellaensis*
- *Spirifer spinosa = Spiriferina spinosa = Reticulariina spinosa*
- *Triplophyllum spinulosum = Zaphrentites spinulosum* (after Rodríguez and Kopaska-Merkel 2014; this species has also been assigned to genera including *Triplophyllites*, *Zaphrentis*, and *Zaphrentoides*).
- "Undetermined horn corals" includes a record of *Streptelasma*? ("simple rugose corals") from the Karnak Member of the Ste. Genevieve Formation (BlackEagle 1989), because *Streptelasma* is an Ordovician–early Silurian genus and the name was used in a general sense.

Typographic Errors in MACA Files

- *Cliothyridina = Cleiothyridina*
- *Eupachicrinus = Eupachycrinus*
- *Martina = Martinia*
- *Talaracrinus = Talarocrinus*
- *Triplophillites = Triplophyllites*

Other Notes

Certain taxa are common in formations found in MACA, but have not yet been reported from the park, such as *Acrocyathus proliferum* (St. Louis Formation) and *Pugnoides* (a small brachiopod found in the Ste. Genevieve Formation). It is likely they will be found eventually. Park staff interested in fossils are suggested to familiarize themselves with figures in Weller et al. (1920), Weller (1931), and Weller et al. (1952), and Figure 65 in Sable and Devers (1990), a table of stratigraphically important Mississippian fossils of Kentucky ("WEST-CENTRAL" column, Glen Dean Limestone down to St. Louis Limestone).

Non-echinoderms in MACA collections should be re-evaluated, as some of the names are outdated or are used for taxa found in other geologic periods (e.g., *Batostomella*, *Spirifer*, *Triplophyllum*).

Taxa in MACA collections from "Sloan's Valley" are omitted (see also Chapter 6 for more discussion).

Chapter 6. Fossil Echinoderms of Mammoth Cave National Park

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Introduction

The cave system of Mammoth Cave National Park (MACA) was formed in massive Mississippian limestones and dolomites with certain beds containing abundant remains of fossil echinoderms, especially crinoids and the now-extinct blastoids (Palmer 2017; Chapter 3). These Mississippian limestones were deposited between ~340–325 million years ago when broad, shallow, tropical seas covered much of the central United States (a geologic time scale is included as an appendix to this inventory, Appendix I). During the Mississippian, central Kentucky was located at approximately 15° south paleolatitude (Scotese 2001). In comparable settings today, environments commonly have a coral reef separating a shallow lagoon landward from deep ocean waters seaward. During the Mississippian shallow-water coral reefs did not exist (Copper 1994). Consequently, Mississippian shallow-water tropical and subtropical environments were broad, gradually deepening shelves (Wright and Faulkner 1990). Abundant seashells along tropical and subtropical beaches today are bivalves (clams) and gastropods (snails), but during the Mississippian the most abundant organisms were brachiopods, bryozoans, crinoids, blastoids, and solitary corals (Chapter 5).

The volumetrically dominant fossil remains in many Mississippian limestones are the disc-shaped pieces (columnals) of crinoid and blastoid columns (Phylum Echinodermata, Classes Crinoidea and Blastoidea, respectively). In environments where crinoids were superabundant, the sea floor must have been dominated by crinoid columnals, and the resultant rock is called an encrinite (Ausich 1997). Many of the Mississippian rocks in central Kentucky are encrinites. In addition to crinoids and blastoids, sea urchins (Phylum Echinodermata, Class Echinoidea) are also preserved in Mississippian rocks of the MACA region.

An interesting historical note is that the blastoids and crinoids from Kentucky are among the earliest fossils described from North America. As noted in Chapter 5, Mitchill (1808, 1818) described and illustrated what may be the first fossils from Mammoth Cave, referring to them as “echinus,” although the provenance is controversial. These fossils are now recognized as the blastoid *Pentremites godoni. Pentremites godoni* was formally described by Defrance in 1819 (as *encrina Godonii*), and the genus *Pentremites* was described by Say (1825). Also, as noted below, the majority of crinoid species known from the MACA region were described during the middle 19th century.

This chapter is a brief, general introduction to crinoids, blastoids, and echinoids and a guide to the common echinoderms in the MACA region (Figures 127 to 129). Twelve species assigned to 10 genera of crinoids, three species assigned to one blastoid genus, two echinoid species, and numerous echinoid spines are identified from cave walls and surface exposures within the park or from

locations immediately adjacent to MACA. An additional genus and four species of echinoderms are present in MACA collections from a location interpreted as Sloans Valley in southeastern Kentucky.

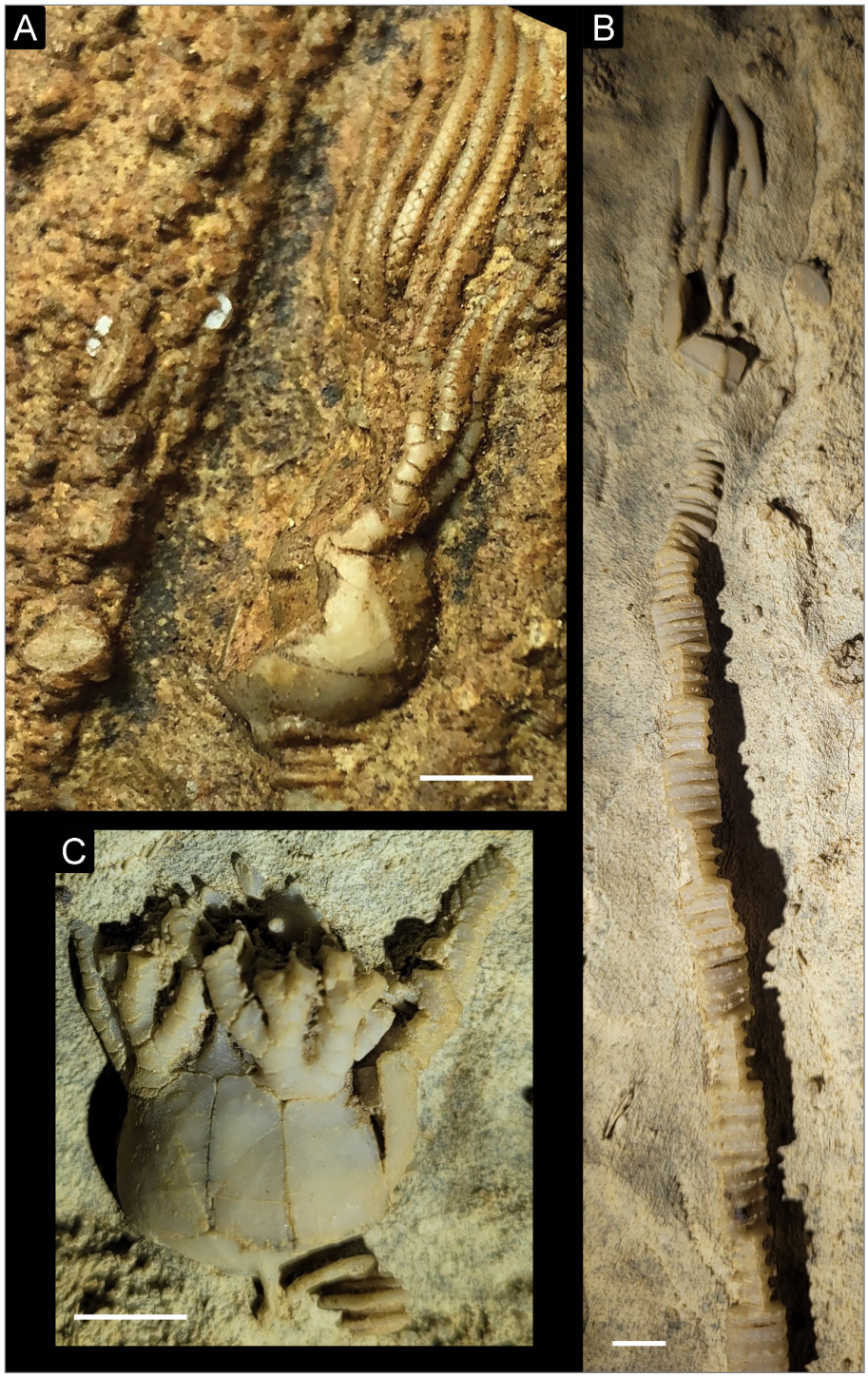


Figure 127. Photographs of *Platycrinites* s.l. *penicillus* preserved in cave walls; specimens illustrate various states of preservation. All scale bars 5 mm (0.2 in). **A.** Partially broken specimen; note biserial brachials and elliptical columnal in lower left portion of the image. **B.** Aboral cup, lower arms, and upper columnals; compare uppermost columnals to other specimens (Colossal Cave, Ste. Genevieve Formation). **C.** Specimen with a high height of the column preserved as well as some arms; the aboral cup is partly disarticulated; (Colossal Cave, Ste Genevieve Formation). **A:** NPS; **B, C:** NPS / KELLI TOLLESON

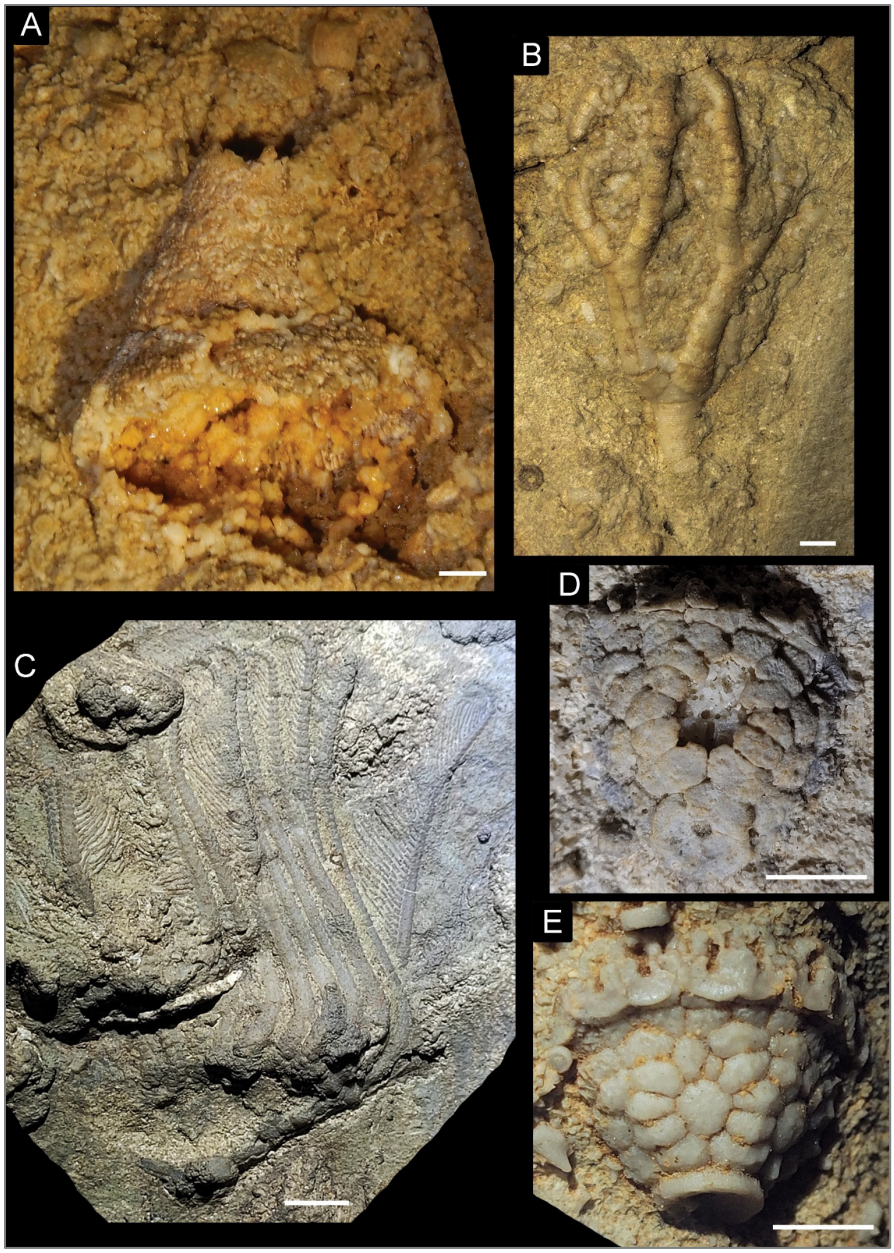


Figure 128. Photographs of crinoids preserved in cave walls. Note the small individual echinoderm plates that are common in the rock surrounding the complete and partially complete specimens. All scale bars 5 mm (0.2 in). **A.** Broken specimen of *Globocrinus unionensis*; the calyx has a low cone shape, but it is broken; the light orange-colored crystals grew within the calyx after burial; the tegmen is a high conical shape and is mostly intact (Echo Passage of Long Cave, Joppa Member, Ste. Genevieve Formation). **B.** Crown and upper column of *Onychocrinus magnus*, arm branching occurs high along the arms (Colossal Cave, Joppa Member; Ste. Genevieve Formation). **C.** Partial crown of *Globocrinus unionensis*; the partial calyx is low cone shaped, and several arms are very well preserved (Colossal Cave, Joppa Member, Ste. Genevieve Formation). **D.** Incomplete calyx of *Globocrinus unionensis*; note the low basal circlet with indentations at the basal plate-basal plate sutures (Cox Avenue, Joppa Member, Ste. Genevieve Formation). **E.** *Globocrinus unionensis*, calyx with well-preserved surface texture on the outer surface of calyx plates (Cox Avenue, Joppa Member, Ste. Genevieve Formation). **A:** NPS; **B–E:** NPS / KELLI TOLLESON

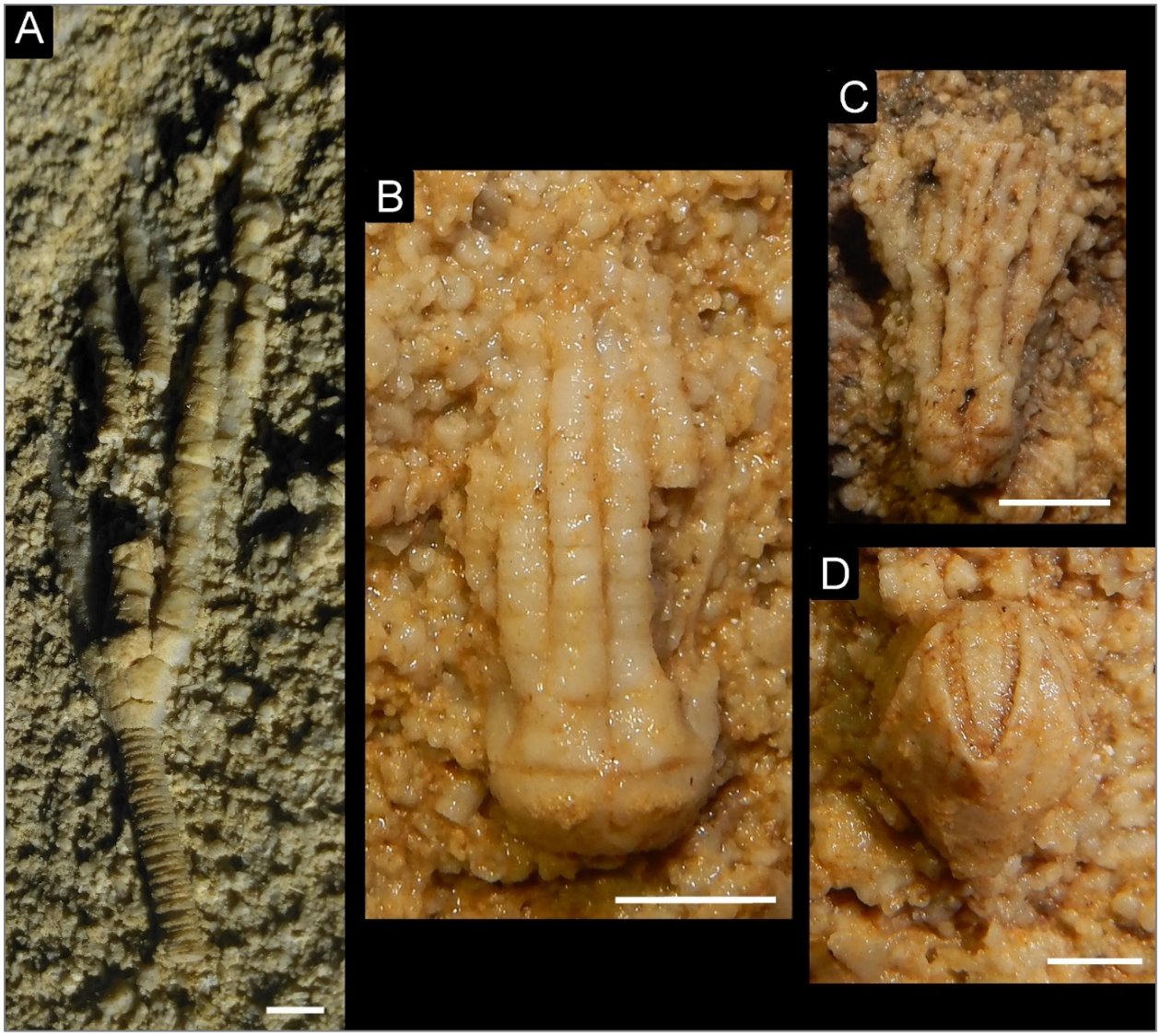


Figure 129. Photographs of eucladids and a blastoid preserved in cave walls. Note the small individual echinoderm plates that are common in the rock surrounding the complete and partially complete specimens. All scale bars 5 mm (0.2 in). **A.** *Culmicrinus missouriensis*; note the first brachial plate does not branch, instead arms branch higher up along the arms; photographed along Specimen Avenue (Joppa Member, Ste. Genevieve Formation). **B.** *Phanocrinus*? *unusualis*; note the arms branch on the first brachial plate (Echo Passage of Long Cave, Joppa Member, Ste. Genevieve Formation). **C.** *Dinotocrinus huntsvillae*; note small nodes or small spines on brachials (Echo Passage of Long Cave, Joppa Member, Ste. Genevieve Formation). **D.** Juvenile specimen of *Pentremites pyriformis* (Echo Passage of Long Cave, Joppa Member, Ste. Genevieve Formation). NPS

Methods

Fossil specimens under consideration herein were collected and/or photographed over many years by employees and volunteers of MACA. They include specimens from surface outcrops as well as limestone exposures within the caves. MACA collections primarily include specimens from the property of MACA and immediately adjacent property, and mostly represent surface outcrops

pertaining to higher stratigraphic units, whereas photographed specimens are primarily from cave walls and represent lower stratigraphic units. The provenance of one locality is equivocal, but the specimens from this site are included for completeness and reference. The vast majority of collected specimens, as well as those in cave walls, are individual columnals or pluricolumnals (one or more columnals preserved together). Although commonly called crinoid columnals, in most cases it is not possible to differentiate crinoid columnals from blastoid columnals. The classification of crinoids and blastoids to genus and species is based on features of the crown and thecae, respectively (see below); unfortunately, except for a few extreme morphologies, Mississippian columnals cannot be assigned to genera and species. Therefore, in this text, columnals and pluricolumnals that cannot be assigned to a genus or species will be referred to as pelmatozoan columnals, where "pelmatozoan" is the group name that includes both crinoids and blastoids. Identifications of crinoids and blastoids were verified using primary paleontological literature, as noted below. The most current genus and species names for crinoids were verified using Webster (2014) and more recent primary literature. Specimens were photographed using various methods, including wet and dry specimens underground on cave walls (Figures 127 to 129). Specimens from surface outcrops were photographed in the laboratory either uncoated or coated with ammonium chloride. A thin coating of ammonium chloride sublimate on a specimen accentuates the relief on the fossil for black and white photography. Figure captions indicate the conditions under which each photograph was taken. All specimens, except one, discussed herein are from collections housed at MACA, which also is the acronym preceding specimen numbers; for identifications see Appendix E. The additional specimen is housed in the United States National Museum/Smithsonian Institution (USNM).

Crinoids, Blastoids, and Echinoids

Living echinoderms include the Class Asteroidea (starfish), Class Crinoidea (feather stars and sea lilies), Class Echinoidea (sea urchins and sand dollars), Class Holothuroidea (sea cucumbers), and Class Ophiuroidea (brittle stars). Extant echinoderms live exclusively in ocean waters, and this was true throughout their evolutionary history. Today echinoderms are distributed in the oceans from the northern polar regions to the southern polar regions and from intertidal pools to great ocean depths. They are more common and abundant in environments with low concentrations of mud and silt deposition, such as settings where modern-day sediments would become limestone rocks, like those in The Bahamas (Zeiller 1974) and the Great Barrier Reef of Australia.

Despite the wide array of body shapes and lifestyles among echinoderms, they all share a suite of characteristics that are distinct from all other organisms, thus defining the Echinodermata as a distinct evolutionary group of organisms (Margulis and Chapman 2009). All echinoderms have a mesodermal skeleton comprised of numerous plates. During life the chemical composition of each plate is high-magnesium calcite; and each plate is constructed of stereom microstructure, which is a porous network of calcite (Figure 130A). All echinoderms have a water vascular system that is a fluid-filled tubular network used for respiration, feeding, and/or locomotion. The peripheral extensions of the water vascular system are tube feet. In starfish, the ends of the tube feet are small suckers that can be used to cling to the glass sides of aquaria. Echinoderms do not have a centralized brain. Instead, they have a diffuse nervous system that modulates bodily functions, including feeding, crawling, and even swimming.

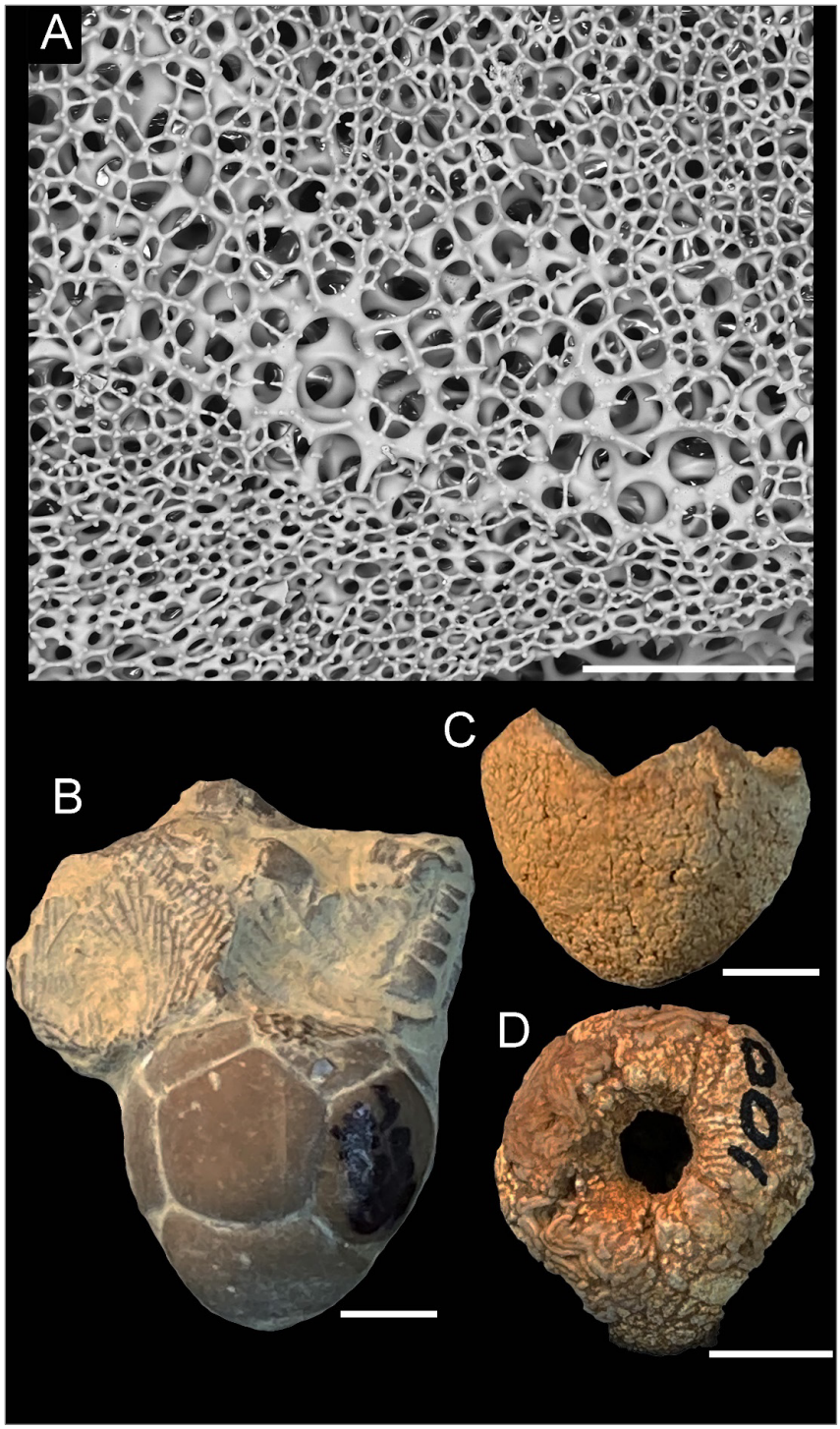


Figure 130. Microstructure and preservation of crinoids. **A**. Stereom microstructure of the extant crinoid *Metacrinus* sp. (scale bar 100 µm [0.004 in]). **B.** Lateral view of *Agassizocrinus occidentalis* with well-preserved calcite plates (MACA 36313; scale bar 5 mm [0.2 in]) (locality unknown). **C.** Lateral view *Agassizocrinus occidentalis* infrabasal cone with calcite plates replaced with a coarse, granular textured quartz (MACA 36284; scale bar 5 mm [0.2 in]) (Girkin Formation). **D.** Basal view of *Zeacrinites magnoliaeformis* with calcite plates replaced with coarse swirled textured quartz (MACA 36288; scale bar 5 mm [0.2 in]) (Girkin Formation). **A:** J. SHEETS; **B–D:** © WILLIAM AUSICH

The five extant echinoderm classes are a mere shadow of the total echinoderm biodiversity that occurred during geologic history. The oldest echinoderms are from near the beginning of the Cambrian (beginning of the Paleozoic) ~540 million years ago (mya). Cambrian echinoderms were an important part of the evolutionary radiation of skeletonized marine life during the Cambrian, and echinoderms were also an important aspect of the "Great Ordovician Biodiversification Event" (Webby et al. 2004) (~465 mya), which was witness to the evolution of the major groups of life that would dominate the ocean floor for the remainder of the Paleozoic (until ~259 mya). At least 25 class-level echinoderm groups evolved during the Cambrian and Ordovician, including all five living classes (Deline et al. 2020). The maximum number of co-existing echinoderm classes occurred during the Middle Ordovician, and since that time the number of living classes has dwindled to the present-day five classes.

Crinoids

The Mississippian has been called the "Age of Crinoids" (Kammer and Ausich 2006), because crinoid peak biodiversity occurred during this time and because in many environments crinoids were the dominant organisms. Blastoid biodiversity and abundance also peaked during the Mississippian, so the conditions that enabled the spectacular biodiversity and abundance of crinoids also enabled significant success among blastoids (Sallan et al. 2011; Ausich and Kammer 2013; and Meyer and Waters 2022). As noted above, in some shallow marine settings, the entire shelf was dominated by crinoids and blastoids, to the extent that crinoid fossils are the dominant remains in the resulting rocks. Extensive rock deposits such as this are called regional encrinites (Ausich 1997).

A detailed description of echinoderm morphology is beyond the scope of this report, but a few basics are needed to understand these fossils. More details are available in Ubaghs (1978), Beaver (1967), and Hess et al. (1999).

A basic crinoid is comprised from top to bottom of arms, tegmen (or oral surface), aboral cup (and/or calyx), column, and holdfast (Figure 131). The arms, tegmen, and aboral cup together make up the crown. The arms are used for feeding and respiration. Arms may branch once or many times, but they can also be unbranched. The plates in the arms are called brachials. They may form a single column of plates (uniserial brachials) or a column of plates in a series of two plates (biserial brachials) (Figures 131A and 121B). An arm may branch in various ways, with pinnulation being a distinctive type in which very fine branches (pinnules) are present on each brachial plate. Individual arms articulate with the radial plates. Radial plates are the top part of the crinoid aboral cup. The aboral cup is comprised of either two or three circlets of plates. If present, the infrabasal plate circlet is at the base of the aboral cup and articulates with the column. The basal plate circlet is either above the infrabasal plate circlet or at the base of the aboral cup and articulates with the column. The radial plate circlet is above the basal plates and, as noted above, articulates with the arms (Figure 131). The typical number of plates in each plate circlet in the aboral cup is five, and each circlet is typically offset by 36° from subjacent (lower) plates. However, the lowest plate circlet (either infrabasal or basal plates) may have a reduced number of plates. The first plate of each arm may move freely on a radial plate or one or more non-moveable arm plate(s) may be fixed into the calyx. In the latter, the portion of the crinoid between the position where arms become free and the column is called the

calyx. If the arms are free immediately above the radial plates, the aboral cup is equivalent to the calyx. In camerates and a few eucladids, the aboral cup is covered by a solidly plated structure called a tegmen. Tegmens are variable in size and shape, and the tegmen covers the mouth. In contrast the mouth is exposed in many other crinoids. Such crinoids are considered to have an oral surface rather than a tegmen.

As noted above, the column is comprised of numerous individual columnals. Typical Mississippian columnals are circular in outline (Figures 131 to 133), but columnals with elliptical, pentagonal, and pentalobate outlines are also known (Figure 132A). A single plate from the column is called a columnal, and two or more attached columnals are called pluricolumnals (Figures 133F to 133H). The base of the column is the holdfast, which is an attachment structure to anchor the crinoid into or onto the sea floor (Figure 132B).

Mississippian crinoids are divisible into four primary groupings that are distinct evolutionary lineages. These are camerates, disparids, flexibles, and eucladids (Wright et al. 2017); a classification is included below for reference. This classification of the Crinoidea follows Cole (2017, 2018), Wright (2017a, b), and Wright et al. (2017). It more closely follows our current understanding of the phylogeny of crinoids than that used in Moore and Laudon (1978).

- Class Crinoidea Miller, 1821
    - Subclass Camerata Wachsmuth and Springer, 1885
    - Subclass Pentacrinoidea Jaekel, 1894
        - Infraclass Inadunata Wachsmuth and Springer, 1885
            - Parvclass Disparida Moore and Laudon, 1943
            - Parvclass Cladida Moore and Laudon, 1943
                - Superorder Flexibilia Zittel, 1895
                - Magnorder Eucladida Wright, 2017a
                - Superorder Cyathoformes Wright, 2017b
                - Superorder Articuliformes Wright, 2017b

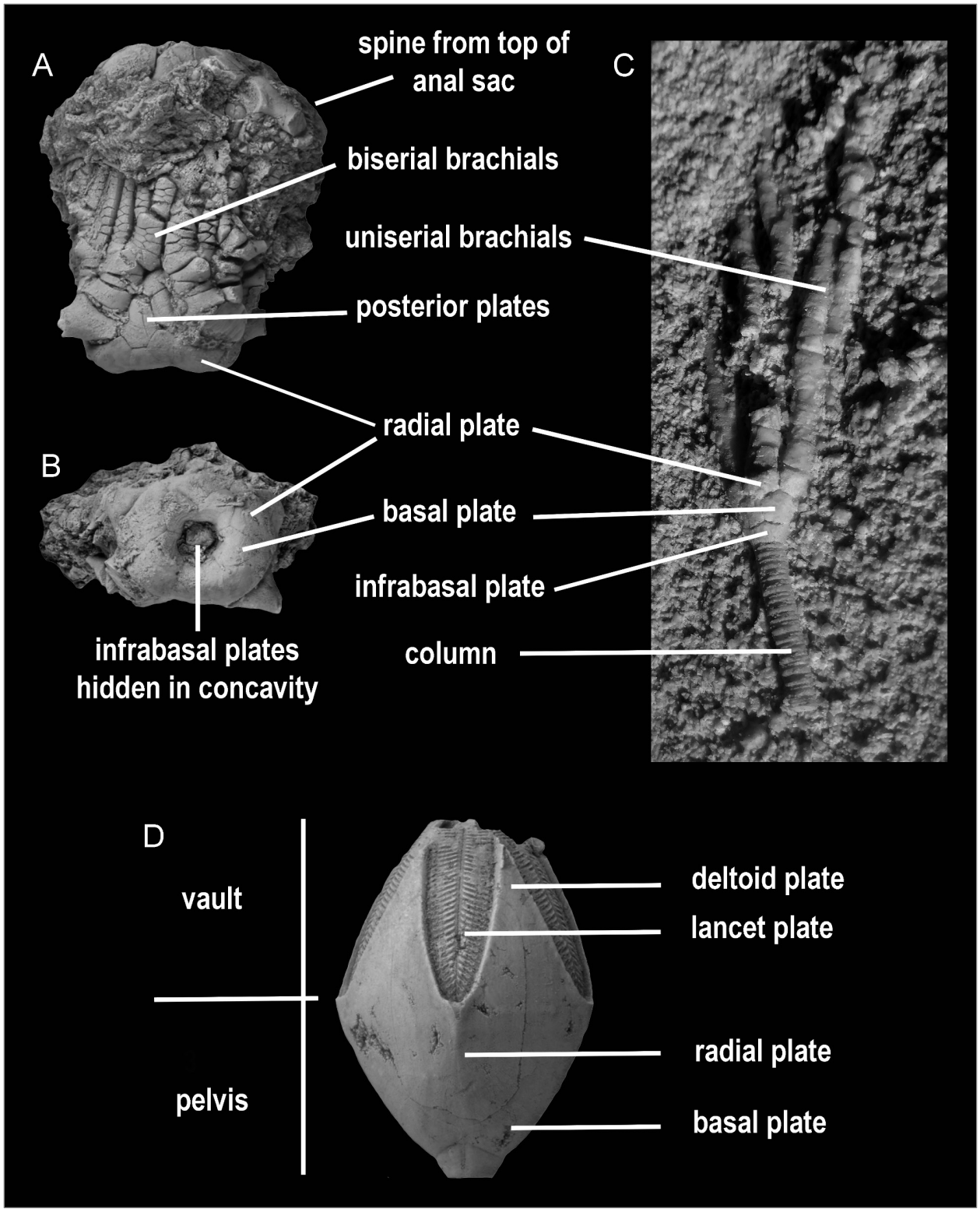


Figure 131. Explanation of morphological features of crinoids and blastoids as discussed in this chapter. All specimens coated with ammonium chloride. **A, B.** *Tholocrinus spinosus*. **C.** *Culmicrinus missouriensis*. **D.** *Pentremites pyriformis*. © WILLIAM AUSICH

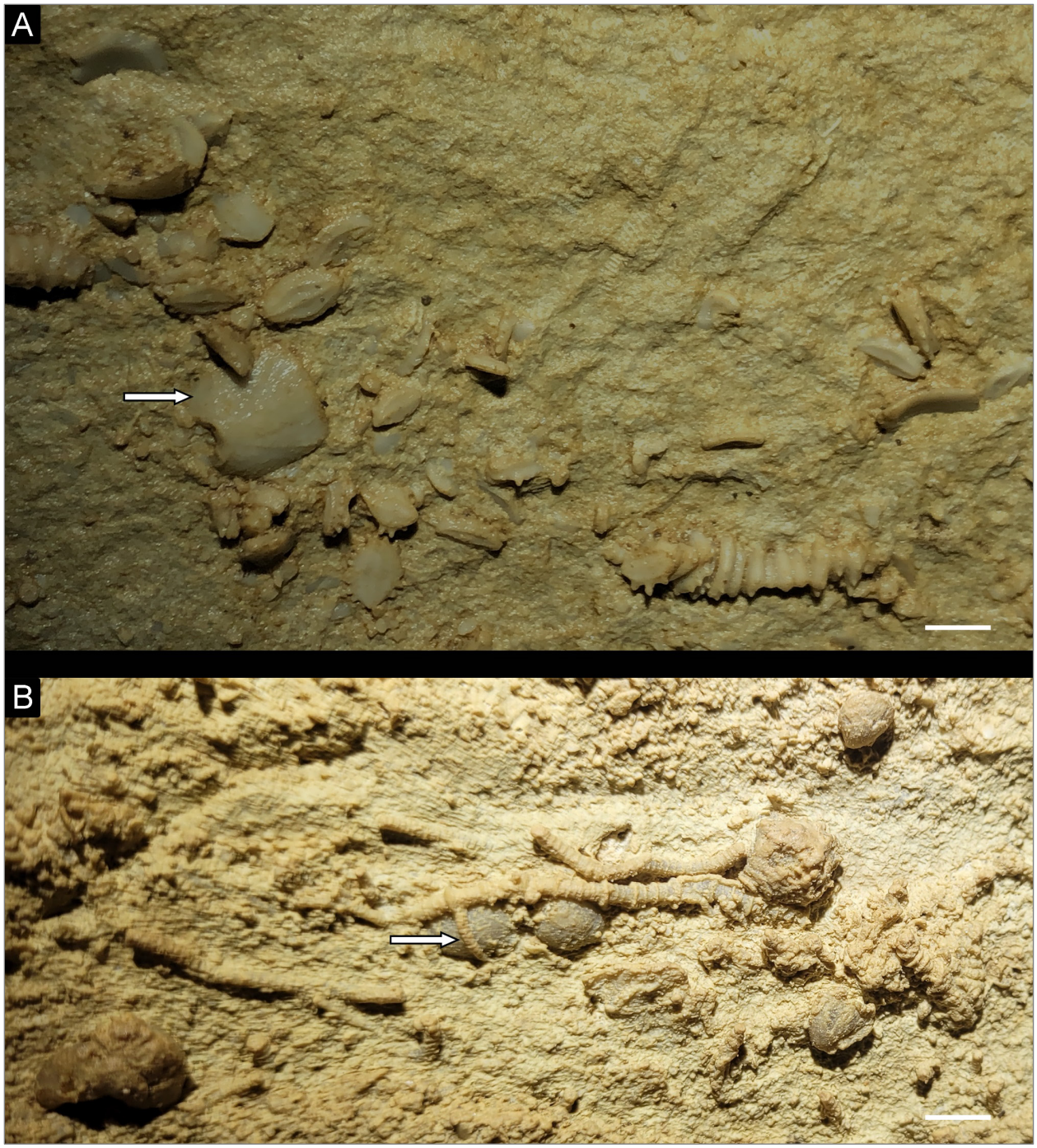


Figure 132. Pluricolumnals, columnals, and calyx plates from the walls of Mammoth Cave. Scale bars 5 mm (0.2 in). **A.** Disarticulated remains of *Platycrinites* s.l. *penicillus*; arrow points to a radial plate, the convex indentation on the left side of this plate is the radial facet, which is the position where arms articulate to the calyx; other plates are columnals in various orientations and pluricolumnals of various height. Note the short spines around the periphery of some of the elliptical columnals (Great Onyx Cave, Joppa Member, Ste. Genevieve Formation). **B.** Pluricolumnals from the distal portion of an unknown crinoid. These pluricolumnals have attached radices (branches from the column), indicating this is the holdfast that anchored a living specimen into the substratum (Great Onyx Cave, Joppa Member, Ste. Genevieve Formation). NPS / KELLI TOLLESON

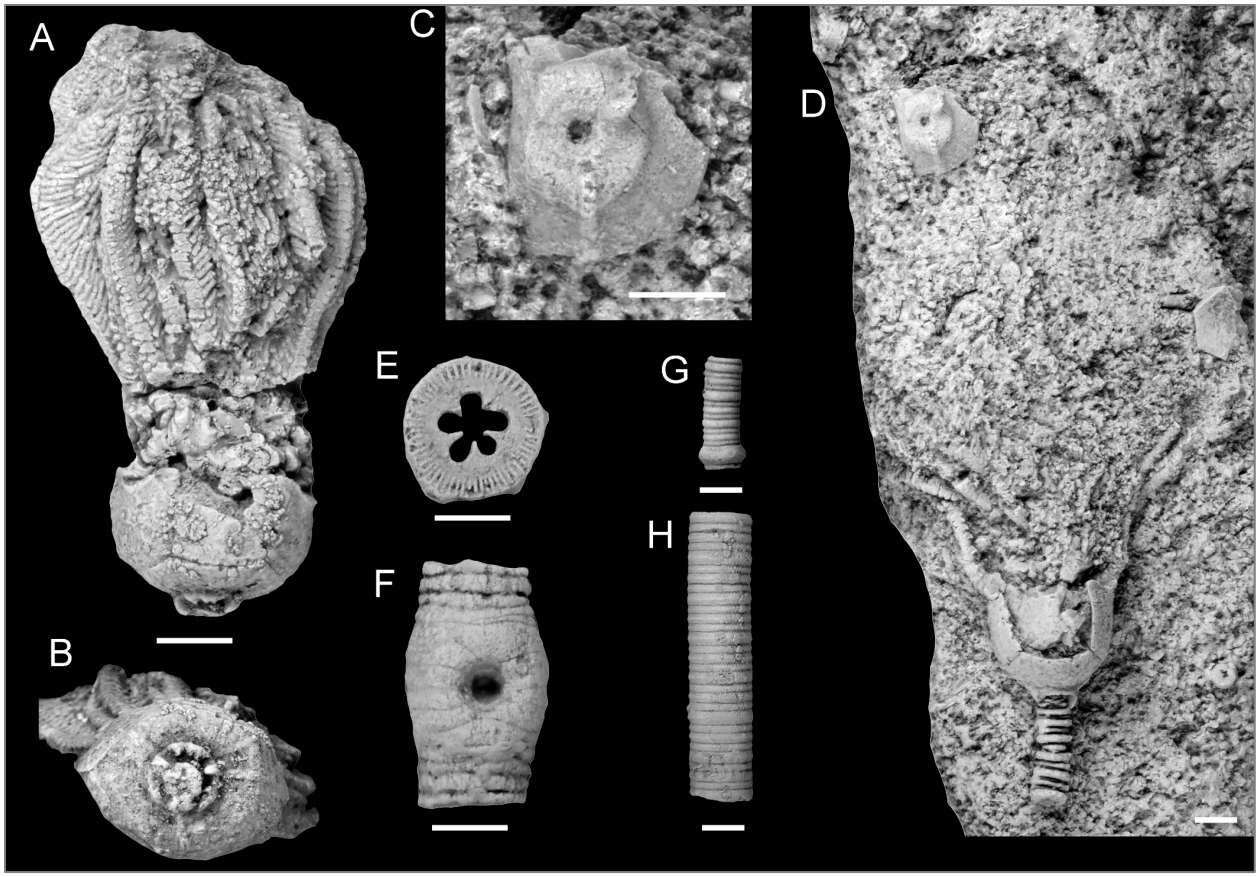


Figure 133. Camerate crinoids from the Mammoth Cave region. Specimens photographed with ammonium chloride coating, scale bars 5 mm (0.2 in). **A**–**D.** *Platycrinites* s.l. *penicillus* (**A, B:** MACA 3203; **C, D:** MACA 62995) (locality unknown). **A.** Side view of a nearly complete calyx; note the biserial brachials and pinnules that branch from brachials. **B.** Basal view showing ridges that diverge away from the column attachment. **C.** Enlargement of the isolated basal circlet in **D** with ridges that divert away from the column attachment. **D.** Side view of a partial specimen with the basal circlet of a different individual in the upper left and enlarged in **C**. **E.** Facet of a circular columnal, with narrow crenulations around the periphery and a pentalobate lumen (MACA 36337) (locality unknown). **F.** Pluricolumnal with a central pit surrounded by swelling, which is thought to be a reaction to a parasite (MACA 36311) (locality unknown). **G, H.** Pluricolumnals with varying height of columnals (MACA 36309 [locality unknown] and MACA 36343 ["1 mile west" of Auburn, Kentucky, Girkin Formation], respectively). © WILLIAM AUSICH

Camerate crinoids typically have lower arm plates cemented into the calyx, but *Platycrinites* s.l. is an exception (The "s.l." in the name *Platycrinites* s.l. *penicillus* is an abbreviation for *sensu lato*, "in the broad sense", and indicates that important aspects of the morphology are unknown so that definite assignment to *Platycrinites* is not possible [Ausich and Kammer 2009]). The arms of Mississippian camerates have biserial brachial plates and pinnules. All of the camerates described here only have two circlets of plates (basals and radials) in the aboral cup.

Mississippian disparids are rare in rocks of the age present in the MACA region. They are typically small and have thin unbranched arms. Although undoubtedly present, to date no disparids have been collected.

As the name implies, the arms and calyx of flexibles are loosely sutured, thus preservation is less likely. They have three circlets of plates in the aboral cup and relatively thick arms with uniserial brachials and no pinnules.

Eucladids are the most diverse group of crinoids during the time when limestones formed in the MACA region. They typically have relatively small cone- or bowl-shaped aboral cups with three circlets of plates. Arms are pinnulate and typically have only uniserial brachial plates (Figures 129B and 131C), although *Tholocrinus* has biserial arms (Figure 131A). The number of arm branches on eucladids varies from few to many.

Blastoids

Blastoids are an extinct class of echinoderms. They are superficially similar to crinoids because they have feeding appendages attached to the main body of the animal that was elevated above the sea floor by a column. However, in detail, blastoids are quite distinct from crinoids (Sprinkle 1987). The feeding appendages are brachioles that are always unbranched and very narrow. It is improbable that brachioles supported the water vascular system like the arms of crinoids. The body of a blastoid is called a theca, and it is comprised of 18 primary plates arranged in four circlets (Figure 131D). The base of the blastoid theca is a circlet of three basal plates, and above the basal plates is a circlet of five radial plates. Each radial plate has a deep central indentation into which is inserted a lancet plate (five total). Brachioles attach to the lancet plates. Five deltoid plates are present in the fourth circlet. Each deltoid plate is positioned on the upper shoulders of two adjacent radial plates and is separated from the adjacent deltoid plates by the lancet plates. Despite a consistent structure of 18 primary plates, blastoid thecae evolved a wide array of shapes by varying the size and shape of these plates. Blastoids have unique internal, infolding structures called hydrospires (Beaver 1967; Waters et al. 2017). Hydrospires have openings along the lancet plates and at the summit of the theca. Hydrospires are thought to have been used for respiration. The blastoid theca is connected to a column, which as in crinoids is comprised of columnals; and the terminus of the blastoid column is a holdfast. Although little is known about blastoid columnals relative to crinoid columnals, blastoid columnals are typically circular.

As a whole, blastoid thecae are divisible into four primary shapes. The two that are relevant for MACA region blastoids are pyriform (pear-shaped with a slender base) and godoniform (with a broader base) (Beaver 1967). In pyriform blastoids the lancet plates are approximately one-half of the thecal height, and the basal plates form a significant part of the thecal height. In contrast, godoniform blastoids are subglobose with the lancet plates forming the vast majority of the thecal height, and basal plates are very low and may not be visible in lateral view. The blastoid genus *Pentremites* occurs in the MACA region and contains species with either pyriform or godoniform shapes.

Crinoid and Blastoid Paleoecology

Typical Mississippian shallow-water marine paleocommunities were dominated by suspension feeders that lived directly on the sea floor or were attached to objects at the sea floor. Suspension feeders extract nutrients that are suspended in sea water that is moving above the sea floor. Most brachiopods lived directly on the sea floor. Most bryozoans lived directly on the sea floor, encrusted

onto other organisms, or grew into colonies that projected a short distance above the sea floor. Horn corals and colonial corals of the Mississippian also projected a short distance above the seafloor. The columns of crinoids and blastoids typically elevated the arms or brachioles much higher than either bryozoans or corals (Figure 134). From a community perspective, the entire community was stratified with different organisms feeding from different parcels of water at varying heights above the sea floor. This structure is termed tiering (Ausich and Bottjer 1982; Bottjer and Ausich 1987). These suspension feeders divided niches further by feeding on different-sized food particles. Food particles were live or dead organic particles ranging in size from a few microns to ~1.3 mm (0.05 in) (e.g., Ausich 1980, Byrne and Fontaine 1983). Among crinoids and blastoids, characteristics of arm branching and brachials resulted in differential size selection of suspended food particles between crinoids and blastoids and between different groups of crinoids (e.g., Ausich 1980; Brower 2011; Cole et al. 2019).



Figure 134. The extant crinoid *Proisocrinus ruberrimus* A. H. Clark, 1910 in a feeding posture. Image from R/V 'Okeanos Explorer' cruise EX1606, "Batfish" Seamount, ~304 km (189 mi) south of Wake Island, Pacific Remote Islands Marine National Monument (PRIMNM), depth ~1,280 m (4,200 ft). NOAA, 2016, https://www.ncei.noaa.gov/waf/okeanos-animal-guide/gal_Sea_Lilies.html
NOAA / PUBLIC DOMAIN

Crinoid and Blastoid Preservation

Complete and even partially complete specimens in the MACA region are extremely rare, which reflects the fact that shallow-marine environments are generally not favorable for preservation of complete echinoderms. During life, the plates of crinoid arms, blastoid brachioles, crinoid and blastoid columns, and plates of echinoids were held together with ligaments and/or muscles that decayed rapidly after death (Meyer 1971; Liddell 1975). The sutures between plates of crinoid calyxes and blastoid thecae are typically more firmly interlocked, but the degree of plate interlocking differed in different groups.

Preservation experiments on extant crinoids, both in the laboratory and in nature, have demonstrated that a dead crinoid on the sea floor will fall apart into individual plates within a few days (Meyer 1971; Liddell 1975). Thus, in order to preserve a complete or nearly complete crinoid, the crinoid must be buried alive or very soon after death. Furthermore, this burial must be permanent, because if a complete specimen with decayed connective tissues is exhumed by a storm or burrowing organisms, it would immediately disarticulate into individual plates. The same basic preservational constraints apply to all echinoderms, which is why MACA limestones have rare complete or partial specimens compared with columnals and pluricolumnals.

During life, the plates that form the skeleton of all echinoderms are comprised of the mineral calcite ($CaCO_3$), but these plates are not solid calcite. As noted above, they have a unique microstructure called stereom, which is a latticework of calcite bars and holes (Figure 130A). After death, the character of these plates changes as a function of the preservation conditions, such as depth of burial, porosity and permeability of the enclosing sediment, and chemistry of the pore water fluids. Crinoids from the MACA area are either preserved in calcite or replaced by quartz (silica; SiO_2). In the former, calcite from pore water crystallized to fill the pore space of the stereom, forming a solid calcite plate (Figure 130B). Many of the identifiable MACA echinoderm plates were replaced by quartz (commonly called silicification). The final texture of a silicified plate can be either a coarse, granular texture (Figure 130C) or a coarse, swirled texture (Figure 130D). The question is “Where did all of the quartz come from to replace all of these fossils?” The most likely answer is from siliceous sponges or wind-blown dust (Cecil et al. 2023). Biogenic quartz in sponge spicules is not stable over geological time, so it dissolves during fossilization and may replace calcareous fossils or may form beds of chert.

Echinoids

Typical Mississippian crinoids and blastoids were sessile, but echinoids were mobile. Like many of their living counterparts, Mississippian echinoids presumably moved along the surface of the sea floor. They were probably herbivores eating only algal and plant material, or they were omnivores eating whatever live or dead organic matter was available. In general, Mississippian echinoids are referred to as regular echinoids because they were spherical to subspherical in shape with spines attached to the echinoid test. (Irregular echinoids include the burrowing sea biscuits and sand dollars that evolved after the Paleozoic, during the Jurassic.) The test is comprised primarily of two plate types that alternate around the test: ambulacrals and interambulacrals. The water vascular system underlies the ambulacral plates, and the interambulacral plates typically have attached spines. The

plates of Mississippian echinoids were typically very loosely articulated, which resulted in rapid disarticulation after death. The most distinctive isolated plates of echinoids from Mississippian rocks are the spine plates and the interambulacral plates with a central boss onto which spines articulated.

The preservation of Mississippian echinoids was no different than crinoids and blastoids. Unlike many living echinoids, Mississippian echinoid skeletal plates were not firmly sutured together. Therefore, Mississippian echinoids were especially susceptible to disarticulation, and preservation or even partial preservation of echinoid tests is rarer than for crinoids and blastoids.

Echinoderms of the MACA Region

Crinoids

MACA collections include numerous crinoid specimens, most of which were collected in the park or within 2–3 km (1–2 mi) of its boundaries. Table 6 lists the crinoids that are identified from the MACA region. These include camerate, flexible, and eucladid crinoids. A single publication describing fossil crinoids from the MACA region does not exist, but the taxa discussed here have been described in various papers from adjacent areas and/or from slightly younger rocks. Among others, these include Burdick and Strimple (1983), Chestnut and Ettensohn (1988), and Keyes (2014).

Table 6. Echinoderm fossils from Mammoth Cave National Park collections. Note: Asterisks (*) indicate taxa that may or may not be from the park or from areas immediately adjacent to the park. Citations are for the original description, not identification from MACA; parentheses indicate the generic assignment of the species has changed since the original description.

Group	Taxon	Taxon Source
Camerate Crinoids	*Globocrinus unionensis*	(Worthen, 1890)
	Platycrinites s.l. *penicillus*	(Meek and Worthen, 1860)
	**Pterotocrinus acutus*	Wetherby, 1879
	**Pterotocrinus bifurcatus*	Wetherby, 1879
	**Pterotocrinus depressus*	Lyon and Casseday, 1860
	Pterotocrinus serratus	Weller, 1920
	Talarocrinus cornigerus	(Shumard, 1858)
	Talarocrinus sexlobatus	(Shumard, 1858)
Flexible Crinoids	*Onychocrinus magnus*	Worthen, 1875
Eucladid Crinoids	*Agassizocrinus occidentalis*	(Owen and Shumard, 1852)
	Culmicrinus missouriensis	(Shumard, 1858)
	Dinotocrinus huntsvillae	(Worthen, 1873)
	Phanocrinus maniformis	(Yandell and Shumard, 1847)
	Phanocrinus? *unusualis*	Burdick and Strimple, 1983
	**Tholocrinus spinosus*	(Wood, 1909)
	Zeacrinites magnoliaeformis	(Troost *in* Wood, 1909)

Table 6 (continued). Echinoderm fossils from Mammoth Cave National Park collections. Note: Asterisks (*) indicate taxa that may or may not be from the park or from areas immediately adjacent to the park. Citations are for the original description, not identification from MACA; parentheses indicate the generic assignment of the species has changed since the original description.

Group	Taxon	Taxon Source
Blastoids	*Pentremites godoni*	(Defrance, 1819)
	Pentremites pyriformis	Say, 1825
	Pentremites tulipaformis	Hambach, 1903
Echinoids	*Melonechinus indianensis*	(Miller and Gurley, 1893)
	Proterocidaridae undetermined	–

Camerate Crinoids

Camerate crinoids typically have fixed brachial plates above the radial plates and biserial brachials. Typically, the preserved adult calyx of most camerates is larger than most flexible and eucladid crinoids.

Four genera of camerate crinoids are known to be present in the MACA region: *Globocrinus*, *Platycrinites*, *Pterotocrinus*, and *Talarocrinus*. *Globocrinus unionensis* (Worthen, 1890) is known from four specimens photographed in the wall of Long Cave: one is a poorly preserved specimen (Figure 128A); one is a partially disarticulated specimen with attached arms (Figure 128C); and the others are partial calyxes (Figures 128D and 128E). All are preserved in cave walls. This is a relatively large crinoid in this fauna. The combined calyx and tegmen form a biconical shape, and the arms are biserial pinnulate. In older literature this crinoid has been called *Batocrinus persculptus* (Ulrich, 1917); however, it is now recognized as *Globocrinus unionensis.* See Ausich and Kammer (2010) and Webster (2014). Note that in nomenclatural convention, the citation that follows a scientific genus and species is the source of the specific name, and is given in parentheses if the genus differs from the original assignment.

Platycrinites is a distinctive camerate crinoid because the biserial arms are free above the radial plates (making it similar to a eucladid) (Figures 127 and 133A to 133D), and its columnals have an elliptical outline (Figure 132A). *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860) (see Ausich 2009 for discussion of valid species name) is present in the MACA region both embedded in the walls of caves and in surficial outcrops. Nearly complete specimens are present, as well as isolated radial plates and distinctive basal circlets (Figures 127 and 133A to 133D). Note the striking change in shape and pattern of columnals along the column. The column closest to the calyx has elliptical columnals with rounded sides, and these columnals are evenly twisted down the column (Figures 127A, 127B, and 133D). In contrast, farther down along the column, the columnals are much more angular, sets of columnals are aligned, and the angle of offset between these sets of columnals is ~90° (Figure 127B).

Pterotocrinus is a very unusual and distinctive Mississippian crinoid. Five prominent “wing plates” are attached to and extend away from the tegmen of this camerate crinoid (Figure 135A). Complete

specimens of *Pterotocrinus* are quite rare, which stands in contrast to the fairly common preservation of the wing plates. Species differentiation in *Pterotocrinus* is based on the shape of the wing plates, and four species are identified in MACA collections. *Pterotocrinus serratus* Weller, 1920 was collected from the park, whereas the provenance of the following three species is uncertain: *Pterotocrinus acutus* Wetherby, 1879; *Pterotocrinus bifurcatus* Wetherby, 1879; and *Pterotocrinus depressus* Lyon and Casseday, 1860. The wing plates of *Pterotocrinus acutus* are long, robust, and slightly curved spines (Figure 135C). *Pterotocrinus bifurcatus* is similar to *Pterotocrinus acutus*, but the wing plates of *Pterotocrinus bifurcatus* divide, resulting in two spines (Figure 135D). The wing plates of both *Pterotocrinus depressus* and *Pterotocrinus serratus* are flat plates. From the attachment to the tegmen, *Pterotocrinus depressus* wing plates expand into a large, subelliptical plate (Figure 135B). In contrast, the wing plates of *Pterotocrinus serratus* are much smaller than those on *Pterotocrinus depressus*, and the outer margin of the *Pterotocrinus serratus* wing plates typically have small spinose extensions (Figure 135E), which give this species its name.

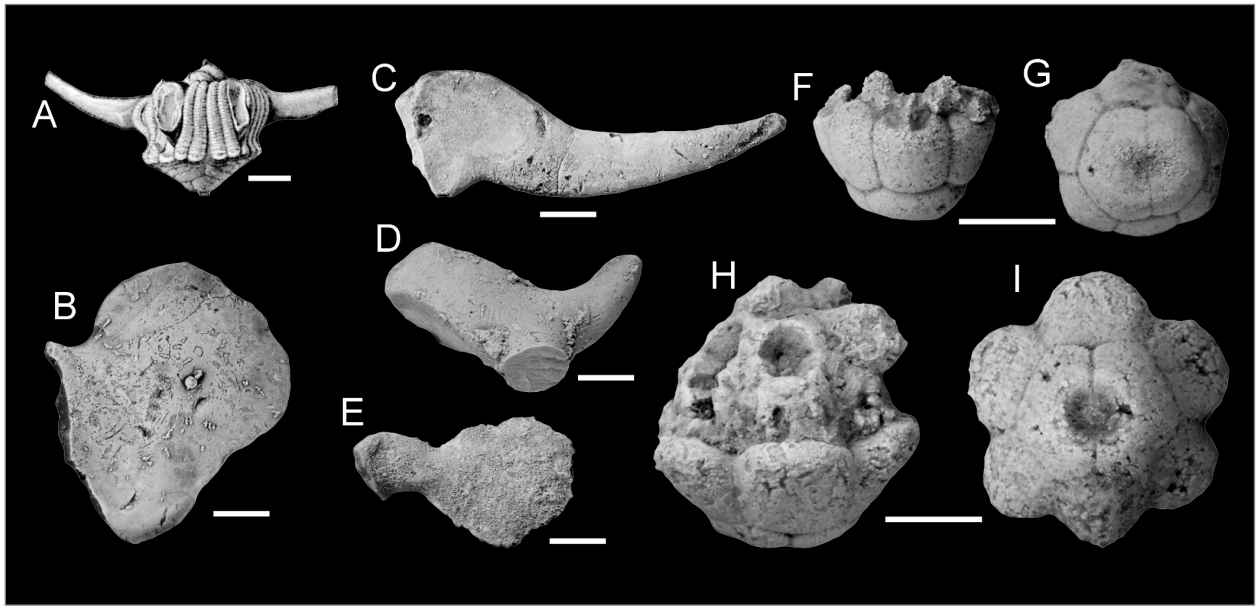


Figure 135. Camerate crinoids from the Mammoth Cave region. Specimens photographed with ammonium chloride coating, scale bars 5 mm (0.2 in). **A.** Side view of a *Pterotocrinus acutus* illustrating a specimen with arms and wing plates intact; wing plates protrude between the arms; the two wing plates that project out of the image are broken (re-illustrated from Wachsmuth and Springer 1897, pl. 79, fig. 3a). **B.** Side view of a wing plate of *Pterotocrinus depressus* (MACA 3052) (from Sloans Valley). **C.** Side view of a wing plate of *Pterotocrinus acutus* (MACA 3050) (from Sloans Valley). **D.** Side view of a wing plate of *Pterotocrinus bifurcatus* (MACA 3951) with one of the terminal spines broken off. **E.** Side view of a wing plate of *Pterotocrinus serratus* (MACA 36372) (locality unknown). **F, G.** Side and basal view, respectively of *Talarocrinus cornigerus*; **F.** Note tegmen not preserved; **G.** Note basal circlet comprised of only two plates (MACA 3097) ("1 mile west" of Auburn, Kentucky, Girkin Formation). **H, I.** Side and basal view, respectively of *Talarocrinus sexlobatus*; **H.** Note prominent tegmen with spinose plates; **I.** Note basal circlet comprised of only two plates (MACA 3096) ("1 mile west" of Auburn, Kentucky, Girkin Formation). © WILLIAM AUSICH

Numerous small camerate crinoids from within MACA boundaries and elsewhere are assigned to *Talarocrinus*. A distinctive feature of this crinoid is that it has two, equal-sized basal plates (Figure 135I), and the tegmen typically has nodes or spines (Figure 135H). Most specimens of *Talarocrinus* are not preserved with the tegmen (Figure 135F), which makes species identification difficult, but two species of *Talarocrinus* are identified from within MACA boundaries. Specimens from elsewhere in Kentucky are also present in the collections (Appendix E). *Talarocrinus sexlobatus* (Shumard, 1858) is a distinctive species with the upper portion of the radial circlet extending outward, and the suture between adjacent radial plates is depressed (Figures 135H and 135I). Thus, the outline of the calyx in basal view is similar to a cogwheel. The majority of specimens assigned to *Talarocrinus sexlobatus* are small and are presumed to be juveniles. These juveniles have less pronounced extensions of the radial plates and depressions at sutures between radial plates.

The second *Talarocrinus* species is *Talarocrinus cornigerus* (Shumard, 1858). It has a higher, cone-shaped calyx with more upright basal and radial plate circlets. The outline of the calyx in basal view is subcircular with only shallow, broad indentations at the radial plate-radial plate sutures (Figures 135F and 135G). Two specimens of this species are present in the collections.

Flexible Crinoid

Onychocrinus magnus (Worthen 1875) is the only flexible crinoid identified from MACA. Figure 128B is a nearly complete aboral cup with arms. The infrabasal plates are very small and hidden beneath the column. Both basal plates and radial plates are visible in lateral view (Figure 128B), and the arms are robust and widely separated. This nearly complete specimen was certainly buried alive, a catastrophe for this crinoid but a stroke of luck that preserved a nearly complete crinoid that helps us to understand ancient life of the MACA region.

Eucladid Crinoids

Eucladid crinoids have three circlets of plates in the aboral cup (infrabasals, basals, and radials) and commonly have a few extra plates in the posterior. Aboral cup shape; relative sizes of aboral cup plates; number, size, and arrangement of posterior plates; the number of arm branches; and shape of the brachial plates are key to identification of eucladids.

Seven eucladids are present in the collections from the MACA region, including *Agassizocrinus occidentalis* (Owen and Shumard, 1852); *Culmicrinus missouriensis* (Shumard, 1858); *Dinotocrinus huntsvillae* (Worthen, 1873); *Phanocrinus maniformis* (Yandell and Shumard, 1847); *Phanocrinus*? *unusualis* Burdick and Strimple, 1983; *Tholocrinus spinosus* (Wood, 1909); and *Zeacrinites magnoliaeformis* (Troost *in* Wood, 1909) (Table 6) (however, note the geographic provenance of the *Tholocrinus* specimen is uncertain). *Agassizocrinus* is a highly unusual Paleozoic crinoid. Like extant feather stars, *Agassizocrinus* juveniles had columns, but during ontogeny, the column was lost and *Agassizocrinus* became a free-living crinoid. Rather than being attached to the sea floor by a holdfast, *Agassizocrinus* is envisioned to have inserted the infrabasal cone into the sediment. In addition to feeding, some arms may have also helped the crinoid to move along the sea floor and to stabilize a favorable position on the sea floor (Ubaghs 1953; Ettensohn 1975). Accordingly, *Agassizocrinus* must have fed from water immediately above the sea floor, unlike other crinoids and blastoids with

columns. The *Agassizocrinus* infrabasal cone is relatively common and easy to identify in many Upper Mississippian strata (Figures 130B, 130C, and 136A to 136E). The size and shape of *Agassizocrinus* infrabasal cones are variable both among species and throughout ontogeny of a single individual. All specimens of *Agassizocrinus* here can be assigned to *Agassizocrinus occidentalis.* Fortunately, two specimens are known from complete or nearly complete aboral cups with some brachials attached (Figures 130B and 136A).

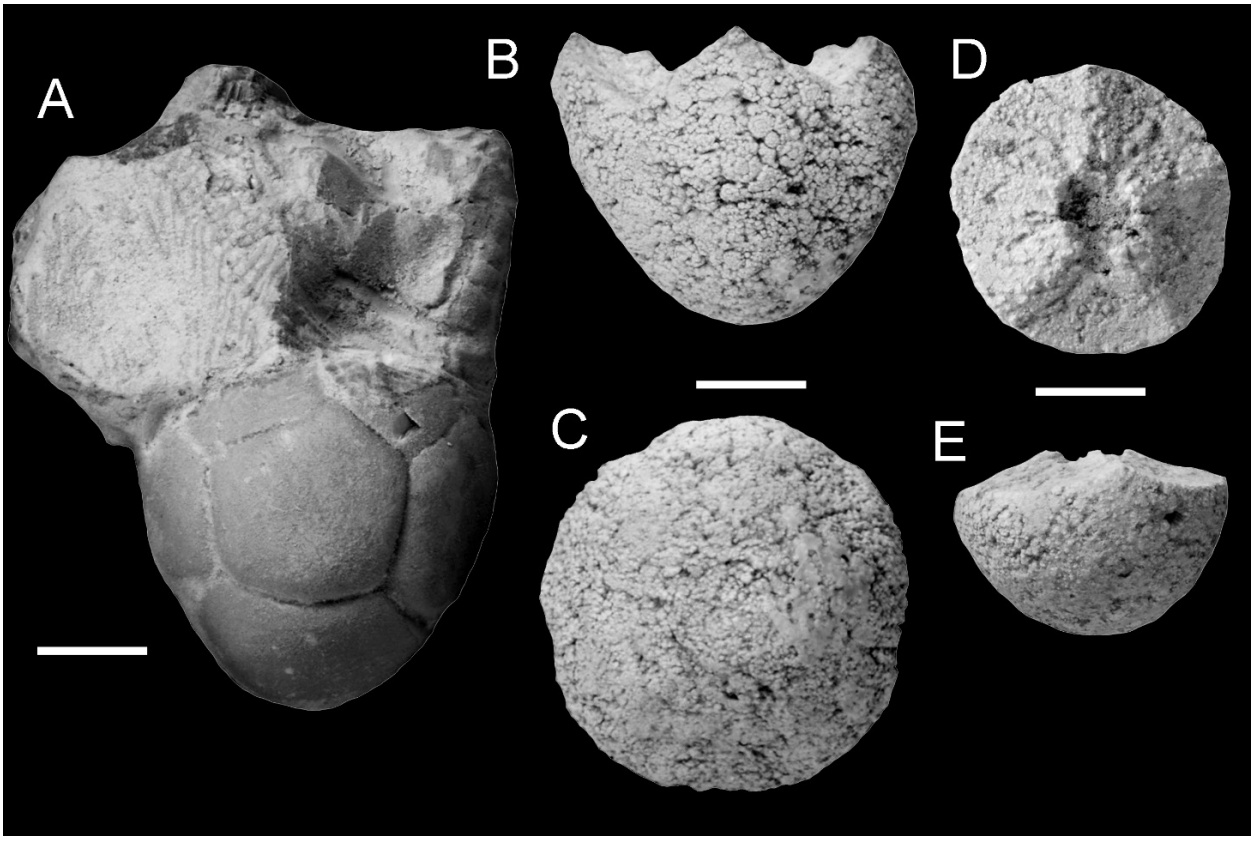


Figure 136. *Agassizocrinus occidentalis* from the Mammoth Cave region. Specimens coated with ammonium chloride, scale bars 5 mm (0.2 in). **A**. Lateral view of partial crown (MACA 36313) (locality unknown). **B, C.** Taller infrabasal cone (MACA 36284) (Girkin Formation); **B.** Lateral view; **C.** Basal view. **D, E.** Shorter infrabasal cone (MACA 36327) (Haney Formation); **D.** Oral view; **E.** Lateral view.
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A single specimen of *Culmicrinus missouriensis* is known in the MACA region. It is a specimen with the lower portion of the arms, aboral cup, and some of the column attached. This specimen is embedded in the wall of Specimen Avenue. *Culmicrinus missouriensis* is distinct from other eucladids discussed here because the aboral cup is cone-shaped, and all three plate circlets (infrabasal, basal, and radial) are visible in lateral view (Figures 129A and 131C). Also, the robust arms of *Culmicrinus missouriensis* branch higher along the arm than other eucladids in the MACA region.

All other eucladids from the MACA region have small, bowl-shaped aboral cups with the infrabasal plates covered by the column and not visible in lateral view, and the arms branch on the first brachial plate. *Dinotocrinus huntsvillae* is distinctive because it has arms that branch equally two times (total of 20 arms) (Figure 129C). Nodes are present on the arm plates where the arms divide, and the sutures between adjacent brachial plates are at an angle. In aboral cups of *Dinotocrinus huntsvillae* the basal concavity is shallow, the basal plates are approximately one-half the cup height in side view, and the radial facets are subhorizontal.

Two species assigned to *Phanocrinus* occur in the MACA region, *Phanocrinus maniformis* (Yandell and Shumard, 1847) and *Phanocrinus*? *unusualis* Burdick and Strimple, 1983. *Phanocrinus* is differentiated from other eucladids in the Ste. Genevieve Formation by having a low bowl-shaped aboral cup with a narrow and shallow basal concavity, only the distal parts of the basal plates visible in side view, subhorizontal radial facets, posterior plates projecting only a short distance above the radial facets, 10 robust arms with uniserial brachials (Figure 129B), and straight sutures between adjacent brachial plates yielding rectangular-shaped brachial plates. *Phanocrinus*? *unusualis* has a slightly higher aboral cup, and the basal circlet of *Phanocrinus maniformis* has a characteristic five-petal shaped basal circlet (Figures 137D and 137E).

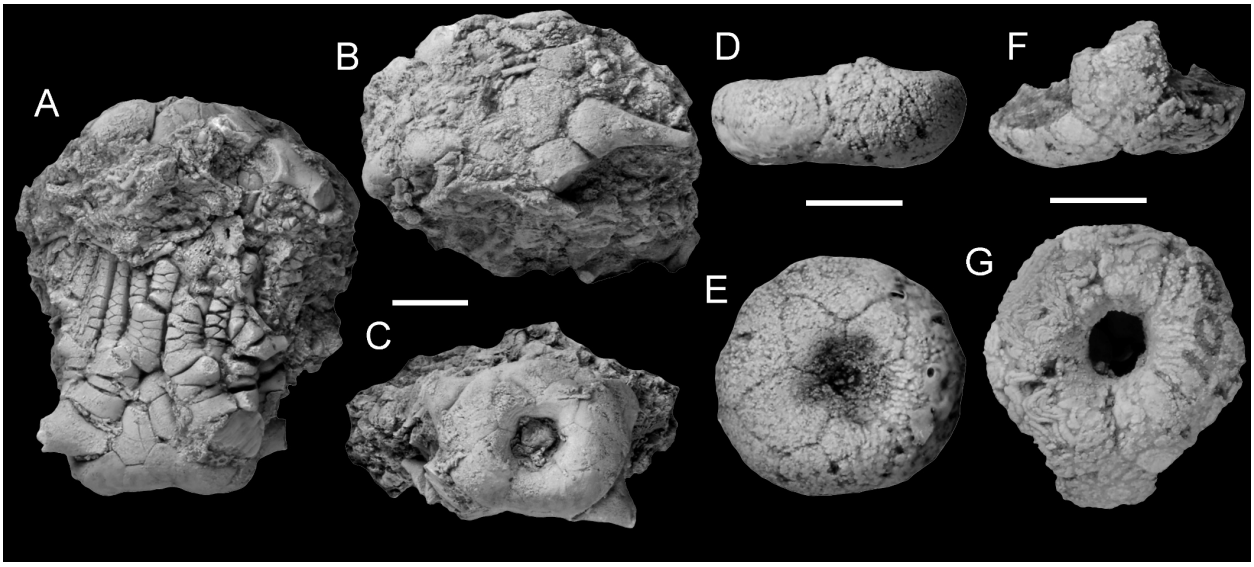


Figure 137. Eucladid crinoids from the Mammoth Cave region. Specimens coated with ammonium chloride, scale bars 5 mm (0.2 in). **A–C.** *Tholocrinus spinosus* (MACA 3053) (from Sloans Valley); **A.** Lateral view of crown, note that arms branch on first brachial plates and broken spines on brachials that branch; **B.** Spinose plates at top of anal sac; **C.** Basal view of aboral cup. **D, E.** *Phanocrinus maniformis* (MACA 36338) (locality unknown); **D.** Lateral view of aboral cup; **E.** Basal view of aboral cup. **F, G**. *Zeacrinites magnoliaeformis* (MACA 36288) (most likely Glen Dean Formation); **F.** Lateral view of aboral cup; **G.** Basal view of aboral cup. © WILLIAM AUSICH

Tholocrinus spinosus also has one primary branching of the arms, but several secondary branches occur higher for a total of as many as 60 arms. The first brachial plate has a prominent spine (Figures 131A, 131B, and 137A to 137C), and progressively higher branching plates have spines that diminish

in length until higher branching plates have only nodes. The tegmen of *Tholocrinus spinosus* is as high as the arms and prominent spinose plates project outward from the top of the tegmen (Figures 137A and 137B). In aboral cups of *Tholocrinus spinosus* the basal concavity is narrow and shallow, only the distal tips of the basal plates are visible in side view, the radial facets slope slightly inward, and posterior plates project only a short distance above the radial facets.

Zeacrinites magnoliaeformis has a very flat aboral cup with the radial facets sloping outward (Figures 130D, 137F, and 137G). Both the infrabasal and basal plates are in a broad and deep concavity at the base of the aboral cup, with only the distal tips of the basal plates visible in side view (Figure 137F). The posterior plates are firmly sutured together and protrude high above the level of the radial facets (Figure 137F). No specimens of *Zeacrinites magnoliaeformis* in the MACA collections have well-preserved arms.

Blastoids

Three species of *Pentremites* are present in the MACA region, two of which are the namesakes for blastoid thecal shapes. *Pentremites pyriformis* Say, 1825 has a pyriform thecal shape. The basal circlet is a steep-sided cone and is ~50% of the thecal height (Figures 129D, 131D, and 138C).

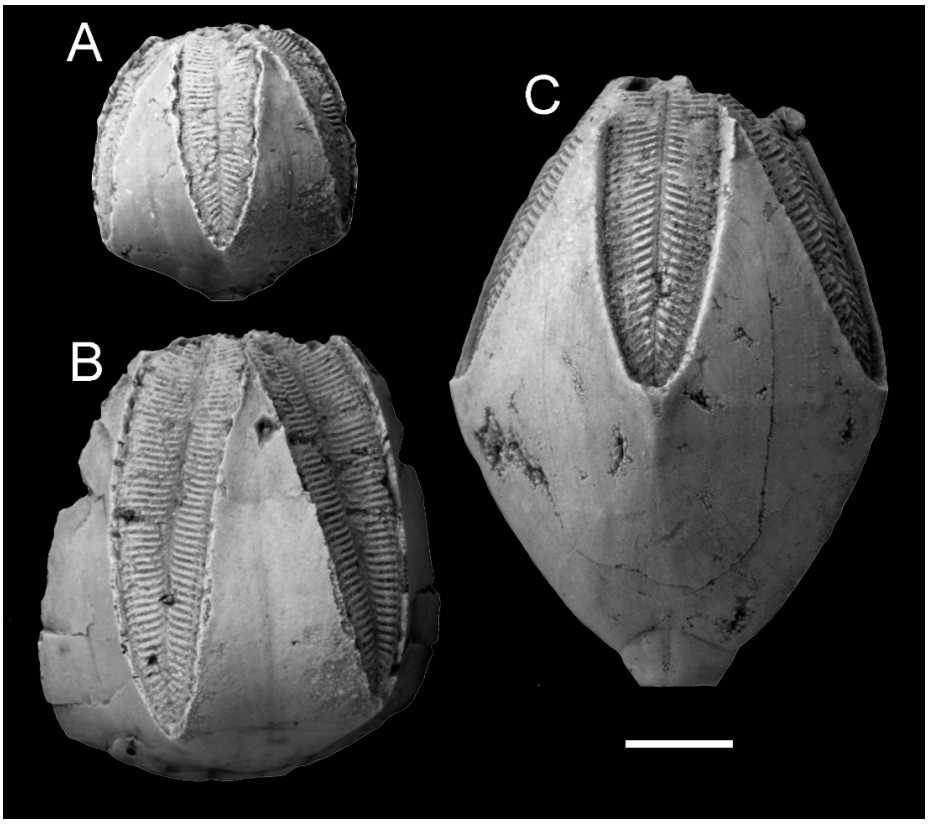


Figure 138. Blastoids. All specimens coated with ammonium chloride, scale bars 5 mm (0.2 in). **A.** Lateral view of *Pentremites godoni* (MACA 36183) (locality unknown). **B.** Lateral view of *Pentremites tulipaformis* (MACA 36184) (locality unknown). **C.** Lateral view of *Pentremites pyriformis* (MACA 3205) (locality unknown). © WILLIAM AUSICH

Godoniform blastoids in the MACA region are *Pentremites godoni* (Defrance, 1819) and *Pentremites tulipaformis* Hambach, 1903. Both of these blastoids have a basal circlet that is a very flat cone. In *Pentremites godoni*, the basal circlet is no more than ~25% of the thecal height (Figure 138A), and the theca is subcircular in outline. Most specimens of *Pentremites godoni* are relatively small. In contrast, *Pentremites tulipaformis* is a much larger and robust species with a subelliptical thecal shape and the basal circlet is ~10% of the thecal height (Figure 138B).

Echinoids

In general, Paleozoic echinoids are more susceptible to rapid disarticulation than most crinoids; however, the thicker plates of *Melonechinus* resulted in slower disarticulation rates. Regardless, two exceptionally well-preserved echinoid taxa are present in the rocks in the MACA region. A single very well-preserved specimen of *Melonechinus indianensis* (Miller and Gurley, 1893) is known. This echinoid has no spines and has very thick plates, which undoubtedly helped to preserve specimens intact (Figure 139C). In contrast, echinoids from the family Proterocidaridae (Figures 139A and 139B) had long spines when they were alive. The specimen in Figure 139A has been flattened, and the spines have fallen off. The exposed surface of this specimen is insufficient to assign this echinoid to a species or even a genus, but it belongs to the family Proterocidaridae. This echinoid is a much thinner-plated specimen, and it is a relatively small individual; both qualities would promote rapid disarticulation.

Because only a few spines are preserved next to the main body of this specimen, it is probable that this proterocidarid laid dead on the sea floor for at least a few days. The spines fell off the echinoid body, and most spines were dispersed away from the specimen. In contrast, the plates of the main echinoid body remained intact until burial. A storm presumably buried this specimen and prevented it from disarticulating further.

Other known echinoid remains in the MACA region are isolated spines (Figure 139B). The base of these spines is slightly expanded to form a socket on which the spines articulated with a rounded boss on an interambulacral plate. Above the base, the spine gradually tapers (Figure 139B).

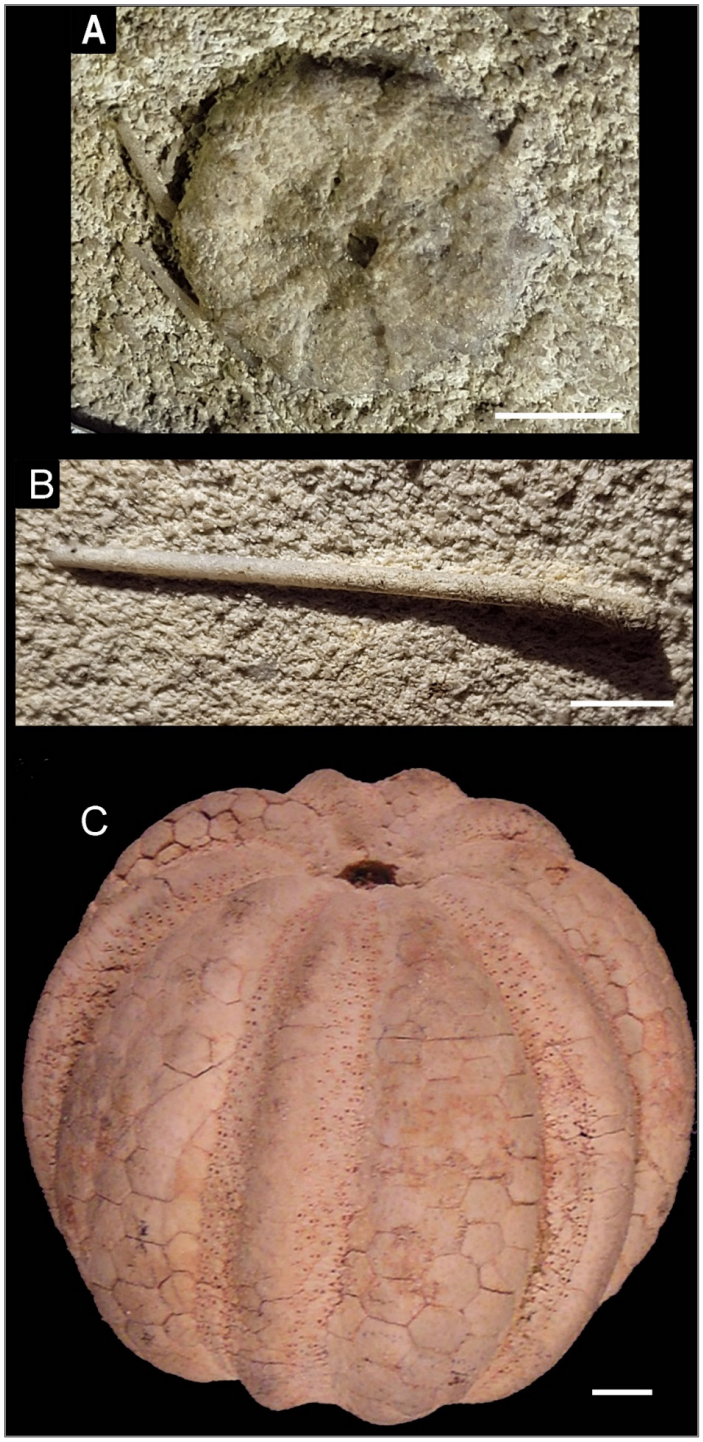


Figure 139. Mammoth Cave echinoids. **A, B.** Echinoids from Ganter Avenue in the Joppa Member of the Ste. Genevieve Formation; scale bars 5 mm (0.2 in). **A.** The body of an echinoid from the family Proterocidaridae whose spines had fallen off before burial; note two spines to the left of the specimen. **B.** Isolated proterocidarid spine. **C.** Oblique view of a very well-preserved *Melonechinus indianensis.* Unlike many Paleozoic echinoids, the plates on *M. indianensis* are thick and presumably disarticulated more slowly (USNM PAL 380837, unknown MACA locality). **A, B:**
NPS / K. TOLLESON; **C:** IMAGE COURTESY OF THE SMITHSONIAN INSTITUTION

Stratigraphic Distribution of Echinoderms

Although there are some caves in higher stratigraphic units in MACA, the namesake cave system is formed within three formations, from the oldest to the youngest the St. Louis, Ste. Genevieve, and Girkin Formations (Palmer 2017; Chapter 3). This limestone succession is capped by sandstones of the Big Clifty Formation. The Big Clifty Formation is succeeded by the Haney, Hardinsburg, and Glen Dean Formations; carbonates of the Haney and Glen Dean Formations also form caves and sometimes contain echinoderm remains. Most specimens collected from surficial localities were weathered free from the host rock, so the precise stratigraphic level from which these specimens originated may be difficult to establish. In contrast, the stratigraphic occurrence is known for specimens preserved on the cave walls. Echinoderm debris is present in the park in the St. Louis, Ste. Genevieve, Girkin, Haney, and Glen Dean Formations (Chapter 3; inventory photos). Few genera and species have previously been identified, apart from taxa mentioned without comment in Pohl and Cushman (1964): *Agassizocrinus* spp. from the Beech Creek Member of the Girkin Formation in the Cedar Sink area; and blastoids (*Pentremites abruptus*, *P. pyriformis*, and *P. welleri*), and crinoids (*Agassizocrinus conicus*, *A. ovalis*, and *Eupachycrinus* sp.) from residual Haney Formation chert at a road cut in the southern part of the park. The present work greatly increases and clarifies taxonomic knowledge of the park's fossil echinoderms, particularly from cave surfaces in the Joppa Member of the Ste. Genevieve Formation. At the present time fossil echinoderms known with certainty from the Joppa Member in and around MACA are the following: crinoids *Culmicrinus missouriensis*, *Dinotocrinus huntsvillae*, *Globocrinus unionensis*, *Onychocrinus magnus*, *Phanocrinus*? *unusualis*, and *Platycrinites* s.l. *penicillus*; blastoids *Pentremites godoni* and *Pentremites pyriformis*; and echinoid remains from the family Proterocidaridae (Appendix E). Fossil echinoderms known with certainty from the Girkin Formation in and near MACA include: crinoids *Agassizocrinus occidentalis*, *Phanocrinus maniformis*, *Pterotocrinus serratus*?, *Talarocrinus cornigerus*, *Talarocrinus sexlobatus*, and *Zeacrinites magnoliaeformis*; and blastoids *Pentremites godoni*, *Pentremites pyriformis*, and *Pentremites tulipaformis* (Appendix E). Notably, the crinoid assemblage is completely different at the species level and almost completely different at the genus level compared to the Joppa Member of the Ste. Genevieve Formation. Fossil echinoderms known with certainty from the Haney Formation in and near MACA include the crinoids *Agassizocrinus occidentalis* and *Phanocrinus maniformis*, and the blastoid *Pentremites pyriformis* (Appendix E). Finally, fossil echinoderms known with certainty from the Glen Dean Formation in and near MACA include the crinoids *Phanocrinus maniformis* and *Zeacrinites magnoliaeformis* and the blastoid *Pentremites pyriformis* (Appendix E).

Conclusions

The passageways and chambers of MACA developed in Mississippian limestone and dolomites, with many beds comprised of numerous individual crinoid, blastoid, and echinoid plates. The most abundant plates are columnals from the columns of crinoids and blastoids; however, only one of the columnal shapes can be identified (*Platycrinites* s.l.). In order to preserve complete echinoderms, an individual must be buried permanently while alive or shortly after death. The depositional environment of these Mississippian limestones was typically not conducive to rapid, permanent burial.

Regardless, partial to complete remains of 12 crinoid species, three blastoids, and two echinoids are identified from the MACA region. The most abundant genera in the park and/or in outcrops immediately adjacent to the park are the crinoids *Platycrinites*, *Pterotocrinus*, *Talarocrinus*, and *Agassizocrinus*, and the blastoid *Pentremites*.

This echinoderm fauna is similar to other age-equivalent shallow marine environments elsewhere in the Midcontinent. These crinoids, blastoids, and echinoids were part of much larger shallow marine communities that also included bryozoans, brachiopods, corals, and sharks, among other organisms (Chapters 5 and 7).

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Appendix E: Mammoth Cave National Park Echinoderm Taxonomy and Distribution

The following presents lists of echinoderm specimens and taxa associated with MACA. The information is divided into three sections: fossils from inside the cave system, including collected specimens and those represented by photographs; fossils from surficial locations in MACA collections, some of which were collected outside of the park; and summary lists of taxa sorted by stratigraphic unit.

Specimens from Inside Caves

Below is a list of echinoderm fossils from the Mammoth Cave System arranged by locality, including fossils photographed on cave walls and collected specimens. This list includes identified specimens in the MACA collection but does not include columnals and pluricolumnals that cannot be identified to genera and species defined by characteristics of the crown. Specimens lacking geographic provenance are not included.

Cave #293 (Haney Formation)

- *Pentremites pyriformis* Say, 1825

Cave #048 (Girkin Formation)

- MACA 63203: *Pentremites godoni* (Defrance, 1819)
- MACA 63200–MACA 63203: *Pentremites pyriformis* Say, 1825

Colossal Cave (Joppa Member, Ste. Genevieve Formation)

- Photos (1–3): *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)
- Photo (10): *Dinotocrinus huntsvillae* (Worthen, 1873)
- Photo (11): *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)?
- Photos (12–20, 23, 33): *Onychocrinus magnus* Worthen, 1875
- Photos (22, 24, 27): *Pentremites godoni* (Defrance, 1819)
- Photos (30, 31): ?*Onychocrinus magnus* Worthen, 1875
- MACA-Colossal Cave Fossils (1, 3–6): *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)
- MACA-Colossal Cave Fossils (17): *Onychocrinus magnus* Worthen, 1875
- MACA-Colossal Cave Fossils (18): Family Proterocidaridae
- Photo 20220910_052818: *Globocrinus unionensis* (Worthen, 1890)

Crystal Cave (Girkin Formation)

- MACA 63204, MACA 63208: *Pentremites pyriformis* Say, 1825
- MACA 63209: *Talarocrinus sexlobatus* (Shumard, 1858)

Cox Avenue, Genie's Pass off Boone Avenue (Joppa Member of the Ste. Genevieve Formation)

- *Globocrinus unionensis* (Worthen, 1890)
- *Onychocrinus magnus* Worthen, 1875
- *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)

Edmondson County, Kentucky (National Park Service locality 6320)

- USNM 380837: *Melonechinus indianensis* (Miller and Gurley, 1893)

Ganter Avenue (Joppa Member of the Ste. Genevieve Formation)

- *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)
- Photos 20210605_1136198; 113455; Photo-20210605; 20210605_113619 20210605_11363220; 220426_194931; 20220430_164132: Family Proterocidaridae (echinoid remains)

Great Onyx Cave (Joppa Member of the Ste. Genevieve Formation or Girkin Formation)

- Photos 20220506-100117; 20220506-100235: 20220506-100306; 20220506-100259: *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)

Jessup Avenue (Joppa Member of the Ste. Genevieve Formation)

- Photos 20220426_194831, 20220426_194836): *Onychocrinus magnus* Worthen, 1875
- Photos 20220430_16382, 20220430_164132, 20220426_192153, 20220426_192156, 20220426_192212: Family Proterocidaridae (echinoid remains)

Long Cave, Echo Passage (Joppa Member of the Ste. Genevieve Formation)

- Photos (12, 40, 45, 46, 63, 64, 80, 81, 82): *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860) *Pentremites godoni* (Defrance, 1819)
- Photos (13, 16, 32, 33, 43, 48, 65, 67, 68, 72, 73, 113, 126): *Pentremites godoni* (Defrance, 1819)
- Photos (17, 18, 22, 38, 42, 53, 120, 121): *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)
- Photos (36, 37, 39, 127): *Phanocrinus*? *unusualis* Burdick and Strimple, 1983
- Photos (51, 83): *Pentremites pyriformis* Say, 1825
- Photos (116, 117, 118): *Phanocrinus*? *unusualis* Burdick and Strimple, 1983
- Photos (122, 123, 124): *Dinotocrinus huntsvillae* (Worthen, 1941)

- Photos (129, 130): *Globocrinus unionensis* (Worthen, 1890)

Specimen Avenue (Joppa Member of the Ste. Genevieve Formation)

- Photo Specimen_Ave_crinoid_nr_saivodus: *Culmicrinus missouriensis* (Shumard, 1858)

Solitary Cave (Joppa Member of the Ste. Genevieve Formation)

- *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)

In addition, the following have been identified from photos without location or stratigraphic information:

- Platy.jpg: *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)
- Photos Questionable crinoid stem segments: *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)
- unknown leaf-like structures: *Pentremites* sp. lancet plates

Specimens from Surface Outcrops

The following are all specimens in MACA collections and represent collections made by Erwin Pohl in the 1930s. Geographic information for sites within or near MACA has been replaced by generic collection numbers and is available to qualified researchers upon request. Stratigraphic information has been determined post hoc. "Interpreted to be from" is a confident assessment with minor likelihood of inaccuracy. "Stratigraphic position uncertain" indicates a lower level of confidence.

Within MACA

Collection 1 (interpreted to be from the Girkin Formation):

- MACA 3009: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 36196: *Pentremites pyriformis* Say, 1825
- MACA 36355: *Talarocrinus sexlobatus* (Shumard, 1858)
- MACA 36357: *Talarocrinus cornigerus* (Shumard, 1858), *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

Collection 2 (interpreted to be from the Girkin Formation):

- MACA 36206: *Pentremites pyriformis* Say, 1825
- MACA 36279: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 36283: *Agassizocrinus occidentalis* (Owen and Shumard, 1852), *Platyceras* gastropod, unidentified plates

Collection 3 (interpreted to be from the Girkin Formation):

- MACA 36284: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

- MACA 36351: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

Collection 4 (interpreted to be from the Glen Dean Formation):

- MACA 36303: *Phanocrinus maniformis* Burdick and Strimple, 1983

Collection 5 (interpreted to be from the Haney Formation):

- MACA 36189: *Pentremites* sp.
- MACA 36327: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 36329: *Phanocrinus maniformis* (Yandell and Shumard, 1847)

Collection 6 (interpreted to be from the Haney Formation):

- MACA 3040: *Phanocrinus maniformis* (Yandell and Shumard, 1847)
- MACA 36194: *Pentremites pyriformis* Say, 1825

Collection 7 (interpreted to be from the Girkin Formation):

- MACA 3065: ?*Pterotocrinus serratus* Weller, 1920
- MACA 3069: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 3073: *Pentremites godoni* (Defrance, 1819)
- MACA 36180: *Pentremites pyriformis* Say, 1825
- MACA 36181: *Pentremites pyriformis* Say, 1825
- MACA 36182: *Pentremites godoni* (Defrance, 1819)
- MACA 36183: *Pentremites godoni* (Defrance, 1819)
- MACA 36184: *Pentremites tulipaformis* Hambach, 1903
- MACA 36187: *Pentremites* sp.
- MACA 36321: *Phanocrinus maniformis* (Yandell and Shumard, 1847), *Zeacrinites magnoliaeformis* (Troost *in* Wood, 1909)
- MACA 36344: Unidentifiable crinoid plates
- MACA 36346: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

Collection 8 (stratigraphic position uncertain, most likely the Haney Formation):

- MACA 3104*: Pentremites pyriformis* Say, 1825
- MACA 3105: *Pentremites pyriformis* Say, 1825
- MACA 3106: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 36290: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

Collection 9 (interpreted to be from the Girkin Formation):

- MACA 36319: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

Outside of but immediately adjacent to MACA
Collection 10 (interpreted to be from the Glen Dean Formation):

- MACA 36195: *Pentremites pyriformis* Say, 1825

Collection 11 (interpreted to be from the Glen Dean Formation):

- MACA 3030: *Pentremites pyriformis* Say, 1825

Collection 12 (stratigraphic position uncertain, Girkin Formation most likely):

- MACA 36306: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

Collection 13 (interpreted to be from the Haney Formation):

- MACA 3039: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)

Collection 14 (stratigraphy uncertain, Glen Dean Formation most likely):

- MACA 36286: Unidentifiable crinoid plate
- MACA 36288: *Zeacrinites magnoliaeformis* (Troost *in* Wood, 1909)

Collection 15 (too vague to provide a stratigraphic interpretation):

- MACA 3119: *Pentremites pyriformis* Say, 1825

Farther afield from MACA
One mile [1.6 km] west of Auburn, Kentucky on US 68 (interpreted to be from the Girkin Formation):

- MACA 3009: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 3086: *Pentremites godoni* (Defrance, 1819)
- MACA 3087: *Pentremites pyriformis* Say, 1825
- MACA 3088: *Pentremites pyriformis* Say, 1825
- MACA 3089: *Pentremites pyriformis* Say, 1825
- MACA 3091: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 3096: *Talarocrinus sexlobatus* (Shumard, 1858)
- MACA 3097: *Talarocrinus cornigerus* (Shumard, 1858)
- MACA 3098: *Talarocrinus sexlobatus* (Shumard, 1858)
- MACA 3100: *Zeacrinites magnoliaeformis* (Troost *in* Wood, 1909)
- MACA 36343: crinoid pluricolumnal

Uncertain but likely distant from MACA

Sloan's Valley: There is some question whether this is Sloans Valley in southeastern Kentucky or an informal name for a valley near Sloan's Crossing in MACA, with the former most likely. The specimens were collected by Pohl on 8/25 and 8/26/1935 during a geologic mapping project of the future parklands, with collecting from known MACA-area locations on both days. Weekly reports are available for some of Pohl's activities, but not this time frame, and likely no longer exist. Sloans Valley is approximately 180 km (110 mi) from the nearest part of MACA by modern roads. In terms of logistics and practicality, either a "within MACA" or "outside MACA" origin are feasible. For the first option, no particular plan of action is suggested, whereas for the second, an overnight collecting trip (perhaps undertaken in search of comparative material) with local collecting before and after is suggested. If the locality is within MACA, the Girkin Formation is the most likely source rock in the Sloan's Crossing area, and the site has produced four unique taxa (the three *Pterotocrinus* species and *Tholocrinus spinosus*). If the locality is outside of MACA in the Sloans Valley area, there is a known Glen Dean Formation site that has produced examples of these taxa (Horowitz 1965), so on these grounds the outside origin is more likely. However, they are still of interest for comparative and reference purposes because the Glen Dean Formation is also present at MACA.

- MACA 3050: *Pterotocrinus acutus* Wetherby, 1879
- MACA 3051: *Pterotocrinus bifurcatus* Wetherby, 1879
- MACA 3052: *Pterotocrinus depressus* Lyon and Casseday, 1860
- MACA 3053: *Tholocrinus spinosus* (Wood, 1909)
- MACA 3054: *Talarocrinus sexlobatus* (Shumard, 1858)
- MACA 3056: *Pentremites* sp.
- MACA 3059: *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- MACA 36193: *Pentremites* sp.

Taxonomic Lists by Stratigraphic Unit

Below are lists of echinoderm fossil taxa identified from photos or specimens and arranged by stratigraphic unit. Single asterisks (*) indicate the only record(s) are from just outside of MACA. Question marks (?) leading a taxon indicate the stratigraphy is particularly questionable ("stratigraphy uncertain…" above). Blastoids are listed first, then crinoids, then echinoids.

Ste. Genevieve Formation (Joppa Member)

- *Pentremites godoni* (Defrance, 1819)
- *Pentremites pyriformis* Say, 1825
- *Culmicrinus missouriensis* (Shumard, 1858)
- *Dinotocrinus huntsvillae* (Worthen, 1873)
- *Globocrinus unionensis* (Worthen, 1890)

- *Onychocrinus magnus* Worthen, 1875
- ?*Onychocrinus magnus* Worthen, 1875
- *Phanocrinus*? *unusualis* Burdick and Strimple, 1983
- *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)
- Family Proterocidaridae (echinoid remains)

Joppa or Girkin

- *Platycrinites* s.l. *penicillus* (Meek and Worthen, 1860)

Girkin Formation

- *Pentremites godoni* (Defrance, 1819)
- *Pentremites pyriformis* Say, 1825
- *Pentremites tulipaformis* Hambach, 1903
- *Pentremites* sp.
- *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- *Phanocrinus maniformis* (Yandell and Shumard, 1847)
- ?*Pterotocrinus serratus* Weller, 1920
- *Talarocrinus cornigerus* (Shumard, 1858)
- *Talarocrinus sexlobatus* (Shumard, 1858)
- *Zeacrinites magnoliaeformis* (Troost in Wood, 1909)
- Unidentifiable crinoid plates

Girkin (MACA) or Glen Dean Formation (outside of MACA) (Sloans Valley)

- *Pentremites* sp.
- *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- *Pterotocrinus acutus* Wetherby, 1879
- *Pterotocrinus bifurcatus* Wetherby, 1879
- *Pterotocrinus depressus* Lyon and Casseday, 1860
- *Talarocrinus sexlobatus* (Shumard, 1858)
- *Tholocrinus spinosus* (Wood, 1909)

Girkin Formation (Auburn, outside of MACA)

- *Pentremites godoni* (Defrance, 1819)

- *Pentremites pyriformis* Say, 1825
- *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- *Talarocrinus cornigerus* (Shumard, 1858)
- *Talarocrinus sexlobatus* (Shumard, 1858)
- *Zeacrinites magnoliaeformis* (Troost *in* Wood, 1909)
- crinoid pluricolumnal

Haney Formation

- *Pentremites pyriformis* Say, 1825
- *Pentremites* sp.
- *Agassizocrinus occidentalis* (Owen and Shumard, 1852)
- *Phanocrinus maniformis* (Yandell and Shumard, 1847)

[This does not include Pohl and Cushman (1964)'s unique Haney residual chert taxa, which cannot be evaluated: *Pentremites abruptus*, *Pentremites welleri*, *Agassizocrinus conicus*, *Agassizocrinus ovalis*, and *Eupachycrinus* sp.]

Glen Dean Formation

- **Pentremites pyriformis* Say, 1825
- *Phanocrinus maniformis* Burdick and Strimple, 1983
- **Zeacrinites magnoliaeformis* (Troost *in* Wood, 1909)
- *Unidentifiable crinoid plate

Unknown MACA

- *Pentremites* sp. lancet plates
- *Melonechinus indianensis* (Miller and Gurley, 1893)

Chapter 7. Mississippian Marine Vertebrates of Mammoth Cave National Park

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Introduction

The underground cave passages of Mammoth Cave National Park (MACA), Kentucky are geologic windows that cut through deep time and reveal a rich history of life from approximately 340 to 325 million years ago. Park visitors are often inspired by the underground geologic splendor of the wide and open passages along the Historic Entrance Tour Route and encounter both a history of human uses of the cave and occasional glimpses of fossils exposed in the cave's walls (O'Connor Olson 2017). The invertebrate fossils are frequently cited in texts that discuss the fossil history of Mammoth Cave, though little of the fossil faunas has been described in detail (Palmer 1981; O'Connor Olson 2017). However, for vertebrates, the remains of Pleistocene and Holocene species are better known and described in reports and scientific literature (O'Connor Olson 2017; Colburn 2017) by comparison to the teeth and spines of lower Carboniferous chondrichthyans recently encountered in many of the passages within the cave.

Fossils of Mississippian chondrichthyans were not unknown to early cave explorers and park interpreters and were often pointed out on special trips into the deeper passages within the park. However, the extent of the occurrence, diversity, and quality of preservation of these Mississippian-age fishes was not well understood until recently. In the last few years, the significance of these Mississippian vertebrate fossils has become recognized, which led to a concentrated effort to document, collect, and identify these important paleontological resources. Starting in late 2019, a team of park scientists, fossil fish specialists, and cave explorers has worked to document the fossils exposed on cave surfaces in an effort to understand the extent of the Mississippian vertebrate record within MACA. Almost immediately, this team was rewarded with a wealth of information and a large number of new fossil specimens for the MACA collections (Hodnett et al. 2024a). At present,

91 distinct taxa of Mississippian fish have been recognized from four geologic formations within the park. Of the 91 fish identified, approximately 90% represent cartilaginous fishes (Class Chondrichthyes).

Presented here is a summary of the results of the recent field work and research on the Mississippian marine vertebrate fossils documented between November 2019 and the present. This summary contains an overview of the rich vertebrate assemblages recovered from the various geologic horizons within the park, a summary of the significance of the Mammoth Cave Mississippian vertebrate record, and recommendations for further research and public interpretations. We intend to show that MACA is one of the most important fossil parks within the National Park Service system.

Previous Work

Until recently, little has been written on the Carboniferous vertebrates occurring at MACA. The earliest account of a Carboniferous vertebrate fossil is two sets of correspondence between Mammoth Cave general manager (pre-park) Mr. W. W. Thompson and University of Chicago geology professor J Harlen Bretz, dated November 29, 1937, and February 11, 1938. In the first letter from Bretz to Thompson, Bretz was returning a fossil fin spine to Thompson with an explanation of the difficulty of identifying isolated shark spines to a specific species. In the second letter, also from Bretz to Thompson, Bretz identified a fin spine as belonging to a *Ctenacanthus*. He also gave an elaborate description of what the fossil shark spine represented, and how it was deposited at Mammoth Cave (see Chapter 2). Whatever happened to this shark spine is unclear as it is not in the MACA museum collection. During the early 1990s a group of Mammoth Cave guides located cartilaginous fossil remains of a large shark during an after-hours trip in Specimen Avenue. When Rick Toomey and Mona Colburn (Illinois State Museum) were documenting (mostly) Quaternary fossils in the park, they visited this site with Rick Olson, Chuck DeCroix, and a Cave Research Foundation (CRF) crew. During this trip, they confirmed that the fossil cartilage existed and took some photographs of the specimen. The photographs of this specimen were provided to NPS Senior Paleontologist Vincent Santucci in the 2010s. Santucci provided photos of this specimen to JP Hodnett for identification. Hodnett recognized the significance of this fossil and began work on Mammoth Cave chondrichthyans. This specimen is the *Saivodus* skeletal material described below.

Several other reports date from this general time frame. While a CRF team was surveying a passage near Marion Avenue in the early 1990s, the survey crew noted the occurrence of a fish jaw with teeth within the passage ceiling. They included a description in a trip report. One of us (RST) found the trip report and was successfully able to relocate this specimen which proved to be the first record of skeletal material for the ctenacanth shark *Glikmanius* (Hodnett et al. 2024b). Rick Toomey and Rick Olson, along with Bob Osburn and Elizabeth Winkler, also collected a chondrichthyan tooth from a pit at the end of Gothic Avenue during a 2000 mapping trip with CRF. It was collected as part of Toomey's Pleistocene fauna survey (ISM). About a dozen other CRF trip reports prepared between the late 1970s and early 2000s reference shark teeth and fin spines from various localities in Mammoth Cave. Many of these have been followed up on in the recent effort, although some are from areas that have not been revisited.

Current Field and Lab Work

Field work for the MACA shark project has taken place since November 2019. To date, as part of a concentrated effort to document, collect, and identify Carboniferous vertebrate fossils, at least 40 cave passages or lesser caves have been surveyed fully or in part and found to contain Mississippian vertebrate fossils. In addition, another dozen lesser caves and numerous cave passages have been examined, but Mississippian vertebrate fossils were not found in them. Paleontological field work in caves has a variety of challenges. Space limitations in packs restrict the amount of collection gear to what is safe to carry while traversing cave passages. Lighting is limited to what can be brought along. Some fossil sites require a rock saw, hammer, and chisel to remove paleontological specimens with limited breakage, while in other passages, specimens can easily be teased out of the cave surfaces with a pointed tool. Traveling to many of the sites requires crawling for long distances on hands and knees, or even belly crawling, due to low ceilings. Some of the paleontological sites themselves are similarly confined. Some underground stream passages require inflatable kayaks that need to be carried to the launch sites. These kayaks are used to traverse long stretches of deep water, many of which have fish fossils exposed along the walls and ceilings. At many passage localities, the fish fossils are most frequently encountered in the cave ceilings, with cave walls in second place. Fish fossils have only been encountered in place in the cave floor at two sites (Roaring River and Logsdon River). At several sites, fish fossils have been found in blocks of limestone that have detached from the ceiling or wall and are now located on the floor (for example, Logsdon River and Forks of the Cave). In addition, in several places (Specimen Ave, Fossil Ave, Colossal Cave–Grand Ave), cave floor sediment was collected to recover small fish material that had weathered from the ceiling.

To protect the fossils for their transport to the surface, the usual procedure has been to wrap each fossil either in paper towels or toilet paper and place it in a hard-sided container. Recently, we have found that screw-capped sampling tubes lined with cotton balls work well. Our primary method is to remove all but one cotton ball, carefully tease the fossil from the cave surface into the tube, place a cotton ball on top, and continue to the next specimen. We repeat this method until the tube is full and record our locality information on the tube. This method is extremely useful in areas where there is a high concentration of vertebrate material in a small area.

For the large and fragile skeletal cartilages of chondrichthyans, we decided that collecting was not an option. These sites are difficult to access even without considering the logistics necessary to bring the needed power tools, or the feasibility of safely and properly operating them in the close confines of the sites, or how to safely transport the resulting slabs. Additionally, traditional casting methods with latex-based compounds might be deleterious to the specimens. Instead, photogrammetry was chosen as the best way to document these fossils. Photogrammetry has been used to make high-quality models of museum specimens (Hamm et al. 2018) and camera equipment is sufficiently easy to transport within the cave passages. We utilized photogrammetry to gather three-dimensional data that was later used to generate computer models that can be three-dimensionally studied and printed without having to remove the specimens. Using the 3D data from photogrammetry, a printed voucher specimen created from rapid prototyping technologies can be placed in the MACA museum collections for description and review purposes. Thus, photogrammetry solves the issue of specimen access that arose from the decision to leave the specimens in situ.

Photogrammetry was achieved by bringing a portable studio into the cave. This was no small effort but was necessary to ensure the integrity of these important specimens while providing detailed spatial information. Equipment included battery-powered LED panel lights, a tripod with swivel camera mount and extension arm, and a portable Wi-Fi network for control of the camera with a tablet computer. This was in addition to the standard caving gear of helmet, three light sources, pack, knee and elbow pads, lunch, and water for the day. Images were captured with a Nikon D810 affixed with a Nikkor 24 mm f/1.4 AF lens. The lights were mounted on tripods to illuminate the fossils; these lights have variable temperature and brightness settings. They were used in lieu of flash units that might be brighter, but tend to have an outwardly dimming circumference of light. Instead, the LEDs provide a more uniform if slightly dimmer illumination. The camera was mounted on the tripod with a counterbalanced extension arm, which permitted inverting the camera to follow the pattern of photography suggested by Mallison and Wings (2014) and Matthews et al. (2016). Images were acquired by remote control and reviewed for clarity on the tablet. Camera settings were set to aperture priority, with the focal ring on the lens set to manual and tapped down to maintain the continuity of optical settings within the camera. Control sticks were placed on the walls and ceiling of the cave passage, with placement determined by where they could remain in place, often with the use of nails, tacky putty, or both. These control sticks provide scaling: the distance between targets is known to 0.1 mm (0.004 in) or better, and errors are ± 0.03 mm (0.001 in) or better. Imagery was recorded to the camera as raw images (NEF format for Nikon) and as .jpg files to provide reference images. The reference images could be downloaded from the camera and processed with the photogrammetry software to ensure image overlap and placement were sufficient.

The 3D surface models of the cave walls and fossils were completed in a multipart process. Processing of raw imagery to finished 3D models was completed on a Windows operating system machine, with an Intel i9 CPU processor, a single NVIDIA GTX 1080 GPU, and 64 Gb RAM. Raw images were converted to .tif format using Adobe Bridge; image exposure, color settings (such as contrast and brightness), and chromatic aberration can be altered without affecting the fidelity of the imagery for processing. Images were then aligned in AGISoft MetaShape professional (version 1.5.4; build 8885) using the high setting. A good alignment is assumed if the pattern of photography is uniformly spaced and the software calculated value for “average tie point multiplicity” is ~3 to ~5 (dimensionless). This is diagnostic of the number of pixels in the sparse cloud generated in alignment and the average number of images used to calculate the coordinates of the point. The image alignment is then refined using a stepwise process with the “gradual selection” tool to winnow those points with lower confidence as identified by the software, until the Max RMS error is approximately 0.5 pixel. The control sticks within the imagery then become key to additional point cloud refinement as the software will solve for a lens factor (e.g., k4, etc.) that is scale-dependent. This highly refined sparse cloud is then the foundation for generation of the dense cloud and the mesh of the final model. All models, source imagery and associated metadata, as well as non-proprietary 3D data format files, are deposited in the National Park Service’s Integrated Resources Management Applications Portal (IRMA), available online.

Cave floor sediments were collected from four localities (Specimen Ave, Colossal Ave, Fossil Ave, and Cox Ave, localities discussed below) to search for microvertebrate specimens (vertebrate fossils

with dimensions 1 mm [0.04 in] or less). These sediments are run through a stack of graded sieves and flushed with flowing water until the heavier concentrations are left behind. The graded concentrations are then picked through using a stereo microscope. Cleaning of fossils from Mammoth Cave typically requires only a pin vise and a toothbrush to remove sediment. Fossils in larger chunks of rock can be cleaned with an electric engraving tool equipped with a carbide needle. To remove fine-grained mud and silt from fossils from river passages, these fossils can be cleaned with a simple solution of diluted acetic acid (white vinegar) and water.

All collected specimens (approximately 400+) are housed in MACA museum collections. A database of collected and in situ specimens is on file in the park archives.

Recently, two abstracts and posters were presented to the 2020 and 2021 Society of Vertebrate Paleontology Virtual Meetings, providing a preliminary account of the vertebrate assemblages of the Joppa Member of the Ste. Genevieve Formation and Horse Cave Member of the St. Louis Formation at MACA (Hodnett et al. 2020, 2021a). They have been succeeded by the first formal publications (Hodnett et al. 2023, 2024a, 2024b).

Institutional Abbreviations—ISM, Illinois State Museum, Springfield, Illinois; **MACA**, Mammoth Cave National Park, Kentucky.

Mississippian Marine Vertebrate Localities and Assemblages of Mammoth Cave National Park

The Carboniferous rocks found at MACA represent one of the southeasternmost portions of the ancient marine Illinois Basin (Palmer 1981). The Illinois Basin is historically significant to early American paleoichthyology because a large number of mid to late Paleozoic fish fossils were collected and described from other states in the basin such as Missouri, Illinois, Iowa, and Indiana (Newberry and Worthen 1870; St. John and Worthen 1875, 1883). At the time, these early collections were compared to similar fossils from Europe, which formed the basis for modern Paleozoic chondrichthyan paleoichthyology. However, even though there is a rich fossil record of Paleozoic fish from the Illinois Basin, these North American assemblages have yet to be compared with better-described assemblages elsewhere around the world.

As stated above we presently recognize 91 distinct taxa of Middle and Late Mississippian fishes within MACA (Appendix F), the majority of which represent the class Chondrichthyes. Both major groups of chondrichthyans are present: the shark-like elasmobranchs (Figure 140) and euchondrocephalans (=holocephalans), including ancestors of extant ratfish and kin (Figure 141). Both of these groups are represented in the St. Louis, Ste. Genevieve, Girkin, and Haney Formations, with some horizons having highly diverse assemblages (Figure 142). Below is a summary of the Carboniferous marine vertebrate assemblages found at MACA. (A geologic time scale is included as an appendix to this inventory, Appendix I.)

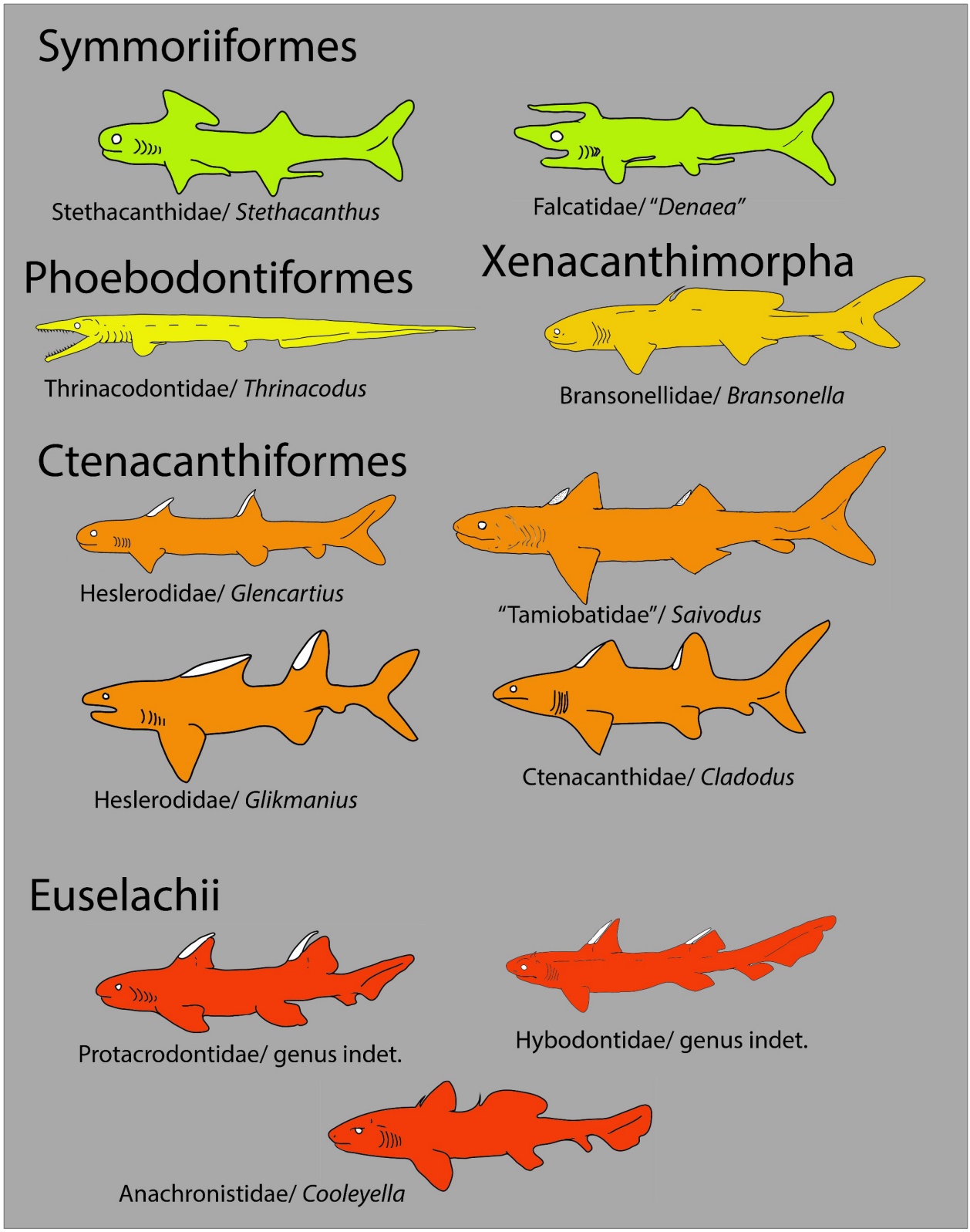


Figure 140. Key to the major shark-like taxa of chondrichthyans found at MACA as seen in Figure 142. Taxa not drawn to scale. NPS / JP HODNETT

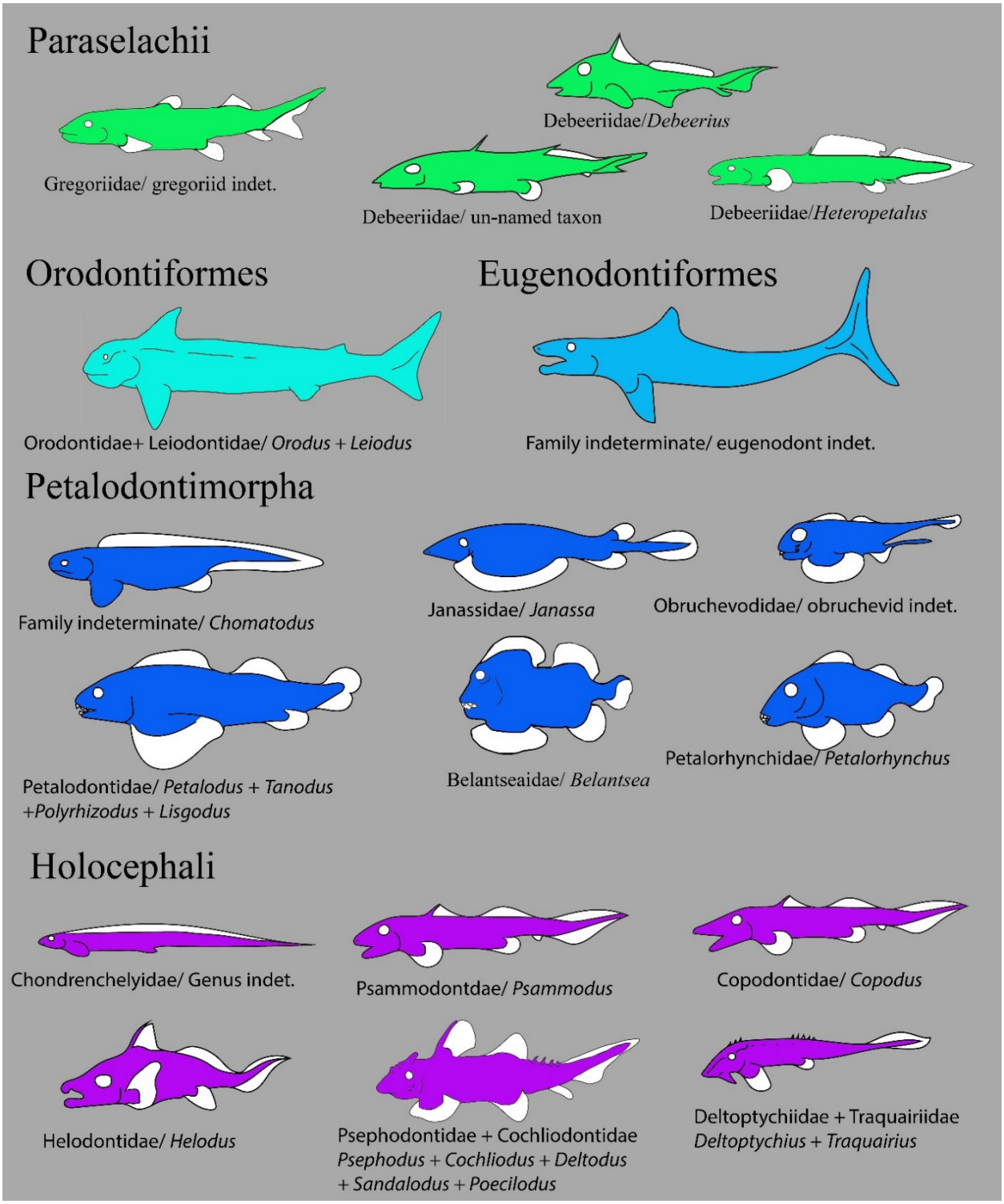


Figure 141. Key to the major “ratfish group” taxa of chondrichthyans found at MACA as seen in Figure 142. Taxa not drawn to scale. NPS / JP HODNETT

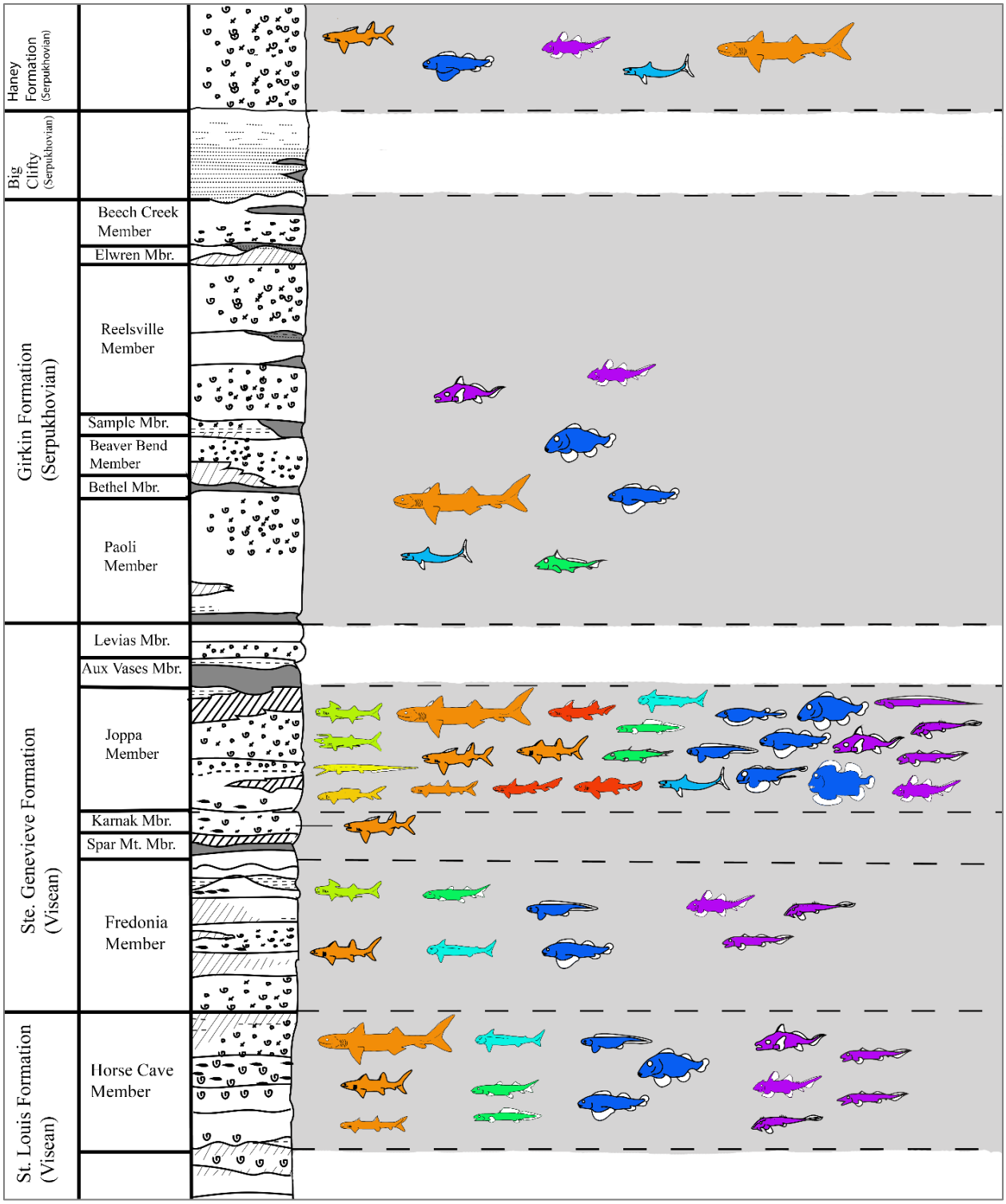


Figure 142. The stratigraphic distributions of the major chondrichthyan taxa found at MACA. NPS / JP HODNETT (MODIFIED FROM PALMER 2007)

Vertebrate-Bearing Geologic Formations of Mammoth Cave National Park

St. Louis Formation (Middle Mississippian: early Viséan)

The St. Louis Formation is an extensive geologic formation in the central United States with a historical place in the early research on Paleozoic fish in North America. The St. Louis Formation is typically characterized by micritic (carbonate grain size approximating a mudstone) to lutitic (approximating a siltstone or claystone) limestone beds, dark shales, and grayish green shales (Sable and Dever 1990). Chert beds and nodules and invertebrate fossils are common within the St. Louis Formation (Butts 1917; Palmer 1981; Chapter 3 in this volume).

The earliest accounts of marine vertebrate fossils from the St. Louis Formation (cited as the St. Louis Limestone) were chondrichthyan teeth and dermal elements described by Newberry and Worthen (1870) and St. John and Worthen (1875, 1883) from Missouri, Illinois, and Iowa. However, these fossils were not put into the overall local stratigraphic context within the St. Louis Formation itself. As a result, descriptions of the various vertebrate faunal assemblages within the St. Louis Formation were never formulated. At present, little work has been done on the vertebrates of the St. Louis Formation with the exception of a few taxa (Hampe et al. 2006), though discoveries by local amateur and hobbyist fossil collectors and cavers are common in the region (JPH, pers. obs. and pers. comm.).

Although it has not been mapped on the surface in the park, approximately the upper 12 m (40 ft) of the Horse Cave Member of the St. Louis Formation is exposed in some of the lowest elevation passages in the Mammoth Cave system. These passages represent some of the youngest passages in the system. All passages in the St. Louis are subject to flooding. The exposures of the St. Louis in cave passages reveal several important paleontological resources including Mississippian marine vertebrates and large fossil burrows.

St. Louis Formation Passage Localities

Vertebrate fossils are presently recognized from three primary passages: Roaring River, Martel Avenue (and nearby Becky's Alley), and Logsdon River/Bridge Avenue.

Roaring River—Numerous vertebrate remains are found along a 1.6 km (1 mi) stretch of the passage in which the namesake underground river flows. This site is accessible from kayaks when the water levels are at their lowest (Figure 143). Teeth and dermal fin spines of chondrichthyans, particularly large dorsal fin spines, are locally common in the passage walls and ceiling. When water levels are at their lowest, teeth and spines are also encountered along exposed areas of the cave floor. These elements are well-preserved, though some show signs of water wear. Hand tools such as chisels, hammers, and portable rock saws were required to remove most of the vertebrate fossils, as the limestone is rather hard. In some cases, a battery-powered angle grinder with a tile blade has been used to remove well-imbedded shark fossils.

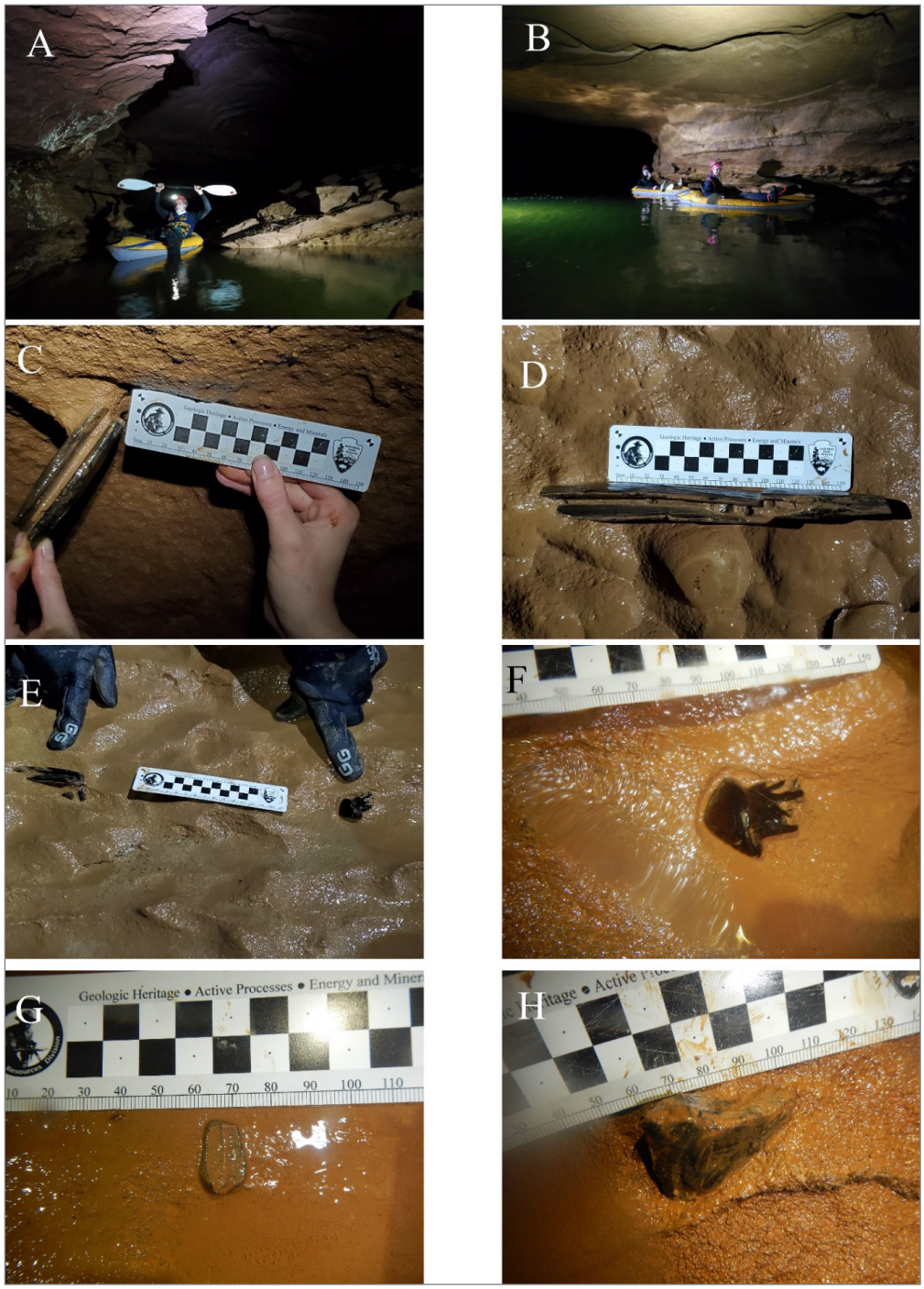


Figure 143. Field work and documentation of St. Louis Formation fossil chondrichthyans from the Roaring River passage locality, October 10, 2020. **A.** Rick Olson in kayak, using a paddle to demonstrate the scale of some of the narrow waterways in Roaring River. **B.** Marissa Schorr (right) and Kelli Tolleson (left) investigating the passage walls for vertebrate fossils in kayaks. **C.** Partial large ctenacanth dorsal fin spine fragment, exposed along cave wall. **D.** Smaller ctenacanth dorsal spine, exposed along the cave wall. **E.** Ctenacanth spine (left) and the tooth of the petalodont *Polyrhizodus concavus*, exposed together on the cave floor. **F.** Close-up of the *Polyrhizodus concavus* tooth. **G.** Tooth plate of the holocephalan *Psephodus* sp. on the cave floor. **H.** Very large *Psammodus* sp. tooth plate in the cave wall. Scale for **C–H** includes centimeters (squares) and millimeters (tick marks). NPS / JP HODNETT & NPS

Martel Avenue—A few exposed teeth and dermal elements are encountered in hard limestone walls of Martel Avenue towards Edna's Dome (Figure 144) and in Becky's Alley. These passages are along MACA's Wild Cave tour route. Only photographic sampling was used as a means of documentation, in order to preserve the specimens for future interpretive tours.

Logsdon River/Bridge Avenue—A number of chondrichthyan teeth and dermal elements, and a partial chondrichthyan neurocranium are exposed along the upper walls and ceiling of the Logsdon River/Bridge Avenue passage (Figure 145). Access to this site is difficult; the most direct access point utilizes an approximately 60 cm (24 in) diameter drilled shaft that people and equipment such as stepladders must descend by rope approximately 24 m (79 ft).

Echo Cave—A single large *Saivodus striatus* tooth was collected from rock fall debris at Echo Cave.

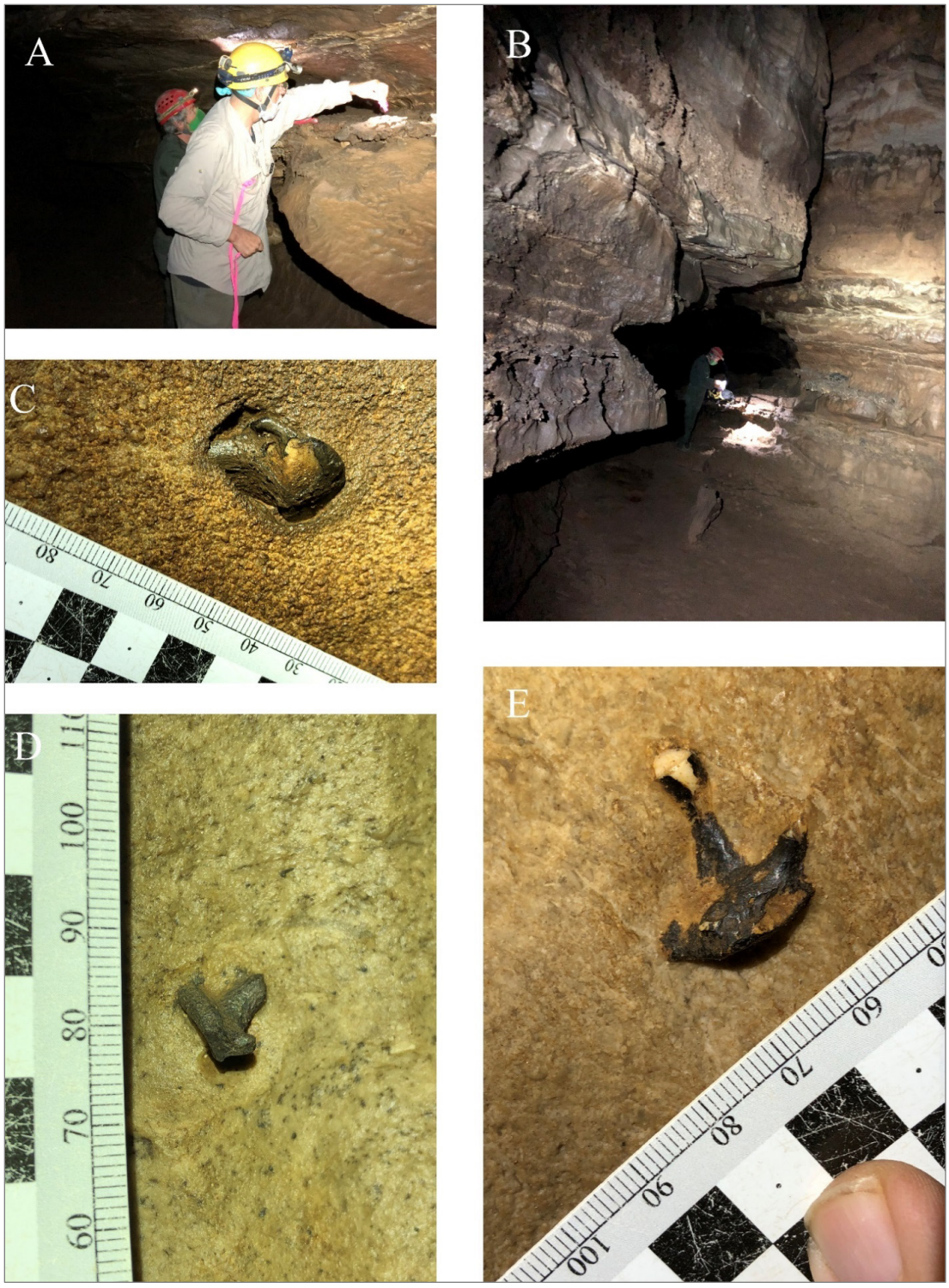


Figure 144. Documentation of chondrichthyan fossils from the St. Louis Formation along Martel Avenue. **A.** Rick Toomey (left) and Rick Olson (right) marking the locality of a petalodont tooth, exposed under the ledge they are standing next to. **B.** Rick Toomey looking for vertebrate fossils. **C.** Tooth of *Polyrhizodus concavus* as exposed under a ledge. **D.** Tooth of a small indeterminate ctenacanthiform. **E.** Large ctenacanthiform tooth. Scale for **C–E** includes centimeters (squares) and millimeters (tick marks). NPS / JP HODNETT & NPS



Figure 145. Field photos of in situ chondrichthyan fossils from Logsdon River. **A.** Tooth of *Polyrhizodus concavus*. **B.** Tooth of *Troglocladodus trimblei*. **C.** Tooth of *Cladodus elegans*. **D.** Tooth of *Leiodus calcaratus*. **E, F.** Partial chondrichthyan neurocranium, in two associated pieces, in the cave ceiling: **E.** The otic region exposed ventrally; **F.** The occipital cotylus exposed ventrally. Scale includes centimeters (squares) and millimeters (tick marks). NPS / RICK OLSON

St. Louis Formation Horse Cave Member Assemblage

At present only the class Chondrichthyes is documented from the Horse Cave Member of the St. Louis Formation at MACA. Currently, 20 taxa (Table 7) of chondrichthyans have been identified from isolated or closely associated teeth, which are more reliable to understand chondrichthyan diversity compared to isolated dermal spines and denticles (Ginter et al. 2010). However, several dorsal fin spine elements were collected as well. Below is a summary of the taxa identified from the Horse Cave Member.

Ctenacanthiformes—Ctenacanthiformes was a distinct order of elasmobranch chondrichthyans that represented a sister group to the modern shark (Infraclass Euselachii) lineage. Several teeth and dorsal fin spines have been collected from the Roaring River passage site, showing a diversity of small to large ctenacanthiform sharks (Figure 146). The name for Ctenacanthiformes, the "comb spine" sharks, is derived from the dorsal fin spines which bear posterior-facing hook-like denticles and longitudinal costae or ridges that bear denticle-like ornamentation. The ornamented sections were externally exposed while the non-ornamented areas were covered by skin and tissues. The largest dorsal spine specimen collected to date from Roaring River is a 10 cm (4 in) long by 4.5 cm (1.8 in) wide section of a dorsal fin spine representing the upper part of the basal insertion shaft and the lower ornamented rows of the main spine body (Figure 146A to 146C). The ornamentation on the spine consists of small circular tubercles that are similar to those of the spine taxon *Bythiacanthus*, a member of the Heslerodidae family of ctenacanths which had deep attachment bases and short spines (Maisey 1982, 2010). In terms of specific designation, the *Bythiacanthus* spine from Roaring River is similar to *Bythiacanthus siderius*, which is also known from the St. Louis Formation near Alton, Illinois (Maisey 2010). A number of smaller fragments of ctenacanth spines from Roaring River could also be allied to *Bythiacanthus*. A smaller (7.5 cm [3.0 in] long) isolated spine fragment collected from Roaring River was partly mediolaterally crushed but exhibits both smooth costae and costae with elliptical tubercles along a longitudinal ridge (Figure 146D and 146E). This spine represents the lower midsection of the ornamented face and the upper insertion base. This morphology is similar to *Ctenacanthus venustus* (Newberry 1873; Maisey 1981).

Table 7. The vertebrate assemblage of the Horse Cave Member of the St. Louis Formation at MACA. All are chondrichthyans.

Higher Classification	Genus and Species	Roaring River	Martel Avenue	Logsdon Bridge	Echo Cave
Elasmobranchii: Ctenacanthiformes: Ctenacanthidae	*Cladodus elegans*	Y	–	Y	–
	cf. *Ctenacanthus venustus*	Y	–	–	–
	Troglocladodus trimblei	Y	Y	Y	–
	Genus and species indet. 1	Y	Y	–	–
Elasmobranchii: Ctenacanthiformes: “Tamiobatidae”	*Saivodus striatus*	Y	–	–	Y
Elasmobranchii: Ctenacanthiformes: Heslerodidae	cf. *Bythiacanthus siderius*	Y	–	–	–
	Glencartius costellatus	–	–	Y	–
	Glikmanius careforum	Y	–	–	–
Elasmobranchii: Euselachii	*Amelacanthus* sp.	Y	–	–	–
Euchondrocephali: Paraselachii	Paraselachid indet. 1	Y	–	–	–
	Paraselachid indet. 2	Y	–	–	–
Euchondrocephali: Orodontiformes: Leiodontidae	*Leiodus calcaratus*	–	–	Y	–
Euchondrocephali: Orodontiformes	Genus and species indet. 1	Y	–	–	–
Euchondrocephali: Petalodontimorpha	*Chomatodus* sp. 1	Y	–	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalodontidae	*Tanaodus pumilis*	Y	–	–	–
	Polyrhizodus concavus	Y	Y	Y	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalorhynchidae	*Petalorhynchus pseudosagittatus*	Y	–	Y	–
Euchondrocephali: Holocephali: Helodontiformes: Helodontidae	*Helodus* sp.	Y	–	Y	–
Euchondrocephali: Holocephali: Cochliodontiformes: Psephodontidae	*Psephodus* sp.	Y	–	Y	–

Table 7 (continued). The vertebrate assemblage of the Horse Cave Member of the St. Louis Formation at MACA. All are chondrichthyans.

Higher Classification	Genus and Species	Roaring River	Martel Avenue	Logsdon Bridge	Echo Cave
Euchondrocephali: Holocephali: Cochliodontiformes: Cochliodontidae	*Cochliodus* sp.	Y	–	–	–
	Deltodus sp.	Y	Y	Y	–
	?*Poecilodus* sp.	–	–	Y	–
	Sandalodus sp.	Y	–	Y	–
Euchondrocephali: Holocephali: Psammodontiformes: Psammodontidae	*Psammodus* sp.	Y	–	–	–
Euchondrocephali: Holocephali: Copodontiformes: Copodontidae	*Copodus cornutus*	Y	–	–	–
Euchondrocephali: Holocephali: Menaspiformes: Deltoptychiidae	*Deltoptychius* sp.	Y	–	Y	–
Euchondrocephali: Holocephali: Menaspiformes: Traquairiidae	cf. *Traquairius* sp.	Y	–	–	–

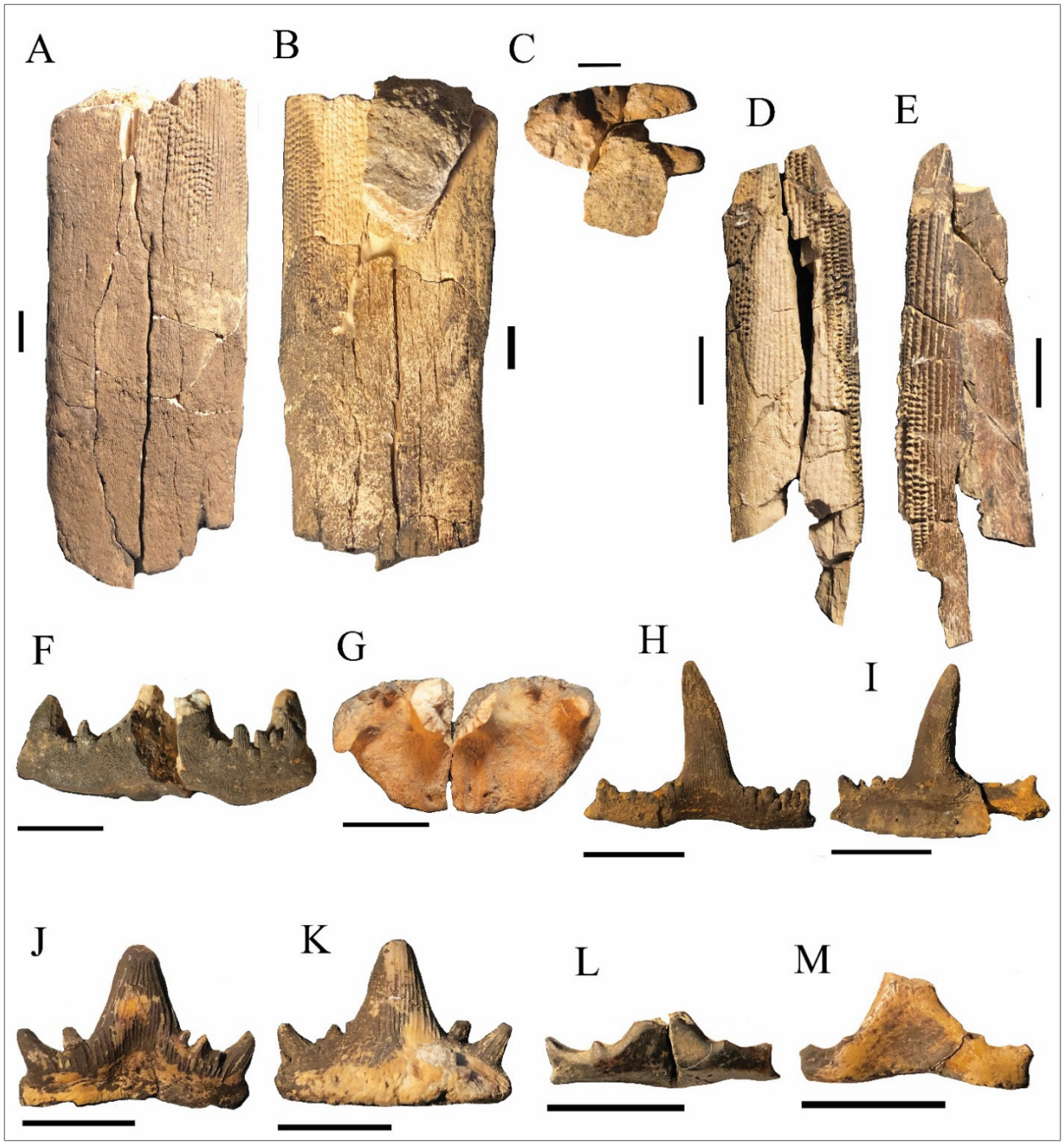


Figure 146. Ctenacanthiform spines and teeth from the St. Louis Formation at MACA. **A–C**, MACA RRCT1, cf. *Bythiacanthus siderius*, dorsal fin spine fragment from Roaring River passage: **A.** Right lateral view; **B.** Left lateral view; **C.** Distal cross-section. **D, E.** MACA RRJPH002, cf. *Ctenacanthus venustus*, dorsal fin spine fragment from Roaring River passage: **D.** Right lateral view; **E.** Left lateral view. **F–I**, *Saivodus striatus* teeth from Roaring River passage: **F, G.** MACA 61966; **F.** Labial view; **G.** Oral view. **H, I**, MACA RR01KT: **H.** Labial view; **I.** Lingual view. **J, K.** MACA 62133, *Troglocladodus trimblei* tooth from Roaring River passage: **J.** Labial view; **K.** Lingual view. **L, M,** *Cladodus elegans* teeth from Roaring River passage: **L.** MACA RRJPH008B, labial view; **M.** MACA RR02RAO, labial view. Scale = 1 cm (0.4 in). NPS / JP HODNETT

Isolated ctenacanth teeth are somewhat common in the Roaring River passage. Presently four taxa can be confidently identified along with a fifth indeterminate form. The largest and presently most common ctenacanth tooth taxon from Roaring River is *Saivodus striatus*, which marks the oldest *Saivodus* samples found at MACA (Figure 146F to 146I). The average *Saivodus* teeth from this site are between 2.0 and 4.0 cm (0.8 and 1.6 in) wide at the tooth base. Teeth of *Saivodus* seem to be common in a number of Mississippian fish fossil localities that include sites in Alabama, Arkansas, Indiana, Iowa, Missouri, and possibly Montana (Duffin and Ginter 2006). A second large ctenacanth tooth taxon, *Trogloclad odus trimblei*, is known from a well-preserved tooth from the Roaring River passage that is 2.0 cm (0.8 in) wide at the tooth base (Figure 146J and 146K). Another potential specimen is located along the old Martel Avenue tour trail. This is a new taxon recognized from both the Middle and Late Mississippian of Kentucky and Alabama (Hodnett et al. 2024b). Two teeth of *Cladodus elegans*, a species that has smaller and thinner crowns compared to the more robust *Trogloclad odus trimblei* teeth, were recently collected from Roaring River. Presently it is only known from the St. Louis Formation at Mammoth Cave (Figure 146L and 146M). This tooth is approximately 1.5 cm (0.6 in) wide at the base. *Cladodus elegans* is also significant as one of the few ctenacanth taxa known to have cranial skeletal material preserved. A partial skull of *Cladodus elegans* with jaws is known from the Lower Limestone Formation of Lugton, Ayrshire, Scotland (Ginter and Maisy 2007). Isolated teeth of *Cladodus elegans* are also known from the St. Louis Formation of Missouri and possibly Iowa (Duffin and Ginter 2006). A fourth identifiable taxon was added in April 2021 when a tooth of *Glencartius costellatus* was collected from Logsdon Avenue. *Glikmanius careforum* was identified from a single tooth from Roaring River (Hodnett et al. 2024b). A sixth and to date indeterminate ctenacanth taxon is based on small crown and tooth base fragments from Roaring River and a small partially exposed tooth along Martel Avenue.

Euselachii—Euselachians is a broad group that includes both hybodonts and neoselachians. A single small spine fragment (7 mm [0.3 in] long) is referable to the spine taxon *Amelacanthus*, which bears smooth, closely spaced, longitudinal costae and posteriorly directed denticles near the upper third of the spine (Maisey 1982). Maisey (1982) suggested that *Amelacanthus* was closer to neoselachians (the modern shark lineage) than to hybodontids or ctenacanths.

Paraselachii—At least three teeth were collected that can be attributed to at least two taxa of paraselachians. Paraselachians are basal members of the Euchondrocephali, the group that contains extant Holocephali (ratfish and chimaeras) (Lund and Grogan 1997a). Paraselachians are known from several complete to nearly complete skeletons from the Late Mississippian of Montana. Unlike holocephalans, paraselachians do not have tooth plates, instead having individual tooth families; nor are the upper jaws (palatoquadrates) fused with the neurocranium, but instead are free mandibular arches attached by ligaments (Lund and Grogan 1997a). At least two distinct families are known within Paraselachii, Debeeriidae and Gregoriidae (Grogan and Lund 2000; Lund and Grogan 2004a).

The three paraselachian teeth collected from Roaring River are 0.5–1.0 cm (0.2–0.4 in) in length, with low enameloid crowns and rather deep but labiolingually compressed bases (Figures 147A to 147E). Two of these teeth have slight triangular peaks and a slight cingulum on the cusp. The other tooth has a rather straight crown. At this time, it is difficult to place these teeth into either of the two

families of paraselachians, and scanning electron microscopy may be necessary to observe their diagnostic features.

Orodontiformes—The Orodontiformes is a diverse group of euchondrocephalan chondrichthyans that contains at least two families, Orodontidae and Leiodontidae (Ginter et al. 2010). Complete specimens from the black shale beds of Indiana and Illinois indicate they had elongated bodies with blunt heads, small pectoral and pelvic fins, and robust jaws with crushing teeth (Zangerl 1981; Ginter et al. 2010). A few small teeth (1.0–1.5 cm [0.4–0.6 in] in length) of an indeterminate orodontid chondrichthyan are recognized from the Roaring River passage (Figures 147F and 147G). This taxon is also known from the Joppa Member of the Ste. Genevieve Formation (see below). These teeth are unique compared to other orodontiforms such as *Orodus* and *Leiodus* in that the Mammoth Cave taxon lacks the glossy enameloid shine seen in the other genera (Ginter et al. 2010). Instead, the Mammoth Cave taxon has a rough, almost fibrous, crown that is either domed or comes to a short triangular point. At this time the Mammoth Cave taxon is considered a unique, possibly new taxon. Recently, a single tooth of *Leiodus calcaratus* (Figures 147H to 147J) was collected from Logsdon Avenue.

Petalodontimorpha—The petalodont chondrichthyans are an extinct sister group to the Holocephali that retained true teeth that are typically petal-like in shape (Ginter et al. 2010; Lund et al. 2014). This group of chondrichthyans had a diverse array of body morphologies, including eel-like, skate-like, and boxfish-like forms (Zangerl 1981; Lund 1986, 1989; Grogan et al. 2014; Lund et al. 2014). At least four petalodontimorphs are recognized at this time from the St. Louis Formation at MACA.

At present, a single tooth of *Chomatodus* sp. is known from the Roaring River passage locality (Figure 148A), whereas in the Ste. Genevieve Formation this taxon is very common. A small tooth of *Tanaodus pumilis* (Figures 148D and 148E) was collected from the Roaring River passage; this species is also known from the St. Louis Formation in Illinois and Iowa (St. John and Worthen 1875; Ginter et al. 2010). A single complete tooth of *Polyrhizodus concavus* (Figures 148B and 148C) was collected from the Roaring River passage, a second seemingly complete tooth is exposed under a short ledge along the Martel Avenue passage trail, and a third specimen has been identified from Logsdon River. *Polyrhizodus concavus* is also known from the St. Louis Formation in Illinois and may have extended into the Middle Pennsylvanian of the Moscow region of Russia (Ginter et al. 2010). Four teeth of *Petalorhynchus pseudosagittatus* (Figures 148F to 148K) were collected from the Roaring River passage, two of which were in close association. *Petalorhynchus pseudosagittatus* is also known from the St. Louis Formation of Illinois, Iowa, and Missouri (St. John and Worthen 1875; Ginter et al. 2010). A cranium of *Petalorhynchus* is known from the Late Mississippian-age Bear Gulch Limestone of the Heath Formation of Montana, demonstrating that this petalodont had a heterodont dentition in which the teeth formed a beak-like arrangement at the end of the upper and lower jaws, and were relatively small in proportion to the cranium itself (Lund et al. 2014).

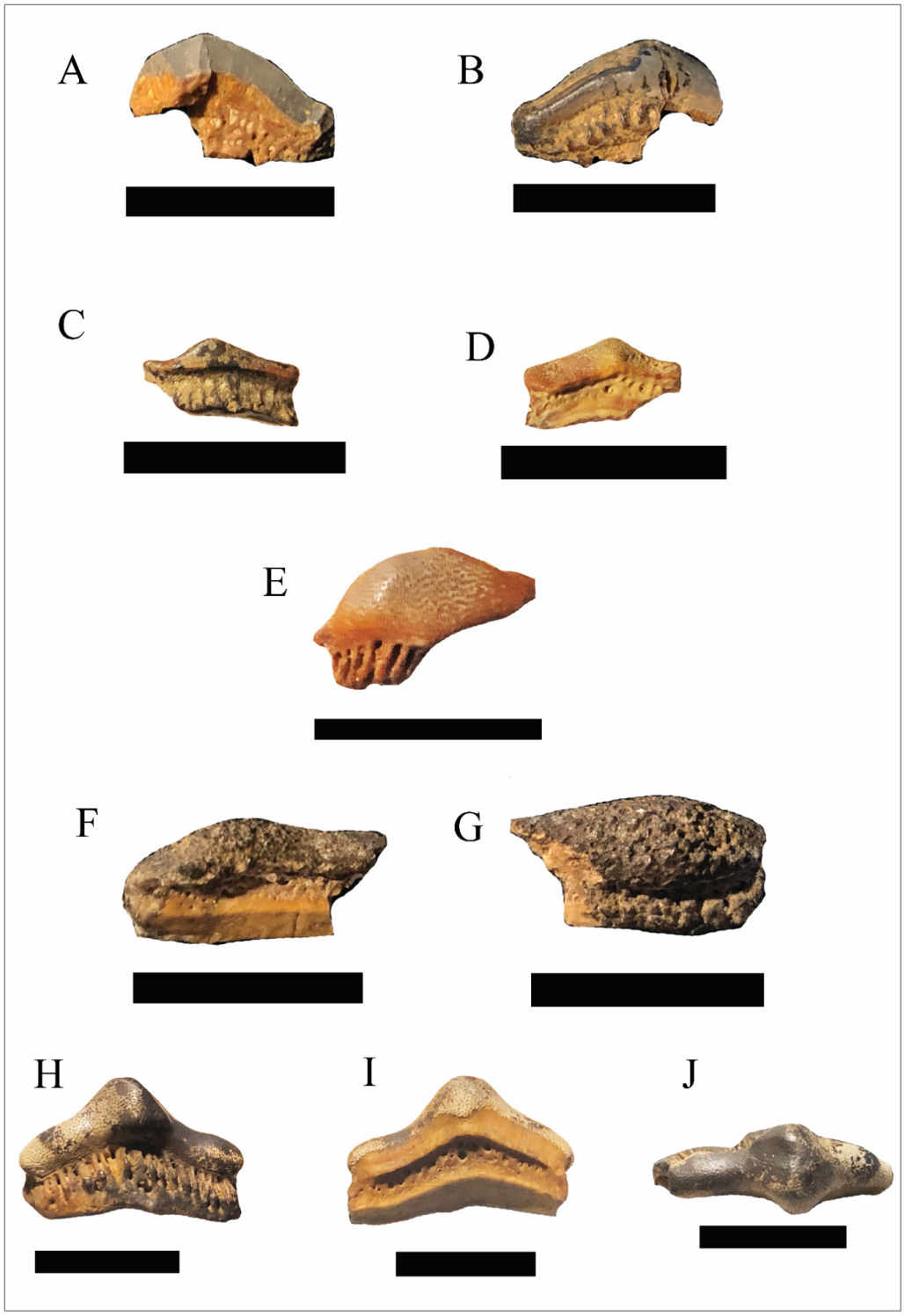


Figure 147. Paraselachian and orodontiform chondrichthyans from the St. Louis Formation at MACA. **A–D.** Indeterminate paraselachian teeth: **A–B.** MACA RR005F, **A.** Labial view; **B.** Lingual view. **C, D.** MACA RR0012C: **C.** Lingual view; **D.** Labial view. **E.** Indeterminate euchondrocephalan tooth, lingual view. **F–J.** Orodontiform teeth: **F, G.** MACA RRMS001, Orodontiformes indet.: **F.** Labial view; **G.** Lingual view. **H–J.** MACA LBBan003, *Leiodus calcaratus*: **H.** Lingual view; **I.** Labial view; **J.** Oral view. Scale = 1 cm (0.4 in). NPS / JP HODNETT

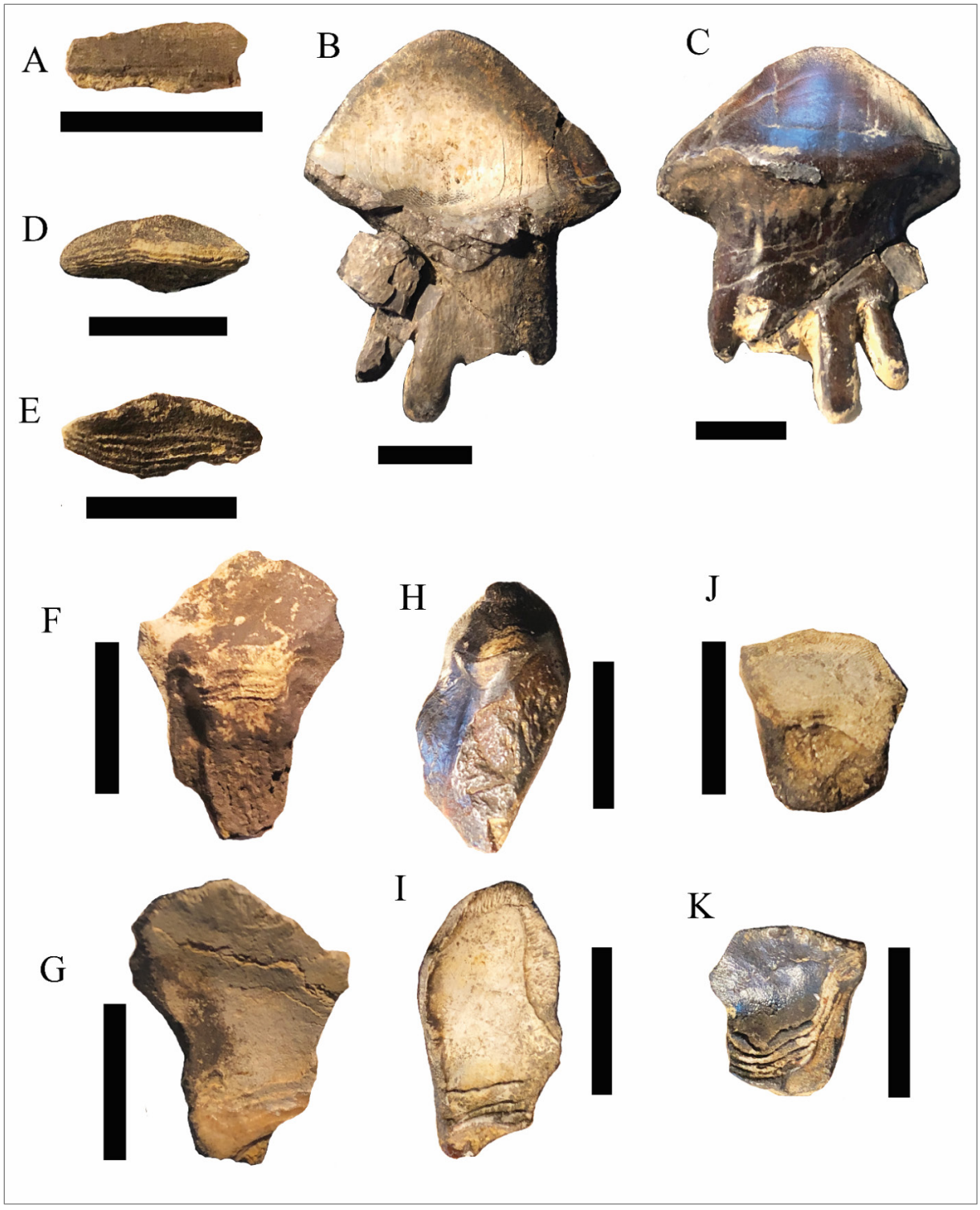


Figure 148. Petalodontimorph fossils from the St. Louis Formation of MACA. **A.** *Chomatodus* sp. in lingual view. **B, C.** MACA RRJPH001, *Polyrhizodus concavus*: **B.** Lingual view; **C.** Labial view. **D, E.** MACA RRPT1, *Tanaodus pumilis*: **D.** Labial view; **E.** Lingual view. **F–K.** *Petalorhynchus pseudosagittatus*: **F, G.** MACA LBBan004: **F.** Labial view; **G.** Lingual view. **H, I.** MACA RR014A: **H.** Labial view; **I.** Lingual view. **J, K.** MACA RRJPH008Q: **J.** Labial view; **K.** Lingual view. Scale = 1 cm (0.4 in). NPS / JP HODNETT

Holocephali—The Holocephali are a group of chondrichthyans that are still extant, with approximately 50 living species identified, as well as a diverse fossil record (Didier 1995; Stahl 1999). The extinct forms had diverse body forms and dental arrangements (Stahl 1999). Holocephalans are characterized by upper jaws that are fused with their cranium and posterior dentition consisting primarily of paired dental plates (Stahl 1999). Some groups have a single narrow elongated anterior dorsal fin spine, which in some extinct male specimens curves forward over the cranium (Stahl 1999). Other extinct species bore elaborate facial spines or pronounced cranial plates (Lund and Grogan 1997b, 2004b; Stahl 1999).

A single partial holocephalan spine was collected from the Roaring River passage locality and consists of two pieces preserved on a small limestone rock. The spine is partially water-worn, making specific diagnosis difficult. Many identifiable teeth and tooth plates of holocephalans were collected from the Roaring River and Logsdon River/Bridge Avenue localities. In addition, a few indeterminate holocephalan tooth plates can be seen in the Martel Avenue passage. Isolated anterior teeth of the basal holocephalan *Helodus* sp. have been collected from the Roaring River and Logsdon River passage localities (Figures 149A to 149C). *Helodus* is a widely distributed taxon, known worldwide from isolated teeth, including examples from the Redwall Limestone and Surprise Canyon Formation at Grand Canyon National Park, Arizona, that are approximately equivalent in age to the Middle Mississippian rocks at MACA (Hodnett and Elliott 2018; Hodnett et al. 2021b). Complete to nearly complete skeletons and isolated crania of the type species, *Helodus simplex*, are known from the latest Mississippian of Great Britain (Stahl 1999). A variety of teeth referable to *Psephodus* sp. were collected from the Roaring River and Logsdon River localities (Figures 149D and 149E). *Psephodus* is also known from single tooth plates from the Redwall Limestone and early Permian Kaibab Formation at Grand Canyon National Park (Hodnett and Elliott 2020; Hodnett et al. 2021b). *Psephodus* is widely distributed in North America, Eurasia and Australia and is known from the Late Devonian to early Permian (Stahl 1999). A single tooth plate of a small *Cochliodus* sp. was collected from the Roaring River passage locality. At least two species have been described from the St. Louis Formation in Missouri and Illinois, *Cochliodus obliquus* and *Cochliodus vanhorni* respectively (St. John and Worthen 1883). However, more specimens will be needed to determine if the Mammoth Cave *Cochliodus* is either of these two species or distinct. *Cochliodus* is primarily known from the Mississippian in North American and Eurasia (Stahl 1999). Tooth plates of *Deltodus* sp. are known from both the Roaring River and Logsdon River/Bridge Avenue localities. *Deltodus* is another widely distributed holocephalan, known from the Mississippian to the early Permian of North America and Eurasia (Stahl 1999), including records in the uppermost Mississippian Surprise Canyon Formation, the Lower Pennsylvanian Watahomigi Formation, and the lower Permian Kaibab Formation of Grand Canyon National Park (Hodnett and Elliott 2018, 2020). Larger tooth plates of *Sandalodus* sp. have been collected from Roaring River and Logsdon Bridge Avenue (Figure 149F). At least two species of *Sandalodus* are known from the St. Louis Formation in Indiana and Illinois, *S. porcatus* and *S. spatulatus* respectively (St. John and Worthen 1883; Branson 1905; Stahl 1999). However, more specimens are required to determine the specific designation of the Mammoth Cave *Sandalodus*.

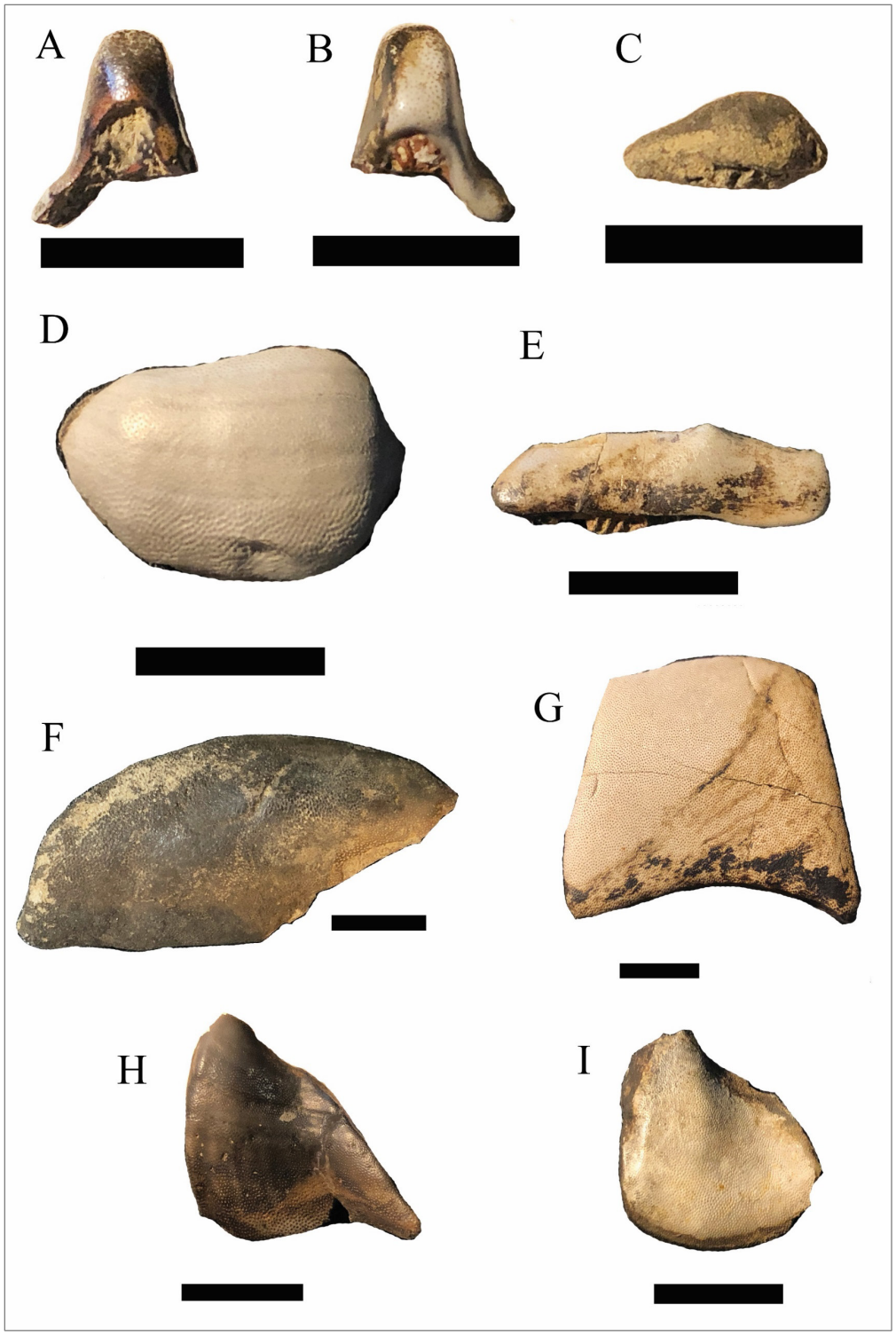


Figure 149. Holocephalan fossils of the St. Louis Formation at MACA. **A–C.** Teeth of *Helodus* sp.: **A, B.** MACA RR012A, anterior tooth? **A.** Mesial; **B.** Distal. **C.** MACA RRJPH008C, posterior tooth, lingual view. **D, E.** Tooth plates of *Psephodus* sp.: **D.** MACA RR013A, posterior tooth plate, oral view; **E.** RR018JPHA, anteromedial tooth plate? oral view. **F.** MACA 61967, *Sandalodus* sp., upper posterior tooth plate. **G.** MACA RR017, *Copodus cornutus*, tooth plate, oral view. **H.** MACA RRJPH008F, *Deltoptychius* sp., oral view. **I.** MACA RRJPH008C, cf. *Traquairius* sp., oral view. Scale = 1 cm (0.4 in). NPS / JP HODNETT

A large tooth plate of *Psammodus* sp. with an approximate width of 5 cm (2 in) was encountered in the wall of Roaring River. The rest of the tooth plate was deeply embedded into the limestone. Tooth plates of *Psammodus* can be quite large, some exceeding 8 cm (3 in) in length, and are typically rectangular and tile-like (Stahl 1999). *Psammodus* is known also from the Ste. Genevieve Formation at MACA (see below) and from the Late Devonian to Late Mississippian of North America, Eurasia, and Australia (Stahl 1999). A single tooth plate of *Copodus cornutus* was collected from the Roaring River locality (Figure 149G). Tooth plates of *Copodus* share the similar plate-like shape seen in *Psammodus* but differ in being more mesiodistally compressed and labiolingually elongated with a U-shaped lingual margin (Stahl 1999). *Copodus* is only known from the Late Mississippian of North America and Eurasia (Stahl 1999). Two representatives of the Menaspiformes order of holocephalans are known from the St. Louis Formation of Mammoth Cave. Menaspiform holocephalans bore elaborate facial spines and cranial plates, based on several complete to nearly complete specimens (Lund and Grogan 1997b; Stahl 1999). Tooth plates of *Deltoptychius* are known from Roaring River and Logsdon River/Bridge Avenue localities (Figure 149H). A possible representative of *Traquairius* is known from the Roaring River locality (Figure 149I).

Ste. Genevieve Formation (Middle Mississippian: late Viséan)

The Ste. Genevieve Formation overlies the St. Louis Formation. It is approximately 33–37 m (110–120 ft) thick. Most of the passages of the Mammoth Cave System occur in the Ste. Genevieve and passages occur throughout the thickness of the formation (Palmer 1981, 2017; Chapter 3 in this volume). This unit consists primarily of light gray limestones and dolomitic limestones with the upper beds alternating with thin beds of dark, silty, granular limestones (Palmer 1981). The large number of passages cutting through the Ste. Genevieve Formation may contribute to the prolific fossil record documented within Mammoth Cave. Of the six geologic members of the Ste. Genevieve Formation, only two members have definitive vertebrate passage locality records. Three passage localities are currently known for the lowest Fredonia Member, while the middle Joppa Member currently has at least seven localities. One passage locality, Below Marion Avenue, which contains an articulated set of ctenacanth shark jaws, gill arches, and dislodged teeth, is either in the lower Joppa Member or the underlying Karnak Member, and work is currently underway to determine its precise stratigraphic position. However, for simplicity of discussion, the Below Marion Avenue locality is here included with the Joppa Member.

Fredonia Member Passage Localities

Three passage localities have been identified from the Fredonia Member of the Ste. Genevieve Formation. These localities are Edna's Dome off Martel Avenue, Grand Central Station Side Passage, and Jessup Avenue.

Edna's Dome—This passage locality is located near the end of the old Martel Avenue tour trail, which cuts primarily through the St. Louis Formation (which also exposes chondrichthyan fossils) (Figure 150). The trail inclines to Edna's Dome, an actively eroding and extremely tall vertical shaft and pit that exposes the Ste. Genevieve Formation. Holocephalan tooth plates were first encountered just below the pit rim.



Figure 150. Documenting chondrichthyans fossils from the Fredonia Member, Ste. Genevieve Formation at Edna's Dome Locality. **A.** Rick Olson looking into the bottom of Edna's Dome. **B.** Looking up into Edna's Dome. **C.** Isolated tooth plate of *Psammodus* sp. NPS / JP HODNETT & NPS

Grand Central Station Side Passage—Part of the Mammoth Cave system; both this passage and the NY Subway are connected to Grand Central Station, leaving the room from opposite sides. The locality known as "Grand Central Station Side-Passage" dips lower in the stratigraphy to the Fredonia Member, while "NY Subway" is in the Joppa Member. This passage has a petalodont tooth and holocephalan tooth plate.

Jessup Avenue—Marine vertebrate fossils, largely consisting of isolated chondrichthyan teeth, are common near the end of Jessup Avenue and presently provide the most specimens for analysis from the Fredonia Member (Figure 151). Many teeth are still in situ in the upper walls and ceiling of the cave in a crinoidal hash bed. This area also contains sensitive historical signatures, in smoke or etched.

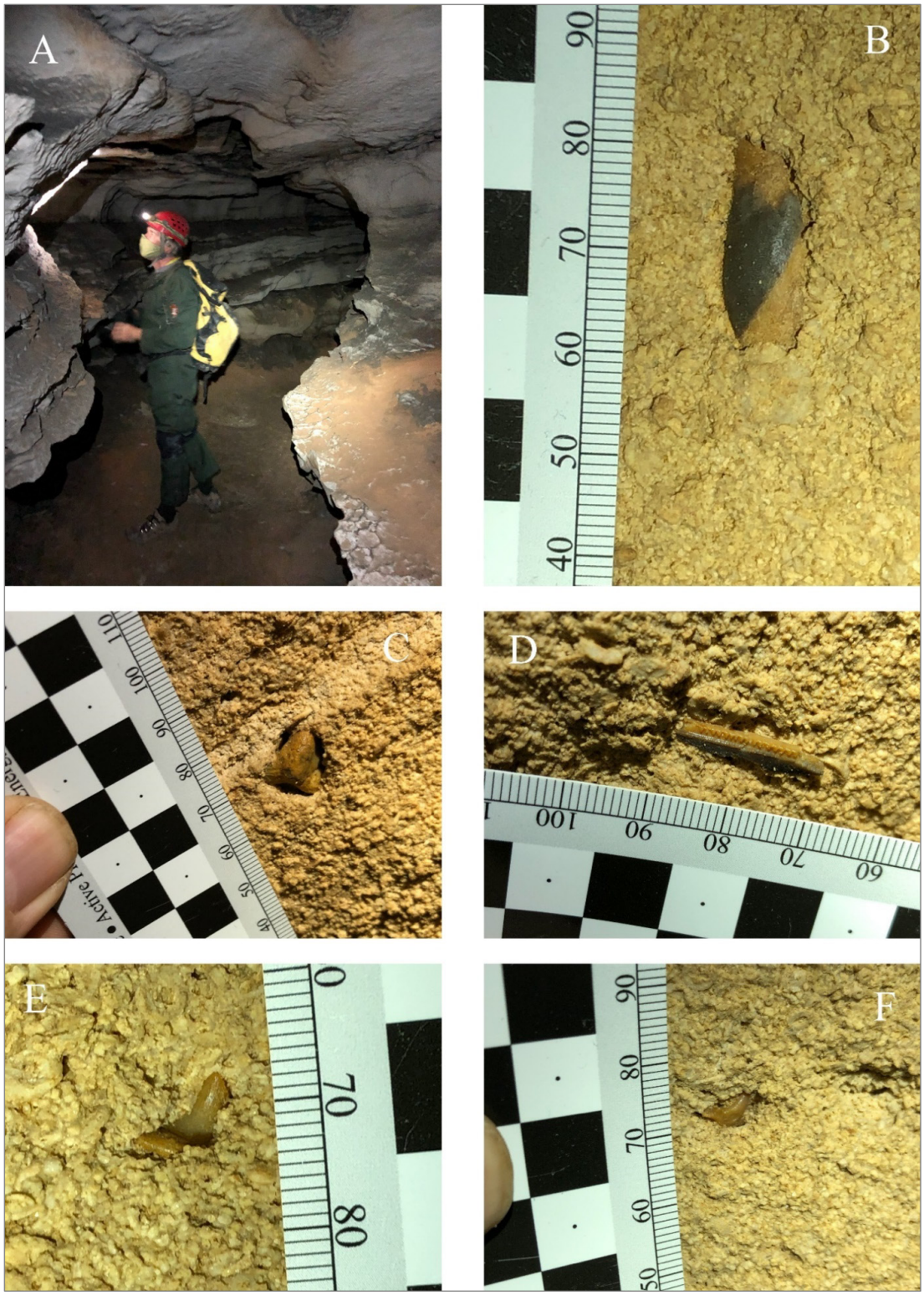


Figure 151. Documenting chondrichthyan fossils from the Fredonia Member of the Ste. Genevieve Formation in Jessup Avenue. **A.** Rick Toomey looking for fossils in Jessup Avenue. **B.** Tooth plate of *Sandalodus* sp. **C.** Distal end of a large *Cladodus*-like tooth exposed in the cave ceiling. **D.** *Chomatodus* tooth. **E.** Partially exposed *Stethacanthus* tooth. **F.** Partially exposed *Stethacanthus* tooth. Scale for **B–F** includes centimeters (squares) and millimeters (tick marks). NPS / JP HODNETT & NPS

Joppa Member Passage Localities

The Joppa Member is one of the most fossil-rich sections in the cave. The lower Joppa (J1 unit) is mostly a micritic limestone with scattered large fossils and some dolomitic zones. The upper Joppa (J2 unit) consists of several fossil hash zones (dense beds of grain-supported limestone in which almost all of the grains are fossils, mainly crinoid fragments, horn corals, brachiopods, shark teeth, and bryozoans). These fossil hash zones are separated by beds that, while still fossil-rich, are matrix-supported micrite with scattered fossils (similar taxa as the fossil hash zones). In many localities only the lowermost fossil hash zone is exposed; however, in a few, notably the Cox Route and Forks of the Cave, several fossil hash zones are exposed. The upper J2 unit of the Joppa Member to date has produced the most vertebrate fossils of all of the Mississippian units at MACA. At present eleven major passages with localities have been identified within Mammoth Cave. These localities are Colossal Cave, Cox Route/Genie's Pass, Forks of the Cave, Fossil Avenue, Below Marion, Marion Avenue, Serena's Arbor, Solitary Cave, Specimen (Roger's) Avenue, NY Subway, and Woodbury.

Colossal Cave—A number of large chondrichthyan teeth were collected from the J2 unit in Colossal Cave (Figure 152). Many of these were collected from the ceiling. Cave floor sediments were collected and screen-washed and are currently under analysis for microvertebrate fossils.

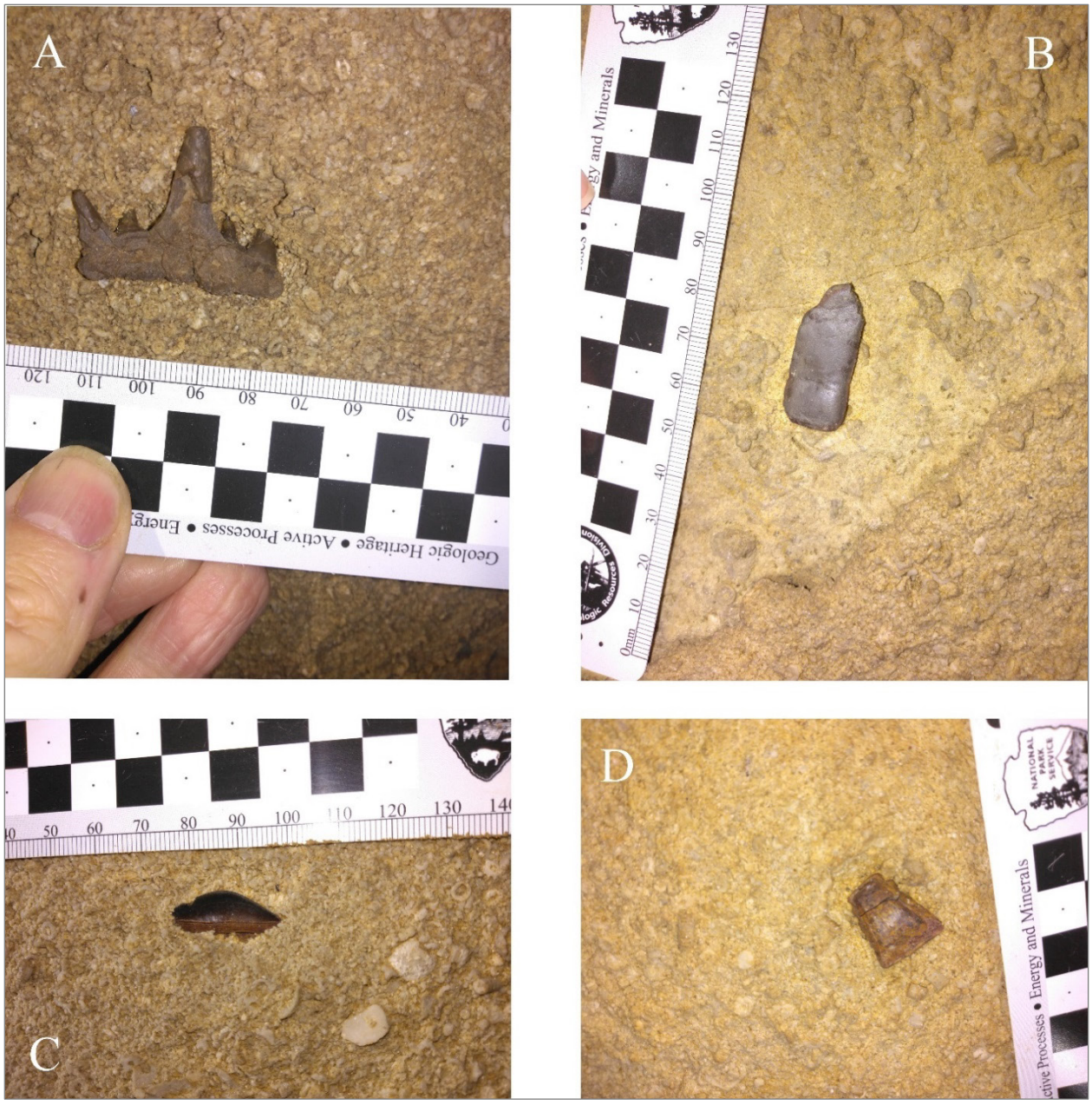


Figure 152. Teeth of chondrichthyans from the Joppa Member of the Ste. Genevieve Formation at Colossal Cave. **A.** Large tooth of *Cladodus mirabilis*. **B.** Tooth plate of *Psammodus* sp. **C.** Tooth of *Petalodus linguifer*. **D.** Tooth plate of a new holocephalan. Scale in millimeters (**A–C**) and centimeters (**D**). NPS / JP HODNETT & NPS

Cox Route/Genie's Pass—A sinuous multi-level canyon passage, this locality has a large number of chondrichthyan and osteichthyan fossils exposed within the passage walls and ceilings of the J2 unit (Figure 153). This is one of the few localities where microvertebrate remains have been encountered in situ and collected. This is also one of the best localities for showing that the J2 unit is comprised of several fossil-rich beds separated by slightly less fossil-rich beds. Cave floor sediments have been collected and screen-washed and are currently under analysis for microvertebrate fossils.

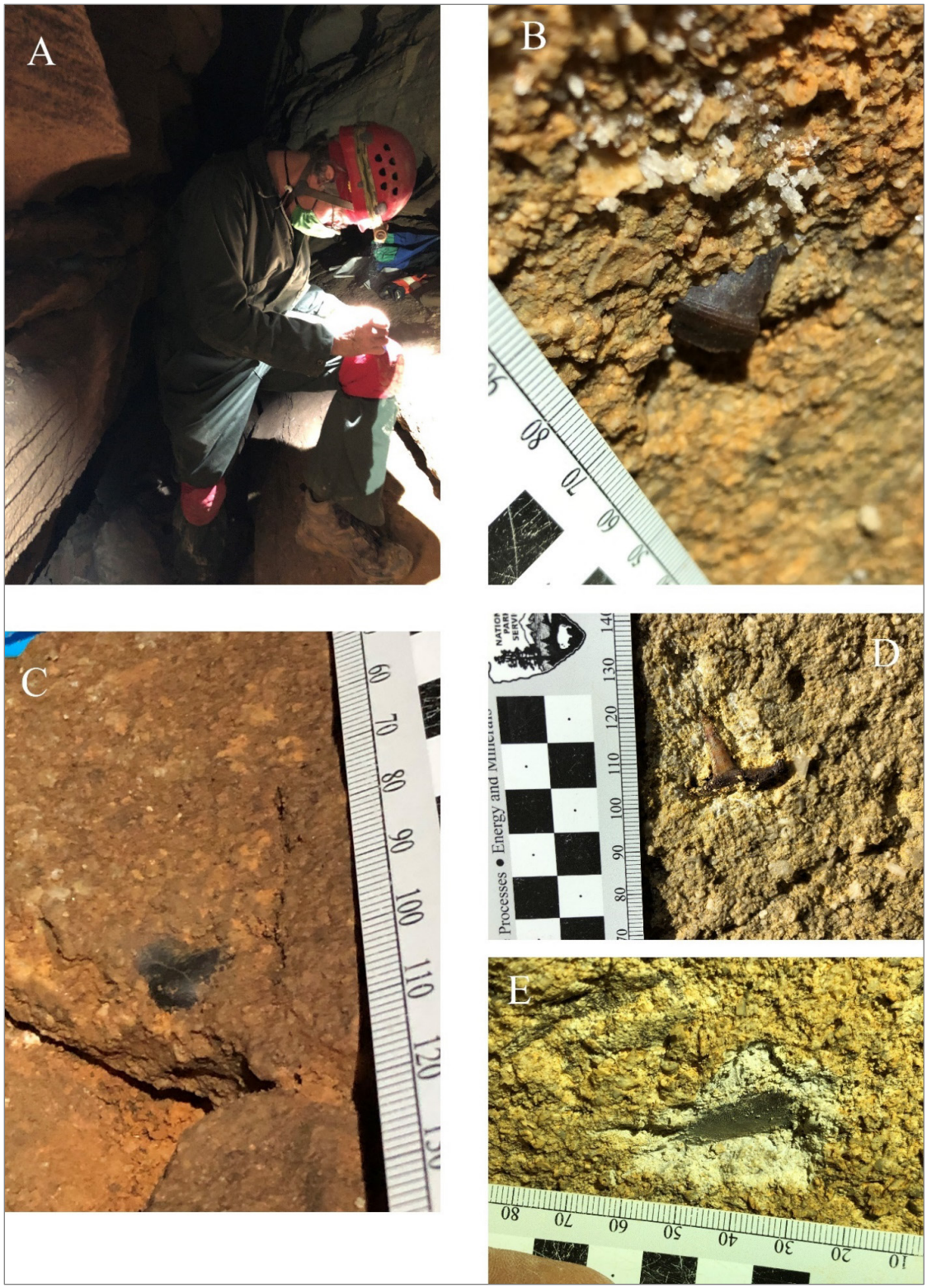


Figure 153. Documenting chondrichthyans from the Joppa Member of the Ste. Genevieve Formation in Cox Avenue. **A.** Rick Toomey documenting fossils. **B.** Exposed tooth of a new species of *Petalodus*. **C.** Partially exposed *Deltoptychius* sp. tooth. **D.** Exposed *Saivodus striatus* tooth on an overhang. **E.** Exposed tooth of *Psammodus* sp. Scale in millimeters. NPS / JP HODNETT & NPS

Forks of the Cave—A side passage with a low ceiling with a diverse assemblage of chondrichthyan fossils in the J2 unit.

Fossil Avenue—This passage locality presently has the largest concentration of Mississippian marine vertebrates in Mammoth Cave (Figure 154). Chondrichthyan skeletal cartilage has been encountered in many areas of this locality, which also has a rich assortment of chondrichthyan teeth and dermal spines. The majority of these fossils were collected from the J2 unit in this passage, but a few were collected in the underlying J1 unit. Cave sediments were collected and screen-washed for microvertebrate fossils. Preliminary results show microvertebrates are present but are encountered infrequently.



Figure 154. Documenting chondrichthyan fossils from the Joppa Member of the Ste. Genevieve Formation in Fossil Avenue. **A.** Rick Olson extracting a tooth in the cave ceiling. **B.** Large section of scapulocoracoid cartilage of a chondrichthyan in the ceiling in the J1 unit. **C.** Partially exposed *Petalorhynchus* cf. *P. spatulatus* tooth in the ceiling. **D.** Large *Saivodus striatus* tooth exposed in an overhang. **E.** Exposed tooth of a new species of the petalodont *Janassa*. Scale for **B–E** includes centimeters (squares) and millimeters (tick marks). NPS / JP HODNETT & NPS

Below Marion—This locality features a single exposed set of jaws, gill arches, and teeth representing new ctenacanth species *Glikmanius careforum* that is still in situ in the winding tight passage (Figure 155). As noted above, this locality represents either the J1 unit of the Joppa Member, or the underlying Karnak Member.



Figure 155. Right set of jaws, gill arches, and teeth (medial view) of *Glikmanius careforum* in Below Marion Avenue in the lower Joppa Member or Karnak Member of the Ste. Genevieve Formation. **A.** Photo of the specimen in situ in the passage ceiling. Scale includes centimeters (squares) and millimeters (tick marks). **B.** Schematic diagram of the *Glikmanius* specimen; dashed lines represent predicted morphology just under the surface. **Abbreviations: Br**, branchial arches; **HY**, hyomandibulum; **rMC**, Right Meckel's cartilage (lower jaw); **MK**, mandibular knob; **rPQ**, palatoquadrate (upper jaw); **T**, teeth.
NPS / JP HODNETT

Marion Avenue—This rather broad passage locality has a few holocephalan teeth exposed (Figure 156). The first is near the elevator access along the sidewalk trail before it opens to the old visitor dining area. Taking the trail towards Marion Avenue proper, the beds seen in the ceiling expose numerous gastropod fossils and a few crinoids. Two holocephalan tooth plates are also present in this area.



Figure 156. Documenting chondrichthyan fossils from the Joppa Member of the Ste. Genevieve Formation in Marion Avenue. **A.** Rick Olson looking at a *Psephodus* sp. tooth. **B.** *Psephodus* sp. tooth plate. **C.** *Psephodus* sp. tooth plate in the cave ceiling. **D.** Exposed *Sandalodus* sp. tooth plate. Scale for **B–D** includes centimeters (squares) and millimeters (tick marks). NPS / JP HODNETT & NPS

Serena's Arbor—This locality is a large breakdown room at the end of Franklin Avenue near the Carmichael Entrance of Mammoth Cave (Figure 157). Vertebrate fossils are common in the ceiling and include chondrichthyan skeletal cartilage.

Solitary Cave—This passage is a paleo upstream continuation of Fossil Avenue. It is separated from Fossil Avenue by a collapse area that is about 6 m (20 ft) long. The presence of the important fossils in Fossil Avenue led teams to look in Solitary Cave to see if the deposits continued there. This more recently identified locality contains rich vertebrate deposits, like those in Fossil Avenue (Figure 158).

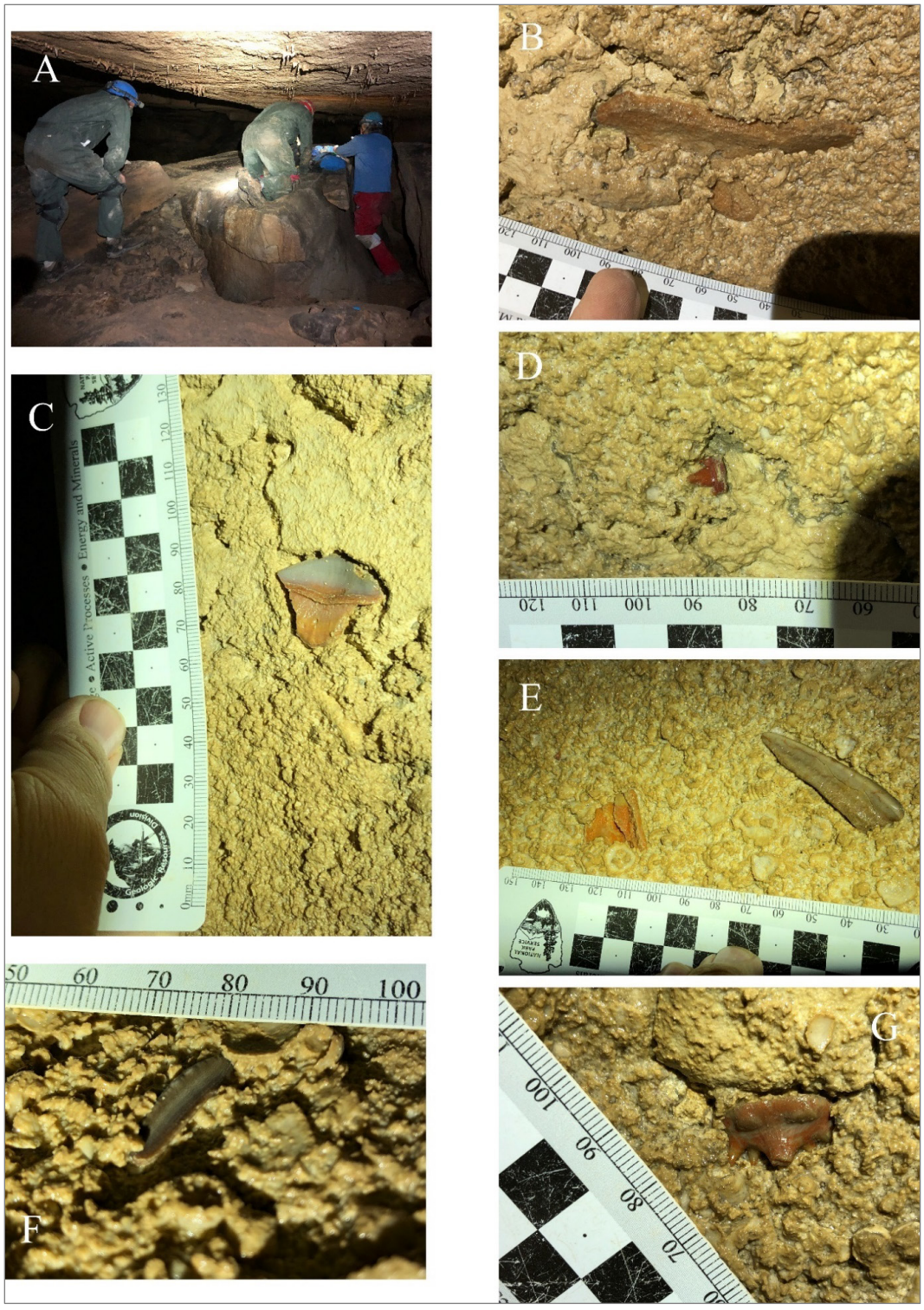


Figure 157. Documenting chondrichthyan fossils from the Joppa Member of the Ste. Genevieve Formation at Serena's Arbor. **A.** MACA crew collecting chondrichthyan fossils in Serena's Arbor. **B.** Large exposed segment of indeterminate chondrichthyan cartilage. **C.** Tooth of *Petalodus linguifer*. **D.** Tooth of *Stethacanthus* sp. **E.** Associated tooth of a new species of *Petalodus* (right) and a portion of chondrichthyan skeletal cartilage (left). **F.** Tooth of *Chomatodus* sp. **G.** Tooth of *Glikmanius careforum*. Scale in millimeters. NPS / JP HODNETT & NPS

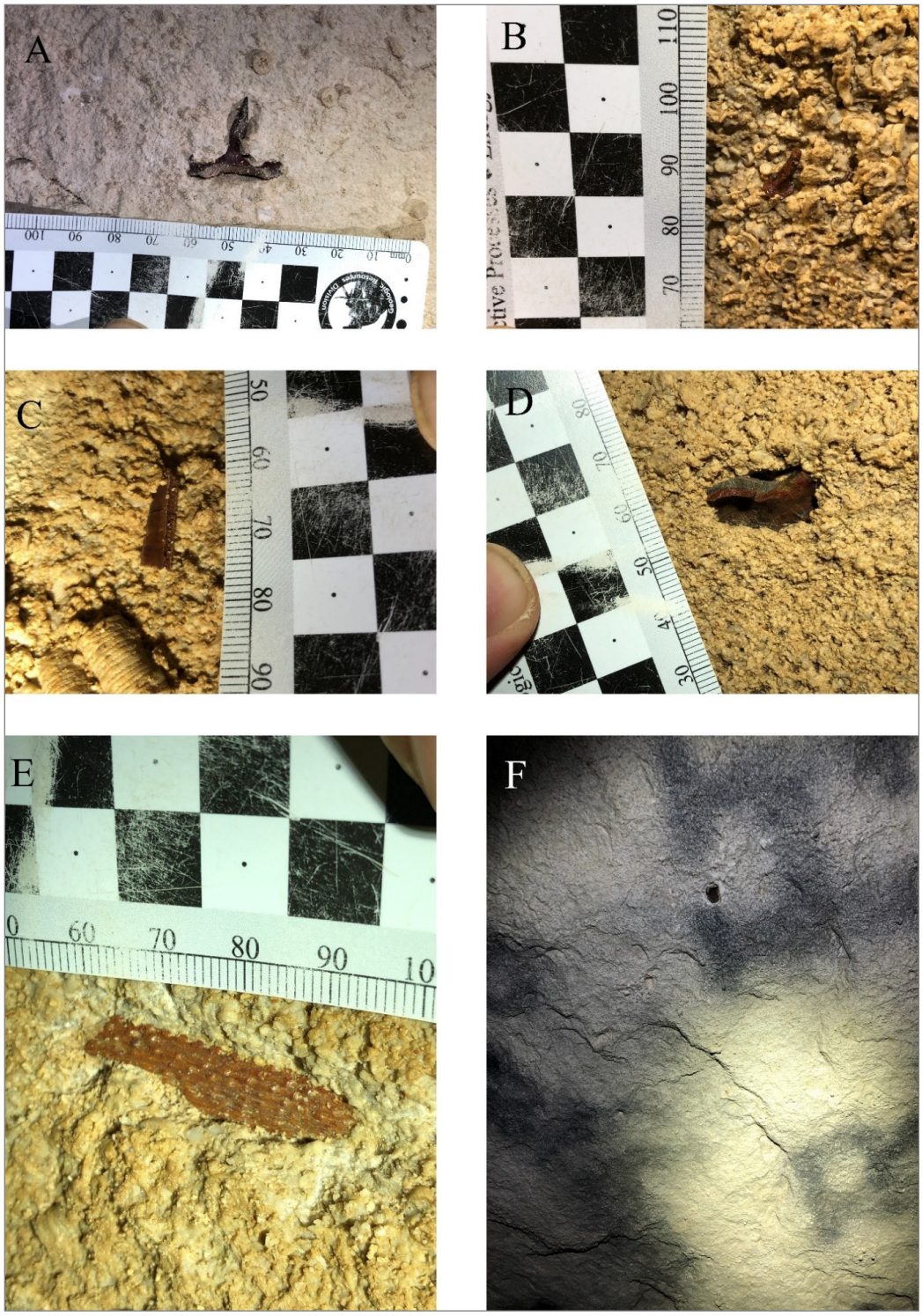


Figure 158. Documenting chondrichthyan fossils from the Joppa Member of the Ste. Genevieve Formation in Solitary Cave. **A.** Large *Saivodus striatus* tooth in the cave ceiling. **B.** Small petalodont tooth. **C.** *Chomatodus* sp. tooth bar. **D.** Partial *Psephodus* sp. tooth plate. **E.** Partial dorsal fin spine of the ctenacanth *Glencartius costellatus*. **F.** Smoke-stained tooth plate of *Psephodus* sp. amongst historic smoke writing. The location of this fossil made it impractical to get a scale to it. Scale in millimeters for other elements. NPS / JP HODNETT & NPS

Specimen (Roger's) Avenue—This passage locality in the J2 unit is unique in that it hosts the only known jaw and other cartilages of the large ctenacanth *Saivodus striatus*, representing the first skeletal material known for this species (Figure 159). The passage itself also has a rich vertebrate record, both at the macro and micro level. Teeth and dermal spines are common near the end of the passage in the walls and ceiling. Cave sediments collected directly under the exposed *Saivodus* skeletal materials were rich in microvertebrate specimens. These included pieces of cartilage that had fallen from the *Saivodus* fossil, as well as dermal denticles known to come from this kind of shark. Additional species of fish, including evidence of several varieties of extinct bony fish not yet observed in other passage localities, were common in the sediment samples.

NY Subway Passage—Part of the Mammoth Cave system; this passage is connected to New Entrance and has a single holocephalan tooth plate.

Woodbury Pass—Part of the Mammoth Cave system; a single large ctenacanth tooth and an indeterminate holocephalan tooth plate have been recorded.



Figure 159. Documenting chondrichthyan fossils from the Joppa Member of the Ste. Genevieve Formation in Specimen Avenue. **A.** MACA crew in Specimen Avenue. **B.** Exposed tooth of a new ctenacanthiform shark. **C.** Lower jaw, teeth, and other cartilages of the *Saivodus striatus*. **D.** Exposed tooth of *Deltoptychius* sp. **E.** Two associated teeth of *Chomatodus* sp. **F.** Tooth of *Orodus elongatus* type. Scale for **B–F** includes centimeters (squares) and millimeters (tick marks). NPS / JP HODNETT & NPS

Ste. Genevieve Formation Vertebrate Assemblages

The vertebrate fossils collected from the Ste. Genevieve Formation at MACA represent the first record of this group of organisms for this geologic horizon, which covers several states in the marine Illinois Basin. This is surprising as the Ste. Genevieve Formation has a rich recorded history of invertebrate fossils (Butts 1917; Palmer 1981). Based on the MACA record the Ste. Genevieve Formation vertebrate assemblage is one of the richest and most diverse Middle Mississippian fish assemblages not only for the park, but perhaps also for the global Viséan marine vertebrate record. At present, 15 different chondrichthyan species have been identified from the Fredonia Member (Table 8). Most impressive, 68 different species of fish have been identified so far from the Joppa Member (Tables 9–11). At present there is little difference between the common chondrichthyan taxa of the Fredonia and Joppa Members, although species abundance does differ between geologic horizons. It should be noted, though, that the Fredonia Member is comparatively under-sampled relative to the Joppa Member. The Fredonia and Joppa vertebrate assemblages offer important information on the transition from the historically better-known early Viséan St. Louis Formation into the younger Serpukhovian beds (such as the local Girkin, Big Clifty, and Haney Formations) in the Late Mississippian.

Table 8. The vertebrate assemblage of the Fredonia Member of the Ste. Genevieve Formation at MACA. All are chondrichthyans.

Higher Classification	Genus and Species	Edna's Dome	Jessup Avenue	Grand Central Station Side-Passage
Cladodontomorphi: Symmoriiformes: Stethacanthidae	*Stethacanthus* sp. 2 (3-cusped teeth)	–	Y	–
Elasmobranchii: Ctenacanthiformes: Ctenacanthidae	?*Cladodus* sp. (large form)	–	Y	–
Euchondrocephali: Paraselachii: Gregoriidae	Genus and species indet.	–	Y	–
Euchondrocephali: Orodontiformes	Genus and species indet. 1	–	Y	–
Euchondrocephali: Petalodontimorpha	*Chomatodus* sp. 1	–	Y	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalodontidae	?*Lisgodus* sp.	–	Y	–
	?*Petalodus* sp.	–	Y	–
	Genus and species indet.	–	Y	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalorhynchidae	*Petalorhynchus* cf. *P. beargulchensis*	–	–	Y
Euchondrocephali: Holocephali: Cochliodontiformes: Psephodontidae	*Psephodus* sp.	–	Y	–
Euchondrocephali: Holocephali: Cochliodontiformes: Cochliodontidae	*Deltodus* cf. *D. sublaevis*	–	Y	–
	Deltodus sp.	–	Y	–
	Sandalodus sp.	–	Y	–

Table 8 (continued). The vertebrate assemblage of the Fredonia Member of the Ste. Genevieve Formation at MACA. All are chondrichthyans.

Higher Classification	Genus and Species	Edna's Dome	Jessup Avenue	Grand Central Station Side-Passage
Euchondrocephali: Holocephali: Psammodontiformes: Psammodontidae	*Psammodus* sp.	Y	–	–
Euchondrocephali: Holocephali: Menaspiformes: Deltoptychiidae	*Deltoptychius* sp.	–	Y	–

Table 9. The acanthodian assemblage of the Joppa Member of the Ste. Genevieve Formation at MACA.

Higher Classification	Genus and Species	Colossal Cave	Cox Ave.	Fossil Ave.	Forks of the Cave	Marion Ave.	NY Subway Entrance	Off Marion	Serena's Arbor	Solitary Cave	Specimen Ave.	Woodbury Pass
Acanthodiformes: Acanthodidae	cf. *Acanthodes* sp.	–	–	–	–	–	–	–	–	–	Y	–

Table 10. The chondrichthyan assemblage of the Joppa Member of the Ste. Genevieve Formation at MACA.

Higher Classification	Genus and Species	Colossal Cave	Cox Ave.	Fossil Ave.	Forks of the Cave	Marion Ave.	NY Subway Entrance	Off Marion	Serena's Arbor	Solitary Cave	Specimen Ave.	Woodbury Pass
Cladodontomorphi: Symmoriiformes: Stethacanthidae	*Stethacanthus* sp. 1 (5-cusped teeth)	–	–	–	–	–	–	–	–	–	Y	–
	Stethacanthus sp. 2 (3-cusped teeth)	–	Y	Y	–	–	–	–	Y	Y	Y	–
Cladodontomorphi: Symmoriiformes: Falcatidae	"*Denaea*" sp. 1	–	–	Y	–	–	–	–	–	–	Y	–
	"*Denaea*" sp. 2	–	–	–	–	–	–	–	–	–	Y	–
	Genus and species indet.	–	–	Y	Y	–	–	–	–	–	–	–
Elasmobranchii: Phoebodontiformes: Thrinacodontidae	*Thrinacodus* cf. *T. dziki*	–	Y	–	–	–	–	–	–	–	Y	–
Elasmobranchii: Phoebodontiformes	Genus and species indet.	–	–	–	–	–	–	–	–	–	Y	–
Elasmobranchii: Xenacanthimorpha: Bransonelliformes	*Bransonella nebraskensis*	–	–	–	–	–	–	–	–	–	Y	–
	Bransonella lingulata	–	–	–	–	–	–	–	–	–	Y	–
Elasmobranchii: Ctenacanthiformes: Ctenacanthidae	*Cladodus mirabilis*	Y	–	Y	–	–	–	–	–	–	Y	–
	Troglocladodus trimblei	–	–	Y	–	–	–	–	–	–	Y	–
	Genus and species indet. 1	–	Y	–	Y	–	–	–	–	–	Y	–
Elasmobranchii: Ctenacanthiformes: "Tamiobatidae"	*Saivodus striatus*	–	Y	Y	Y	–	–	–	–	Y	Y	Y

Table 10 (continued). The chondrichthyan assemblage of the Joppa Member of the Ste. Genevieve Formation at MACA.

Higher Classification	Genus and Species	Colossal Cave	Cox Ave.	Fossil Ave.	Forks of the Cave	Marion Ave.	NY Subway Entrance	Off Marion	Serena's Arbor	Solitary Cave	Specimen Ave.	Woodbury Pass
Elasmobranchii: Ctenacanthiformes: Heslerodidae	*Glikmanius careforum*	–	–	Y	–	–	–	Y	Y	–	Y	–
	Glencartius costellatus	–	–	Y	–	–	–	–	–	Y	Y	–
	Genus and species indet.	–	Y	Y	–	–	–	–	–	–	Y	–
Elasmobranchii: Euselachii: Protacrodontiformes	Genus and species indet.	–	–	–	–	–	–	–	–	Y	Y	–
Elasmobranchii: Euselachii: Hybodontiformes	Genus and species indet.	–	–	–	–	–	–	–	–	Y	Y	–
Elasmobranchii: Euselachii: Neoselachii: Anachronistidae	cf. *Cooleyella* sp.	–	Y	–	–	–	–	–	–	–	–	–
Elasmobranchii: Euselachii: Neoselachii	*Amelacanthus* sp.	Y	Y	Y	Y	–	–	–	–	–	Y	–
	?*Eunemacanthus* sp.	–	–	Y	–	–	–	–	–	Y	–	–
Euchondrocephali	*Euglossodus* sp.	–	–	Y	–	–	–	–	–	–	–	–
	Venustodus sp. 1	–	–	–	–	–	–	–	–	–	Y	–
	Venustodus sp. 2	–	Y	Y	Y	–	–	–	–	–	–	–
	Genus and species indet. 1	Y	Y	Y	Y	–	–	–	Y	–	Y	–
	Genus and species indet. 2	Y	Y	Y	Y	–	–	–	Y	Y	Y	–
Euchondrocephali: Paraselachii: Debeeriidae	*Heteropetalus* sp.	–	–	–	–	–	–	–	–	–	Y	–
	Genus and species indet.	–	–	–	–	–	–	–	Y	–	–	–
Euchondrocephali: Orodontiformes: Orodontidae	*Orodus* sp. 1 (*O. ramosus* type)	–	–	Y	–	–	–	–	–	–	–	–
	Orodus sp. 2 (*O. elongatus* type)	–	–	Y	–	–	–	–	–	–	Y	–
Euchondrocephali: Orodontiformes: Leiodontidae	*Leiodus* sp.	–	–	Y	–	–	–	–	–	–	–	–
Euchondrocephali: Orodontiformes	Genus and species indet. 1	–	–	Y	–	–	–	–	Y	Y	Y	–
Euchondrocephali: Eugenodontiformes	Genus and species indet.	–	Y	Y	–	–	–	–	–	–	–	–

Table 10 (continued). The chondrichthyan assemblage of the Joppa Member of the Ste. Genevieve Formation at MACA.

Higher Classification	Genus and Species	Colossal Cave	Cox Ave.	Fossil Ave.	Forks of the Cave	Marion Ave.	NY Subway Entrance	Off Marion	Serena's Arbor	Solitary Cave	Specimen Ave.	Woodbury Pass
Euchondrocephali: Petalodontimorpha	*Chomatodus* sp. 1	–	Y	Y	Y	–	–	–	Y	Y	Y	–
	Chomatodus sp. 2	–	–	Y	–	–	–	–	Y	Y	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Janassidae	*Janassa* sp.	–	–	Y	–	–	–	–	–	–	–	–
	Strigilodus tollesonae	Y	–	Y	–	–	–	–	Y	–	Y	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalodontidae	*Antilodus* sp.	Y	–	–	–	–	–	–	–	–	–	–
	Harpacodus sp.	–	–	–	Y	–	–	–	–	–	–	–
	?*Lisgodus* sp.	–	–	Y	–	–	–	–	Y	Y	Y	–
	Petalodus hastingsii	–	–	Y	–	–	–	–	–	–	–	–
	Petalodus linguifer	Y	–	Y	–	–	–	–	Y	–	–	–
	Petalodus sp. nov.	–	Y	Y	–	–	–	–	Y	–	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalorhynchidae	*Petalorhynchus* cf. *P. beargulchensis*	–	–	–	–	–	Y	–	–	–	–	–
	Petalorhynchus cf. *P. spatulatus*	–	Y	Y	–	–	–	–	Y	–	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: "Obruchevodidae"	*Netsepoye* sp.	–	–	–	–	–	–	–	–	–	Y	–
	Genus et species nov.	–	Y	–	–	–	–	–	–	–	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Belantseidae	cf. *Belantsea* sp.	–	–	Y	–	–	–	–	–	–	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes:	Genus and species indet. 1	Y	Y	Y	Y	–	–	–	–	Y	Y	–
	Genus and species indet. 2	Y	–	Y	Y	–	–	–	–	Y	Y	–
Euchondrocephali: Holocephali: Chondrenchelyiformes: Chondrenchelyidae	Genus and species indet.	–	–	Y	Y	–	–	–	–	–	–	–
Euchondrocephali: Holocephali: Helodontiformes: Helodontidae	*Helodus* sp.	Y	–	Y	–	–	–	–	Y	–	Y	–

Table 10 (continued). The chondrichthyan assemblage of the Joppa Member of the Ste. Genevieve Formation at MACA.

Higher Classification	Genus and Species	Colossal Cave	Cox Ave.	Fossil Ave.	Forks of the Cave	Marion Ave.	NY Subway Entrance	Off Marion	Serena's Arbor	Solitary Cave	Specimen Ave.	Woodbury Pass
Euchondrocephali: Holocephali: Cochliodontiformes: Psephodontidae	*Psephodus* sp.	–	–	Y	–	Y	Y	–	–	Y	Y	–
Euchondrocephali: Holocephali: Cochliodontiformes: Cochliodontidae	*Cochliodus* sp.	Y	–	Y	–	–	–	–	Y	–	–	–
	Deltodus sp.	Y	Y	Y	Y	–	–	–	Y	–	Y	–
	Poecilodus sp.	–	–	–	–	–	–	–	–	–	Y	–
	Sandalodus sp.	Y	Y	Y	–	Y	–	–	Y	Y	Y	–
Euchondrocephali: Holocephali: Psammodontiformes: Psammodontidae	*Psammodus* sp.	Y	–	Y	–	–	–	–	–	Y	Y	–
Euchondrocephali: Holocephali: Menaspiformes: Deltoptychiidae	*Deltoptychius* sp.	Y	Y	Y	–	–	–	–	Y	–	Y	–
Euchondrocephali: Holocephali	Indeterminate holocephalan	–	–	–	–	–	–	–	–	–	–	Y

Table 11. The osteichthyan assemblage of the Joppa Member of the Ste. Genevieve Formation at MACA.

Higher Classification	Genus and species	Colossal Cave	Cox Ave.	Fossil Ave.	Forks of the Cave	Marion Ave.	NY Subway Entrance	Off Marion	Serena's Arbor	Solitary Cave	Specimen Ave.	Woodbury Pass
Actinopterygii: Palaeonisciformes	Genus and species indet. 1	–	–	Y	–	–	–	–	–	–	Y	–
	Genus and species indet. 2	–	–	–	–	–	–	–	–	–	Y	–
	Genus and species indet. 3	–	–	–	–	–	–	–	–	–	Y	–
	Genus and species indet. 4	–	–	–	–	–	–	–	–	–	Y	–
	Genus and species indet. 5	–	–	–	–	–	–	–	–	–	Y	–
Actinopterygii: ?Eurynotiformes	Genus and species indet. 1	–	–	–	–	–	–	–	–	–	Y	–
	Genus and species indet. 2	–	Y	–	–	–	–	–	–	–	Y	–

Acanthodii

Acanthodians are a basal group of shark-like fishes that first appeared during the Silurian and have been suggested as the ancestral group to the crown group of Chondrichthyes (elasmobranchs and euchondrocephalans) (Maisey et al. 2019). Acanthodians are characterized by cartilaginous skeletons, minute rhombic scales, prominent spines on the pectoral, pelvic, and dorsal fins, and additional ventral paired spines (Long 1996). By the Carboniferous, many acanthodians were filter-feeding fishes (Long 1996). A number of rhombic scales referable to the small filter-feeder *Acanthodes* were collected from the Specimen Avenue sediments below the skeletal material of *Saivodus striatus*.

Chondrichthyes

Fossils of chondrichthyans, including partial to complete skeletal cartilages, isolated teeth, and dermal spines and denticles of at least ten orders, are the most frequently encountered vertebrate fossils in the Fredonia and Joppa Members.

Symmoriiformes—The symmoriiform chondrichthyans had shark-like bodies and "cladodont" teeth, and the males of many taxa had elaborate brush-spines for the anterior dorsal fin. Females and some males in some species had only one dorsal fin. Symmoriiforms first appeared in the Late Devonian and extended into the Permian (Ginter et al. 2010). At least three families are recognized: Symmoriidae, a group where the males did not bear a brush-spine complex; Stethacanthidae, a group where the males had a roughly anvil-shaped brush-spine with the dorsal surface covered in tooth-like denticles; and Falcatidae, a group where the males had a sickle-shaped brush-spine bearing tooth-like denticles on the ventral tip of the spine. Debate on the taxonomic position of this group is ongoing, with some specialists suggesting symmoriiforms were closely related to elasmobranch sharks, while others place them as the most basal members of the Euchondrocephali (Ginter et al. 2010; Coates et al. 2017).

Fredonia Symmoriiforms—Three teeth of the three-cusped form of *Stethacanthus* sp. were collected from Jessup Avenue (Figures 160A to 160E).

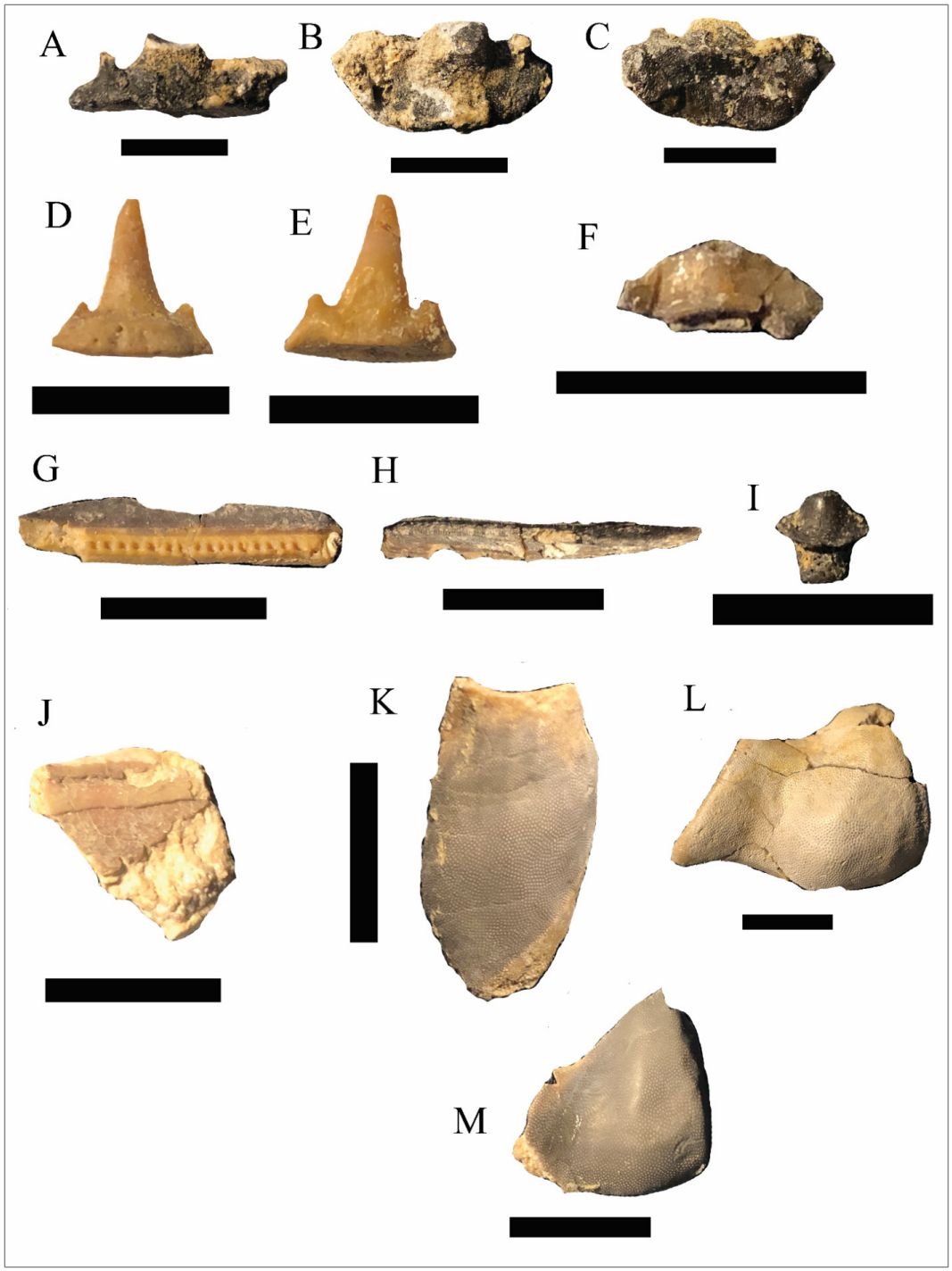


Figure 160. Chondrichthyan fossils from the Fredonia Member of the Ste. Genevieve Formation at MACA. **A–E.** Teeth of *Stethacanthus* sp. 2.: **A–C.** MACA JA018JPH, large *Stethacanthus* sp. tooth: **A.** Labial view; **B.** Oral view; **C.** Aboral view. **D, E.** MACA JA015JPH, small *Stethacanthus* sp. tooth: **D.** Lingual view; **E.** Labial view. **F.** MACA JA004JPH, gregoriid indet., in lingual view. **G, H.** MACA JA014JPH, *Chomatodus* sp.: **G.** Lingual view; **H.** Oral view. **I.** MACA JA016JPH, *Lisgodus* sp., in labial view. **J.** MACA JA008RO, ?*Petalodus* sp., in lingual view. **K.** MACA JA002JPH, *Sandalodus* sp., in oral view. **L.** JA001BOBO, *Deltodus* cf. *D. sublaevis*, in oral view. **M.** MACA JA001JPH, *Deltoptychius* sp., in oral view. Scale = 1 cm (0.4 in). NPS / JP HODNETT

Joppa Symmoriiforms—Two brush-spine bases of a small falcatid were collected from the Fossil Avenue passage. Isolated tiny teeth of two species of falcatid referable to the "*Denaea*" tooth morph were collected from sediments collected from Specimen Avenue at the *Saivodus* site (Figures 161I and 161J). Two types of teeth, a three-cusped morph and a five-cusped morph referable to *Stethacanthus*, were collected from Cox Avenue, Fox Avenue, Serena's Arbor, and Specimen Avenue (Figures 161E to 161H). Of the two tooth morphs, the three-cusped form is the most common.

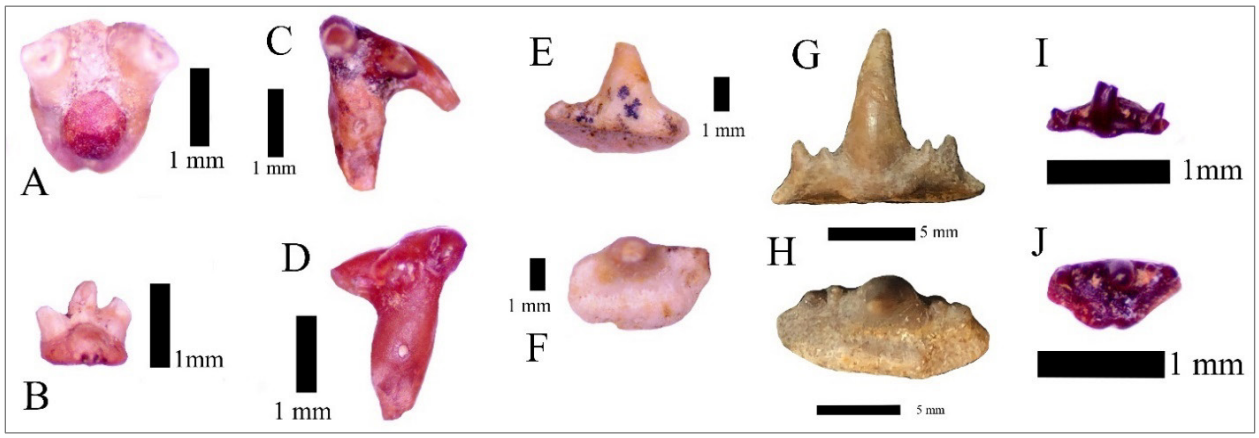


Figure 161. Xenacanthimorph, phoebodontiform, and symmoriiform fossils of the Joppa Member of the Ste. Genevieve Formation at MACA. **A, B.** Teeth of *Bransonella*: **A.** *Bransonella nebraskensis* in oral view; **B.** *Bransonella lingulata* in lingual view. **C, D.** Teeth of *Thrinacodus* cf. *T. dziki* in oral views. **E, F.** cf. *Stethacanthus* sp.: **E.** Labial view; **F.** Oral view. **G, H.** *Stethacanthus* sp.: **G.** Labial view; **H.** Oral view. **I, J.** *Denaea* sp.: **I.** Labial view; **J.** Oral view. NPS / JP HODNETT

Phoebodontiformes—Phoebodont sharks are a basal group of elasmobranch chondrichthyans that appeared in the early Late Devonian and went extinct by the end of the Mississippian. At present at least two families, Phoebodontidae and Thrinacodontidae, are recognized (Grogan and Lund 2008; Frey et al. 2019). Complete skeletons of phoebodont sharks indicate they had elongated, almost eel-like bodies and grappling-hook-like teeth (Grogan and Lund 2008; Frey et al. 2019). Isolated teeth of *Thrinacodus* cf. *T. dziki* have been collected from the Cox Route and Specimen Avenue (Figures 161C and 161D). An indeterminate phoebodont is also known from Specimen Avenue.

Xenacanthimorpha—Xenacanth sharks are well-known as freshwater sharks occurring in the Pennsylvanian and Permian around the world (Long 1996). This group of elasmobranch sharks bore a single elongated dorsal fin and had teeth with broad lateral cusps and reduced central cusps. Teeth of two species of the small basal xenacanthimorph *Bransonella*, which represents one of the few forms known from marine sediments (Ginter et al. 2010), are present. Teeth of *Bransonella nebraskensis* (Figure 161A) and *Bransonella lingulata* (Figure 161B) were collected from the Joppa Member sediments at the *Saivodus* site in Specimen Avenue. These two taxa are known elsewhere from the Viséan in North America and Eurasia (Ginter et al. 2010).

Ctenacanthiformes—The Ste. Genevieve Formation has the highest diversity of ctenacanth sharks at Mammoth Cave. However, unlike the Roaring River locality for the St. Louis Formation, no large dorsal fin spines have been identified from the Ste. Genevieve Formation and most dorsal spines found represent small forms.

Ctenacanthiformes from the Fredonia Member—At present only a single large tooth of a large *Cladodus*-like taxon has been found, in situ at Jessup Avenue (Figure 151C). Only the lateral cusp and part of the tooth base of this specimen are exposed and heavier tools would be required to extract it. However, its close proximity to historic smoke and scratched-in signatures restricts the ability to extract and identify this fossil.

Ctenacanthiformes from the Joppa Member—At least seven different species of ctenacanthiform sharks have been identified from the Joppa Member at Mammoth Cave (Figure 162). An articulated set of jaws, gill arches, and associated teeth of *Glikmanius careforum* were identified from the Below Marion locality (Figures 162C and 162D). Additional isolated teeth of *Glikmanius* were also identified from Fossil Avenue, Serena's Arbor, and Specimen Avenue (Figure 162A and 162B). These fossils, along with a single tooth from the St. Louis Formation at Roaring River, represent the oldest record of *Glikmanius* and the first definitive skeletal material identified for this taxon (Hodnett et al. 2024b). Previously, the oldest record of *Glikmanius* was an isolated tooth from the Serpukhovian (Late Mississippian) Heath Formation in central Montana (Ginter et al. 2010). *Glikmanius* is otherwise well-known from the Pennsylvanian to Permian (Ginter et al. 2010). A smaller relative of *Glikmanius*, *Glencartius costellatus*, was collected from Fossil Avenue and Specimen Avenue and is recognized from both dorsal fin spine fragments and isolated teeth. *Glencartius* is well-known from the Viséan of Eurasia, including two nearly complete skeletons, but is also known from isolated teeth in the younger Serpukhovian rocks of the Surprise Canyon Formation at Grand Canyon National Park (Ginter et al. 2010; Hodnett and Elliott 2018). *Troglocladodus trimblei* has been identified from Specimen Avenue and Fossil Avenue (Figures 162E and 162F). This new taxon differs from *Cladodus* in having complex coarse longitudinal ridges on the cusps and lateral cusps that are splayed outwards (Hodnett et al. 2024b). Restorations of *Glikmanius careforum* and *Troglocladodus trimblei* are included as Figure 163. Large teeth (up to 3.5 cm [1.4 in] in width) of *Cladodus mirabilis* have been collected from Colossal Cave and Specimen Avenue, making this the second-largest ctenacanthiform to be identified from MACA (Figure 162G). Presently, *Cladodus mirabilis* is well-known in Europe, particularly in the Armagh region of Northern Ireland and the Derbyshire region of England (Duffin and Ginter 2006). The only North American record of *Cladodus mirabilis* is from an Early Mississippian (Tournaisian)-age Kinderhookian locality of Iowa (Duffin and Ginter 2006). Isolated juvenile to large adult teeth of *Saivodus striatus* are known from the Cox Route, Fossil Avenue, Solitary Cave, and Specimen Avenue (Figure 162H). The lower jaw, indeterminate cranial cartilages, and associated teeth of a fairly large *Saivodus striatus* are exposed in the Specimen Avenue passage (Figure 162I). This is the first identified skeletal material of *Saivodus*. Isolated teeth of an indeterminate ctenacanth taxon are known from the Cox Route, Fossil Avenue, and Specimen Avenue.

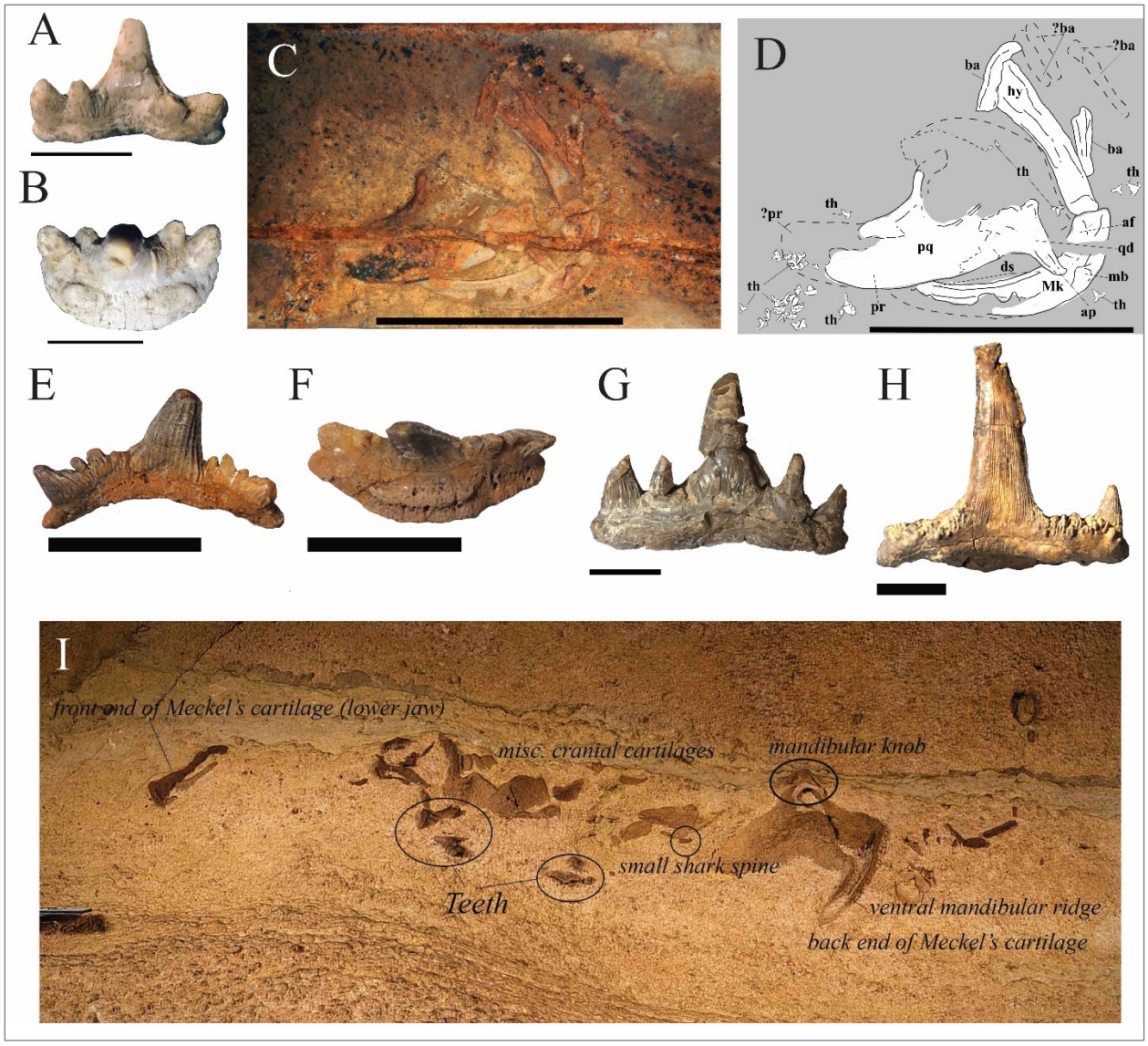


Figure 162. Ctenacanthiform fossils from the Joppa Member of the Ste. Genevieve Formation, MACA. **A–D.** *Glikmanius careforum*, **A, B.** MACA 64335, holotype tooth in **A**. labial and **B.** oral views, scale equals 1 cm (0.4 in); **C, D.** MACA 64342, the visceral cartilages and teeth of *Glikmanius careforum* in situ in the Ste. Genevieve Formation in Off Marion; **C.** Photograph of the specimen. **D.** Line diagram of the exposed and subsurface cartilages. Scale bars equal 10 cm (4 in). **E, F.** MACA 62062, the holotype of *Troglocladodus trimblei*, in **E.** labial and **F.** oral views, scale equals 1 cm (0.4 in). **G.** MACA 62078, tooth of *Cladodus mirabilis* in labial view, scale equals 1 cm (0.4 in). **H.** MACA 62534, tooth of *Saivodus striatus* in labial view, scale equals 1 cm (0.4 in). **I.** Field photo of the Meckel's cartilage (lower jaw), teeth, and other visceral cartilage fragments of *Saivodus striatus* in Roger's Specimen Ave. Abbreviations for **D**: **af**, articular facet; **ap**, articular process of the palatoquadrate; **ba**, branchial arch; **ds**, dental sulcus; **hy**, hyomandibula; **mb**, mandibular knob; **Mk**, Meckel's cartilage; **pq**, palatoquadrate; **pr**, palatine ramus; **qd**, quadrate process of the palatoquadrate; and **th**, tooth or teeth. NPS / JP HODNETT & NPS



Figure 163. Reconstruction of the ctenacanthiforms *Glikmanius careforum* (foreground) and *Troglocladodus trimblei* (background). NPS / BENJI PAYSNOE

Protacrodontiformes—Protacrodont sharks are a basal group that are ancestral to the modern shark lineage (Euselachii). Most protacrodonts have small teeth made for holding and crushing prey, although some species evolved teeth for slicing prey (Hodnett and Elliott 2018). Tiny isolated teeth of this group have been found in sediments from the *Saivodus* site in Specimen Avenue and bear some resemblance to those of *Microklomax carrieae*, a crushing-tooth species, from the Surprise Canyon Formation at Grand Canyon National Park (Hodnett and Elliott 2018).

Hybodontiformes—Hybodonts are another basal group of the Euselachii, unique in that males bore specialized horn-like denticles on the sides of their head (Ginter et al. 2010). A few small teeth of an indeterminate hybodont were collected from the *Saivodus* site in Specimen Avenue. Several species of hybodonts are known from the Viséan of North America and Eurasia (Ginter et al. 2010).

Neoselachii—A single tiny tooth tentatively referred to *Cooleyella* was collected from the Cox Route. *Cooleyella* is considered to be one of the earliest known neoselachians and is known from the Viséan of North America and Eurasia (Ginter et al. 2010).

Paraselachii—A number of basal euchondrocephalans have been collected from both the Fredonia Member and Joppa Member of the Ste. Genevieve Formation.

Paraselachii from the Fredonia Member—A single tooth of an indeterminate gregoriid was collected from the Jessup Avenue locality (Figure 160F). Gregoriids are shark-like basal members of the Euchondrocephali that had pronounced ridged teeth with petalodont-like wide but flattened tooth bases, rhombic scales, and elongated crania (Lund and Grogan 2004a). The gregoriid *Srianta* is known from the Late Mississippian Surprise Canyon Formation at Grand Canyon National Park (Hodnett and Elliott 2018).

Paraselachii from the Joppa Member—Teeth of the debeeriid *Heteropetalus* were collected from sediments at the *Saivodus* site in Specimen Avenue (Figure 164A). *Heteropetalus* was a small elongate chondrichthyan with a single prominent dorsal fin, a paddle-like pectoral fin, and small multi-cusped clipping teeth (Lund 1977). *Heteropetalus* is best known from complete skeletons from the Late Mississippian Bear Gulch Limestone of central Montana but is also known from the Surprise Canyon Formation at the Grand Canyon (Hodnett and Elliott 2018). A single tri-cuspid tooth of an unnamed taxon known from the Bear Gulch Limestone is also present in the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave. This taxon, informally referred to as “L2SP”, is known from a number of complete or nearly complete male and female individuals in Montana and represents a relative of *Debeerius* and *Heteropetalus* (Andermann 2011). It had a series of clipping teeth with three prominent cusps (Andermann 2011). Two additional basal euchondrocephalans are known from the Joppa Member. *Venustodus* sp. is known from isolated teeth at localities including Fossil Avenue and Specimen Avenue (Figure 164B). *Venustodus* is well known from V-shaped teeth with small cusps from Mississippian and Pennsylvanian rocks, and it has been debated if it represents a paraselachian or holocephalan (Stahl 1999; Ginter et al. 2010). Another enigmatic taxon, *Euglossodus*, is known from a single tooth from Fossil Avenue. *Euglossodus* was originally placed with the petalodonts, but that assessment is currently under scrutiny (Ginter et al. 2010). *Euglossodus*

is much more abundant in the Viséan of Great Britain but is known from the Viséan of Iowa (St. John and Worthen 1875; Ginter et al. 2010). A small number of teeth representing at least two indeterminate paraselachian taxa are also known from Colossal Cave, the Cox Route, Fossil Avenue, Serena's Arbor, and Specimen Avenue.

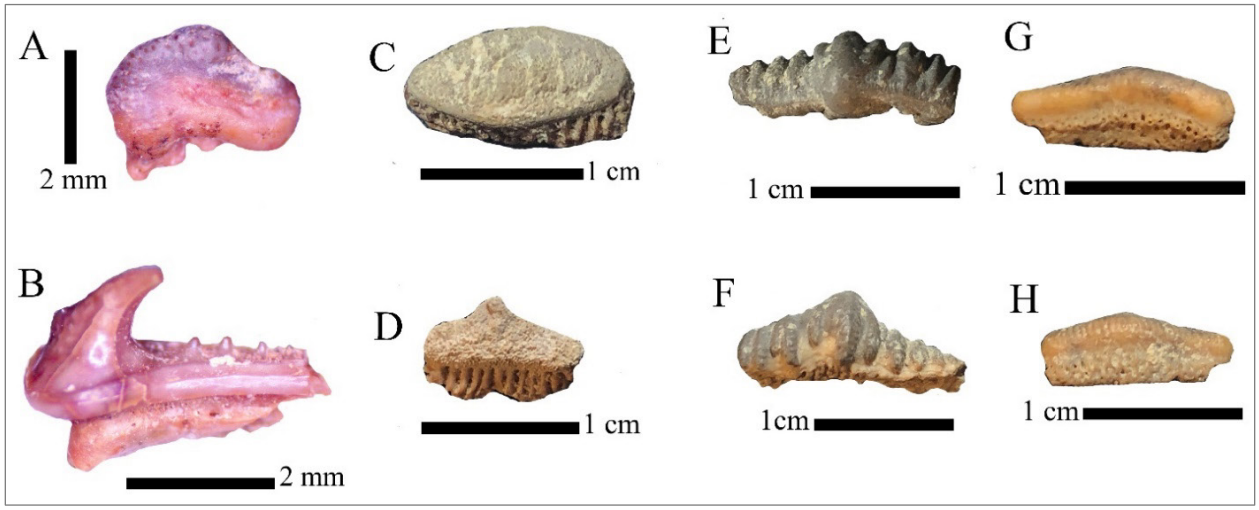


Figure 164. Euchondrocephalan fossils from the Joppa Member of the Ste. Genevieve Formation at MACA. **A.** *Heteropetalus* sp. in lingual view. **B.** *Venustodus* sp. in labial view. **C, D.** Euchondrocephalan indeterminate 1, in lingual views. **E, F.** *Orodus* sp. 1: **E.** Oral view; **F.** Lingual view. **G, H.** *Orodus* sp. 2: **G.** Labial view; **H**. Lingual view. NPS / JP HODNETT

Orodontiformes—Both the Fredonia Member and the Joppa Member have occurrences of orodontid chondrichthyans.

Orodontiforms of the Fredonia Member—Teeth of an indeterminate orodontiform, nearly identical to the type found in the St. Louis Formation, were collected from the Jessup Avenue locality.

Orodontiforms of the Joppa Member—At least five different species of orodontiform chondrichthyans have been identified from the Joppa Member. Ginter et al. (2010) comment that the family Orodontidae is in need of critical review. Currently, Ginter et al. (2010) has broken down this family into "type genera" until the taxonomic issues are sorted, which we are following here. A single tooth of the "*Orodus ramosus* type", which are heavily crinkled crushing teeth, was collected from the Fossil Avenue locality (Figures 164E and 164F). A small number of smaller "*Orodus elongatus* type" teeth, small bar-like teeth with minute ridges, were collected from the Fossil Avenue and Specimen Avenue localities (Figure 164G and 164H). Teeth of *Leiodus* sp., a small orodontiform which has bar-like teeth with a raised pointed central cusp, are recognized from the Fossil Avenue locality. There is also a number of indeterminate orodontiform teeth known from both the St. Louis Formation and the Fredonia Member of the Ste. Genevieve Formation. In the Joppa Member, they have been found at Fossil Avenue, Serena's Arbor, and Specimen Avenue (Figures 164C and 164D). It should be noted here that the Serena's Arbor sample was collected in near close association and

may represent dentition of a single individual, which would show that this taxon has some degree of heterodonty.

Eugenodontiformes—The eugenodontiforms, also referred to as "whorl-toothed sharks", are a diverse group of chondrichthyans that are known for the enlarged lower symphysial whorl of teeth developed in some forms, and well-developed rows of small bar-like teeth, forming a crushing pavement dentition in the upper and lower jaws (Zangerl 1981; Ginter et al. 2010). A partial small symphysial blade-like tooth of a eugenodont was collected from Fossil Avenue. This may represent one of the oldest eugenodonts currently known.

Petalodontimorpha—The petalodonts of the Ste. Genevieve Formation are fairly diverse within Mammoth Cave, with at least four species known from the Fredonia Member and ten species identified from the Joppa Member.

Petalodonts from the Fredonia Member—A small number of *Chomatodus* teeth have been collected and documented from the Jessup Avenue locality (Figures 160G and 160H). A fragmentary tooth referable to *Petalodus* (Figure 160J) and a complete tooth of *Lisgodus* (Figure 160I) were also collected from Jessup Avenue, together with an indeterminate petalodont tooth. A tooth of *Petalorhynchus* cf. *P. beargulchensis* was recently identified from a side passage along the tour trail just off Grand Central Station. *Petalorhynchus beargulchensis* is presently only known from the Heath Formation in central Montana from both isolated teeth and a nearly complete skeleton, and is unique as a species in that the teeth have serration-like structures on the carina (cutting edge) of the tooth (Lund 1989; Lund et al. 2014). The tooth from Grand Central side-passage is the first record of a *Petalorhynchus* similar to *P. beargulchensis* known outside of Montana.

Petalodonts from the Joppa Member—Teeth of *Chomatodus* are very common in most localities within the Joppa Member, particularly Fossil Avenue, Serena's Arbor, and Specimen Avenue (Figures 165A and 165B). Two species of *Chomatodus* are recognized in the Joppa Member. The less-common species is recognized by teeth that are more robust than the much thinner, blade-like teeth of the common form. This second robust species of *Chomatodus* is known from Fossil Avenue and Serena's Arbor. A new species of skate-like janassid petalodont, *Strigilodus tollesonae*, has been recently described from the Joppa Member at Colossal Cave, Fossil Avenue, Serena's Arbor, and Specimen Avenue (Hodnett et al. 2023) (Figures 165J, 165K, and 166). A few teeth of *Janassa* sp. are also reported from Colossal Cavern (Hodnett et al. 2023). Mississippian records of *Janassa* are known from the Viséan and Serpukhovian of North America and Eurasia (Ginter et al. 2010). Three species of *Petalodus* are known from the Joppa Member. *Petalodus hastingsii* is a smaller species found so far only at Fossil Avenue (Figure 165H). This species is otherwise known primarily from Europe (Ginter et al. 2010). *Petalodus linguifer* (Figure 165I) is more common in the Joppa Member at Mammoth Cave but is less known in the literature, as the last descriptive reference to this taxon was in the late 1800s (St. John and Worthen 1875). Teeth of *Petalodus linguifer* are known from Colossal Cave, Fossil Avenue, and Serena's Arbor. Finally, a possible new larger species of *Petalodus* has been identified from the Joppa Member (Figures 165F and 165G). This new *Petalodus* has a rather low and blunt crown, and a long tooth base. This new species has been identified from

the Cox Route, Fossil Avenue, and Serena's Arbor. Tiny teeth of *Lisgodus* are known from Fossil Avenue, Serena's Arbor, and Specimen Avenue (Figure 165C). Additional taxa include the recently collected (2022) *Antilodus* sp. from Colossal Cave.

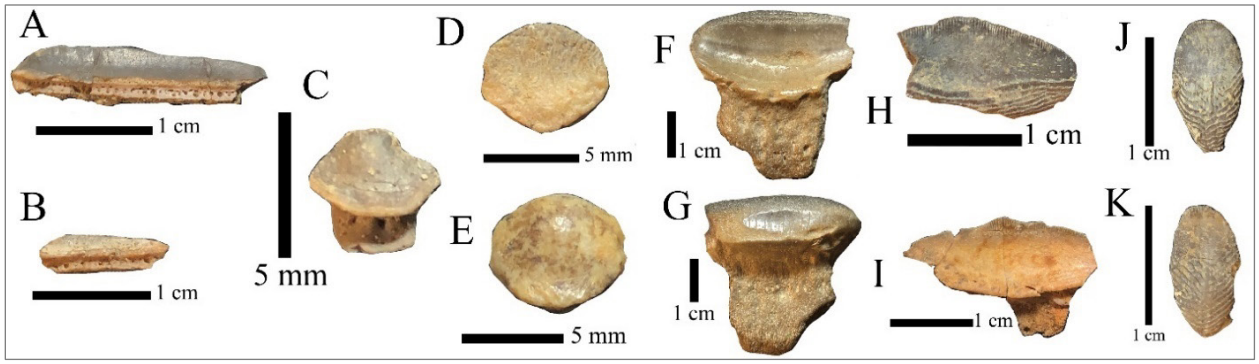


Figure 165. Petalodontiform fossils of the Joppa Member of the Ste. Genevieve Formation at MACA. **A, B.** *Chomatodus* sp. 1: **A.** Posterolateral tooth in lingual view; **B.** Anterolateral tooth in labial view. **C.** *Lisgodus* sp. in lingual view. **D, E.** Petalodont indeterminate 1: **D.** Lingual view; **E.** Labial view. **F, G.** *Petalodus* n. sp.: **F.** Lingual view; **G.** Labial view. **H.** *Petalodus hastingsii*, in lingual view. **I.** *Petalodus linguifer*, in lingual view. **J, K.** Two specimens of *Strigilodus tollesonae* in lingual view.
NPS / JP HODNETT



Figure 166. Reconstruction of the janassid petalodont *Strigilodus tollesonae*. NPS / BENJI PAYSNOE

Smaller petalodonts such as *Petalorhynchus* cf. *P. spatulatus* are relatively common at the Cox Route, Fossil Avenue, and Serena's Arbor. A tooth of an *Obruchevodus*-like taxon was found within sediments collected at the *Saivodus* site in Specimen Avenue. A tooth referable to *Belantsea* was collected from Fossil Avenue. *Belantsea* is known from a complete individual specimen with preserved pigmentation patterns from the Late Mississippian Bear Gulch Limestone in Montana (Lund 1989). A number of small teeth referable to two indeterminate petalodont taxa have been identified at Colossal Cave, the Cox Route, Fossil Avenue, and Specimen Avenue. Recently (2022) a specimen of a new genus and species of *Fissodopsis*-like petalodont was collected.

Holocephali—Both the Fredonia and Joppa Members of the Ste. Genevieve have a diverse record of holocephalan chondrichthyans, which are relatively abundant in most passage localities. The Fredonia Member has at least six species of holocephalans while the Joppa Member has at least ten.

Holocephalans from the Fredonia Member—Two species of *Deltodus*, *Deltodus* cf. *D. sublaevis* (Figure 160L) and *Deltodus* sp., are known from Jessup Avenue. A tooth plate of *Sandalodus* sp. is known from Jessup Avenue and Marion Avenue (Figure 160K). A tooth plate of *Psammodus* sp. was collected from Edna's Dome. Single tooth plates of *Deltoptychius* sp. were collected from Edna's Dome and Jessup Avenue (Figure 160M).

Holocephalans from the Joppa Member—The presence of eel-like holocephalans belonging to Chondrenchelyidae is confirmed by a number of elongated small triangular tooth plates from Fossil Avenue. Chondrenchelyids are otherwise presently represented by at least three genera which are primarily known from the Late Mississippian of North America and Eurasia (Stahl 1999). A large number of isolated teeth of *Helodus* (Figure 167C) are known from Fossil Avenue, Serena's Arbor, and Specimen Avenue. Tooth plates of *Psephodus* (Figure 167F) are known from Fossil Avenue and Specimen Avenue. A tooth plate of *Psephodus* sp. can be seen from the Marion Avenue passage near the elevator access (Figure 152B). Tooth plates of *Cochliodus* are known from Fossil Avenue and Serena's Arbor. Tooth plates of *Deltodus* (Figure 167G) are known from the Cox Route, Fossil Avenue, Serena's Arbor, and Specimen Avenue. *Sandalodus* is the most common holocephalan encountered in the Joppa Member, having been found in Colossal Cave, the Cox Route, Fossil Avenue, Marion Avenue (Figure 160K), Serena's Arbor, and Specimen Avenue. The tooth plates of *Poecilodus* (Figure 167H) are rare, currently only known from Specimen Avenue. A unique tooth plate with a washboard-like crown was collected from Colossal Cave (Figures 167A and 167B). This tooth is similar to those of the Permian *Solenodus* from Russia but differs in terms of the development of the horizontal cusps, which are less developed in the Russian taxon (Stahl 1999). Large and small tooth plates of *Psammodus* (Figure 167E) are known from Colossal Cave, Fossil Avenue, and Specimen Avenue. Tooth plates of *Deltoptychius* (Figure 167D) are relatively common in the Joppa Member and are known from Colossal Cave, the Cox Route, Fossil Avenue, Serena's Arbor, and Specimen Avenue.

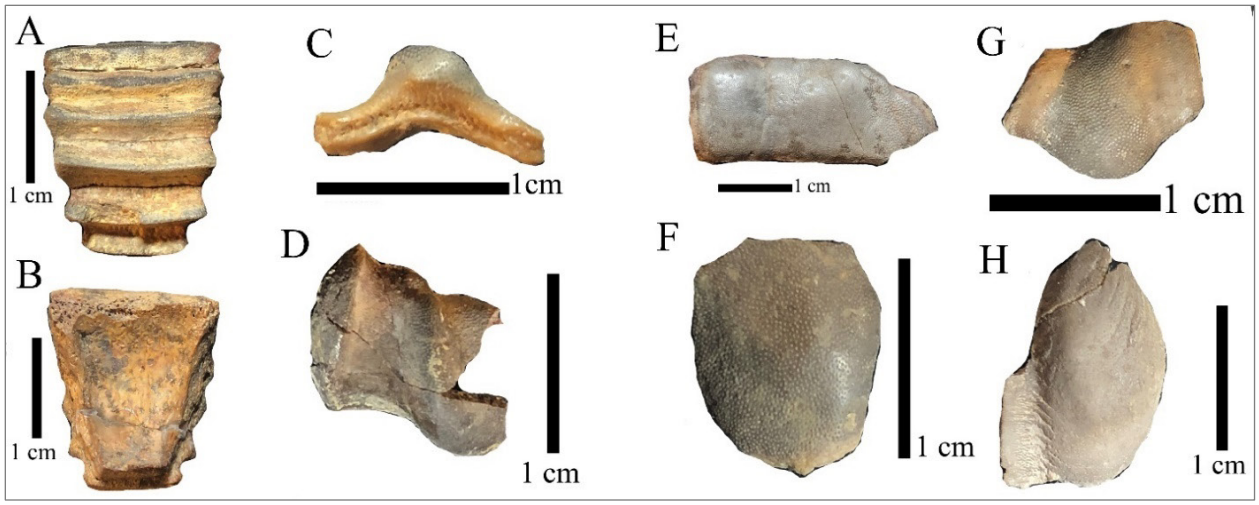


Figure 167. Holocephalan fossils of the Joppa Member of the Ste. Genevieve Formation at MACA. **A, B.** Holocephalan indeterminate 1, tooth plate: **A.** Oral view; **B.** Aboral view. **C.** Tooth of *Helodus* sp. in lingual view. **D.** Upper tooth plate of *Deltoptychius* sp. in oral view. **E.** Tooth plate of *Psammodus* sp. in oral view. **F.** Median tooth plate of *Psephodus* sp. in oral view. **G.** Lower posterior tooth plate of *Deltodus* sp. in oral view. **H.** Upper tooth plate of *Poecilodus* sp. in oral view. NPS / JP HODNETT

Actinopterygii

The actinopterygians, or ray-finned fishes, first appeared in the Devonian and represent one of the largest vertebrate groups alive today (Long 1996). During the Mississippian actinopterygians were diverse but most were small (Long 1996). All of our knowledge of the Carboniferous ray-finned fishes from Mammoth Cave comes from the Joppa Member of the Ste. Genevieve Formation.

Palaeonisciformes—Palaeonisciformes is a group of basal ray-finned fishes, many retaining fusiform bodies, diamond-shaped scales, and needle-like teeth (Long 1996). A large number of isolated scales, teeth, and bones were collected from cave sediments from the *Saivodus* site in Specimen Avenue. The variable morphology of these scales and teeth suggests there are five species of these basal ray-finned fishes in the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave.

?*Eurynotiformes*—Eurynotiformes is a group of deep-bodied basal ray-finned fishes that first appeared in the Early Mississippian and diversified by the Pennsylvanian (Friedman et al. 2018). These fishes had dorsoventrally deep body scales and button-like crushing teeth (Long 1996). A few isolated jaws and scales were collected from the Cox Route and Specimen Avenue that can be tentatively referred to this group of bony fish.

Girkin Formation (Middle–Late Mississippian: late Viséan–early Serpukhovian)

The Girkin Formation consists primarily of dolomitic and shaly limestones as well as thin greenish-gray shale beds and is 40–43 m (130–140 ft) thick. It represents the uppermost sections of the bedrock in which the passages of the Mammoth Cave System are developed (Palmer 1981). Invertebrate fossils are common in some beds that are exposed in passageways, but vertebrate fossils are rare. However, they have been collected from multiple members of the Girkin Formation. Precise placement of these fossils within the formation's stratigraphic framework is still underway. For

simplicity, we are currently reporting these chondrichthyans as coming from the Girkin Formation, undivided. The Girkin Formation is dated to the early Chesterian, spanning the Middle–Late Mississippian boundary (Viséan into Serpukhovian). This time frame is close in age to the Surprise Canyon Formation at the Grand Canyon National Park and the Heath Formation (Bear Gulch Limestone) of Montana (Hodnett and Elliott 2018).

Girkin Formation Localities

At present, five localities have collectively produced a significant collection of marine vertebrates from the Girkin Formation at MACA.

Cave #030—A few chondrichthyan teeth and spines were collected from the Paoli Member of the Girkin Formation at Cave #030 (Figure 168). Cave #030 is an isolated cave at MACA, not connected to the main passages of Mammoth Cave itself. The vertebrate remains were collected from the low ceiling in a side chamber towards the back of the cave. Gastropods and blastoids were fairly common at this site.

Cave #048—A few chondrichthyan teeth were collected from two indeterminate members from Cave #048, a sinkhole cave outside of the main Mammoth Cave system (Figure 169).

Great Onyx Cave—At this popular tour cave, chondrichthyan remains are rare and occur high along the cave wall overhangs (Figure 170). The chondrichthyan fossils consist primarily of holocephalan tooth plates. A possible cartilage fragment was also seen. These fossils were left in place due to the nature of the limestone they were exposed in and their relative proximity to a tour trail.

Crystal Cave—Crystal Cave is a segment of the Mammoth Cave System. A portion of it was previously used as a show cave. A single holocephalan tooth plate and probable actinopterygian cranial material were identified in the ceiling towards the end of one segment of the former tour trail (Figure 171).

New Entrance—The New Entrance of Mammoth Cave is an artificial entrance put into the cave in 1921. It is a series of steps, catwalks, and sidewalks that descends through several pits and canyons. It exposes the lower half of the Girkin Formation and the upper Ste Genevieve Formation. Multiple indeterminate holocephalan tooth plates have been seen in the Girkin as it is exposed along the tour trail.



Figure 168. Documentation of chondrichthyan fossils from the Paoli Member of the Girkin Formation at Cave #030, MACA. **A.** Rick Olson in Cave #030. **B.** Rick Toomey looking for vertebrate fossils in the low ceiling of Cave #030. **C.** Large tooth of *Saivodus striatus* exposed in the cave ceiling. **D.** Small tooth of an eugenodont chondrichthyan. **E.** Small dorsal spine fragment, possibly belonging to a paraselachian chondrichthyan. **F.** Tiny tooth (the small purple-brown speck) of a debeeriid paraselachian chondrichthyan. Scale for **C–F** includes centimeters (squares) and millimeters (tick marks).
NPS / JP HODNETT & NPS

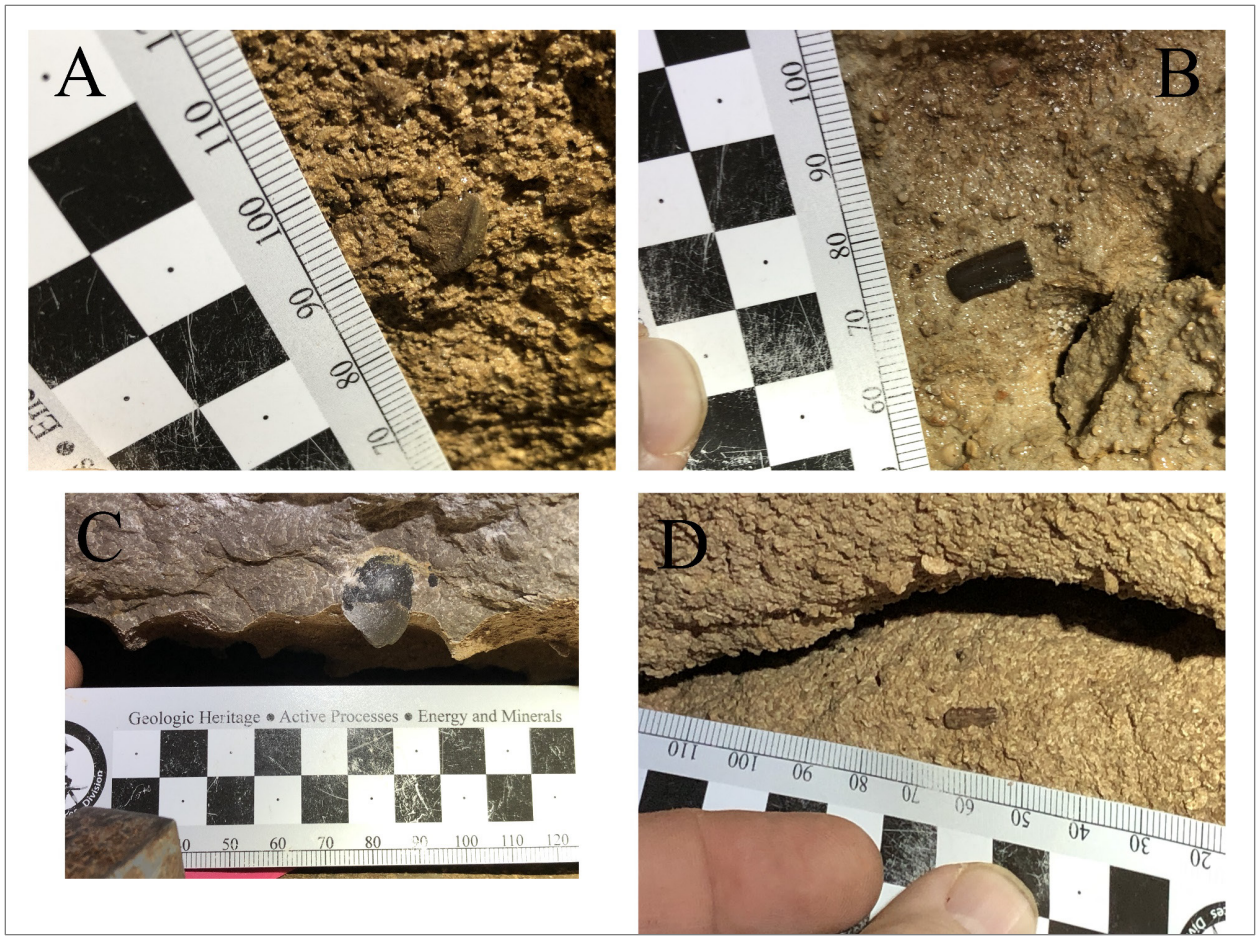


Figure 169. Documentation of chondrichthyan fossils from the Girkin Formation at Cave #048. **A.** Small petalodont tooth. **B.** *Cochliodus* sp. tooth plate in the cave wall of the lower level of Cave #048. **C.** Indeterminate euchondrocephalan tooth on an overhang in the upper level of Cave #048. **D.** Fragment of a holocephalan cephalic tenaculum in the lower level of Cave #048. Scale for **A–D** includes centimeters (squares) and millimeters (tick marks). NPS / JP HODNETT & NPS

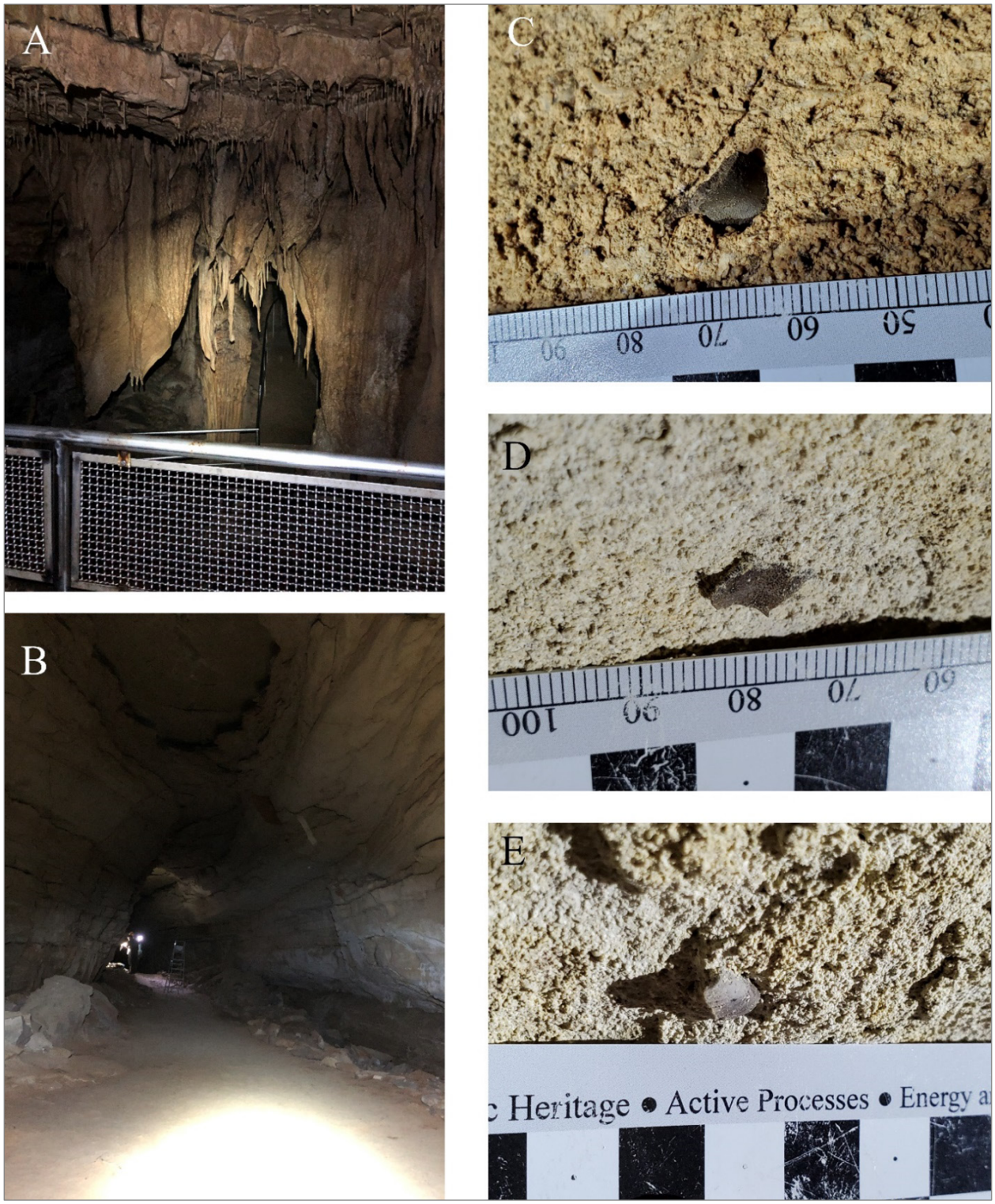


Figure 170. Documenting chondrichthyan fossils from the Girkin Formation at Great Onyx Cave. **A.** Stalactite formations in the upper level of the Great Onyx Cave entrance. **B.** The main pathway of Great Onyx Cave, where the chondrichthyan fossils were encountered. **C.** Holocephalan tooth plate in an overhang off the main pathway. **D.** Segment of chondrichthyan cartilage. **E.** Fragment of a holocephalan tooth plate. Scale in millimeters (**C, D**) and centimeters (**E**). NPS / JP HODNETT & NPS

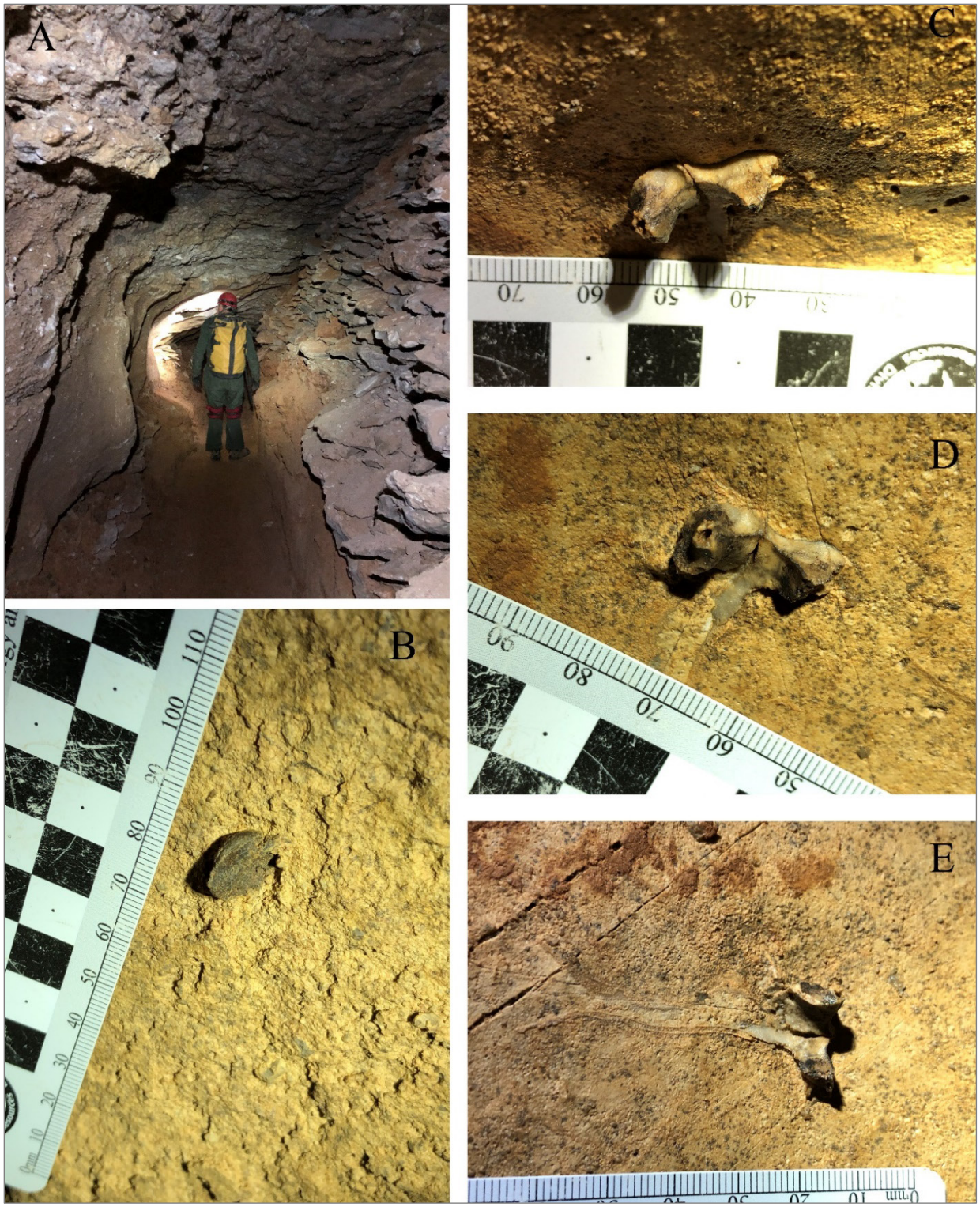


Figure 171. Documenting vertebrate fossils from the Girkin Formation at Crystal Cave. **A.** Rick Toomey leading the way through the main passage of Crystal Cave. **B.** Tooth plate of *Psephodus* sp. in the ceiling near the end of the main passage. **C–E.** Three views of a probable actinopterygian cranial bone in the ceiling of Crystal Cave. Scale for **B–E** includes centimeters (squares) and millimeters (tick marks).
NPS / JP HODNETT & NPS

Girkin Formation Assemblage

At present, no published accounts of fossil vertebrates are known for the Girkin Formation, making the fossils at MACA the first vertebrate record for the entire formation. Presently, nine distinct chondrichthyan taxa and an actinopterygian have been identified (Table 12; Figure 172).

Ctenacanthiformes—A single large tooth (4 cm [1.6 in]-wide tooth base) of *Saivodus striatus* was first encountered by Kristen Bobo, Jim Honaker, and Joe Douglas (Figures 172A to 172C). Presently, this is the largest example of *Saivodus striatus* found at MACA.

Paraselachii—A single tooth of a debeeriid paraselachian was collected in association with two dorsal fin spine fragments. This small tooth (approximately 2 mm [0.08 in] in width) bears closer resemblance to the teeth of *Debeerius ellefseni* than to *Heteropetalus elegantulus*, being more flattened and chisel-like. Both taxa occur in the roughly contemporaneous Bear Gulch Limestone (Lund 1977; Grogan and Lund 2000). The dorsal fin spine fragments collected with the tooth are also similar in morphology to those seen in both *Debeerius* and *Heteropetalus*.

Eugenodontiformes—A single small lateral pavement tooth of a eugenodontiform chondrichthyan was collected in Cave #030. The tooth shares similar morphology to those of *Campodus,* which are elongate and bear labial and lingual knob-like projections. *Campodus* is known from partial jaws from the latest Mississippian of Missouri and isolated teeth from the Early Pennsylvanian of Belgium. Similar small eugenodont pavement teeth were also identified from the Surprise Canyon Formation at Grand Canyon National Park (Hodnett and Elliott 2018).

Petalodontiformes—A well-preserved small indeterminate petalodontid petalodont was collected from Cave #048 in April of 2021 (Figures 172E and 172F).

Holocephali—Several holocephalan chondrichthyans have been recently identified from the Girkin Formation at MACA. *Helodus* sp. was recently collected from Cave #048 (Figure 172G). *Psephodus* sp. (Figure 172H) is known from Crystal Cave and New Entrance. A well-preserved tooth plate of *Cochliodus* sp. was collected from Cave #048 (Figure 172I). A questionable tooth plate of *Deltodus* sp. has been identified along the tour passage of Great Onyx Cave. A number of indeterminate holocephalan tooth plates were also identified from Cave #048 and Great Onyx Cave.

Actinopterygii—Possible bony fish cranial elements were documented in Crystal Cave. This is the first bony fish material identified for the Girkin Formation. The exact identification of the taxon is unknown at this time (Figures 171C to 171E).

Table 12. The vertebrate assemblage of the Girkin Formation at MACA. The first three localities are separate caves from the main Mammoth Cave system, whereas the last two are cave passages within the main Mammoth Cave system.

Higher Classification	Genus and Species	Cave #030	Cave #048	Great Onyx Cave	Crystal Cave	New Entrance
Chondrichthyes: Elasmobranchii: Ctenacanthiformes: “Tamiobatidae”	*Saivodus striatus*	Y	–	–	–	–
Chondrichthyes: Euchondrocephali: Paraselachii: Debeeriidae	Genus and species indet.	Y	–	–	–	–
Chondrichthyes: Euchondrocephali: Eugenodontiformes: Eugenodontidae	Genus and species indet.	Y	–	–	–	–
Chondrichthyes: Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalodontidae	Genus and species indet.	–	Y	–	–	–
Chondrichthyes: Euchondrocephali: Holocephali: Helodontiformes: Helodontidae	*Helodus* sp.	–	Y	–	–	–
Chondrichthyes: Euchondrocephali: Holocephali: Cochliodontiformes: Psephodontidae	*Psephodus* sp.	–	–	–	Y	Y
Chondrichthyes: Euchondrocephali: Holocephali: Cochliodontiformes: Cochliodontidae	?*Cochliodus* sp.	–	Y	–	–	–
	?*Deltodus* sp.	–	–	Y	–	–
Chondrichthyes: Euchondrocephali: Holocephali	Indeterminate holocephalan	–	Y	Y	–	–
Osteichthyes: Actinopterygii	Indeterminate actinopterygian?	–	–	–	Y	–

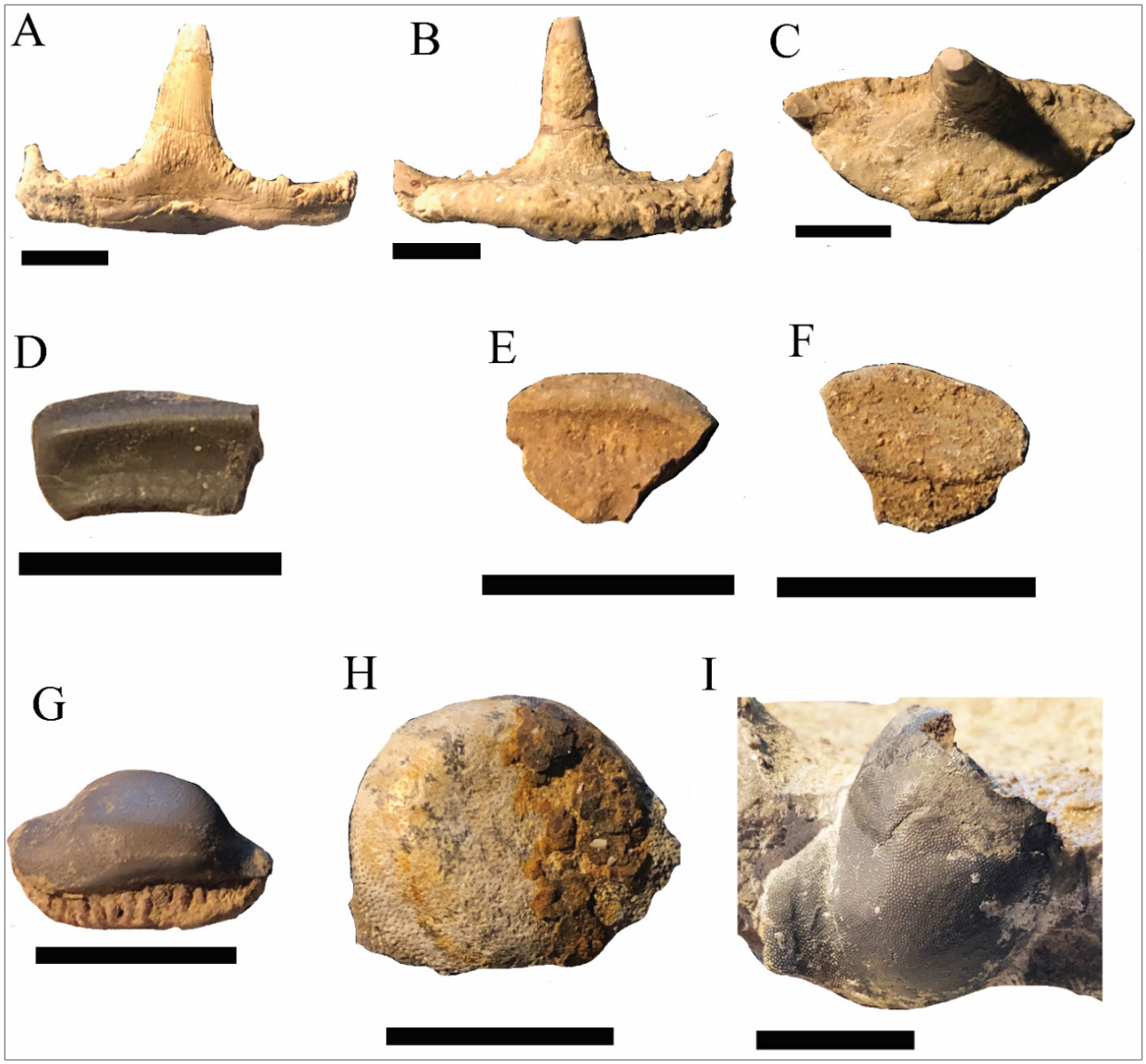


Figure 172. Chondrichthyan fossils from the Girkin Formation at MACA. **A–C.** Tooth of *Saivodus striatus* from Cave #030: **A.** Labial view; **B.** Lingual view; **C.** Oral view. **D.** Indeterminate euchondrocephalan tooth from Cave #048 in oral view. **E, F.** Tooth of indeterminate petalodont from Cave #048: **E.** Labial view; **F.** Lingual view. **G.** Tooth of *Helodus* sp. from Cave #048 in lingual view. **H.** Tooth of *Psephodus* sp. from Crystal Cave in oral view. **I.** Tooth of *Cochliodus* sp. from Cave #048 in oral view. Scale = 1 cm (0.4 in). NPS / JP HODNETT

Big Clifty Formation (Late Mississippian: early Serpukhovian)

The Late Mississippian Big Clifty Formation consists primarily of massive sandstone beds, though basal limestone and shaly beds are known within the park (Palmer 1981). At present no vertebrate fossils have been identified from the Big Clifty Formation within the park. However, the Big Clifty Formation does have a significant record of chondrichthyans from the vicinity of Sulphur, Indiana, located approximately 115 miles north of MACA. Lund (1988, 1989) reported on the petalodont *Lisgodus* sp. and multiple new species of the small early chimaeriform (modern ratfish lineage)

holocephalan *Echinochimaera*. These records were based on isolated dental elements, collected from the Indian Springs Shale Member of the Big Clifty Formation. Unpublished chondrichthyans from the Indian Springs Shale Member also include *Saivodus striatus*, *Thrinacodus* sp., *Harpacodus dentatus,* and *Deltodus* sp. (JPH, pers. obs., 2020). Big Clifty outcrops within MACA should be monitored for potential vertebrate fossils.

Haney Formation (Late Mississippian: early–middle Serpukhovian)

The Haney Formation consists primarily of biomicritic limestones, with lesser skeletal limestones and micritic dolomite. Shales may also occur within this formation. On the park, the Haney generally averages about 10–13 m (33–43 ft) thick. The Haney is a karst-forming unit, and all of the known shark localities are associated with caves/cave entrances developed in it. The Haney Formation overlies the Big Clifty Formation and is overlain by the Hardinsburg Formation. The Haney Formation has not been subdivided into members. The age of the Haney Formation is considered to be Chesterian/Serpukhovian (Late Mississippian). Records of chondrichthyans and other vertebrates from the Haney Formation are rare. Carlson (2014) reported on two teeth of the xenacanthimorph *Bransonella nebraskensis* from a road cut on Illinois Route 146, near Interstate 57, in Union County, Illinois. Petalodont teeth referable to *Petalodus acuminatus* have also been reported from the Haney Formation near Sulphur, Indiana (image available at https://www.kyanageo.org/mississippian.html).

Haney Formation Localities

At present, only three isolated cave localities within MACA are known to contain vertebrate material from the Haney Formation: Cave #293 (Figure 173), Cave #203 (Figure 174), and the Salts Cave sinkhole entrance to Mammoth Cave.

Cave #293—Three chondrichthyan teeth were collected from this spring-fed cave, not only from the cave walls, but also from the spring-fed stream flowing out of the cave entrance. This is the only locality where chondrichthyan teeth were found and collected from a surface locality outside of a cave at the park.

Cave #203—This stream cave where two chondrichthyan teeth were collected has a spring flowing out of it. An indeterminate chondrichthyan dorsal spine was also identified but left in place.

Salts Cave—The Salts Cave entrance to the Mammoth Cave System has developed up through the Big Clifty Formation from a Girkin Passage. The entrance exposes a small Haney bluff and a spring flowing from the Haney into the cave. At the floor of the entrance, a large block of Haney limestone which had fallen from the bluff into the entrance contained a large shark tooth. Of note is the presence of the large ctenacanthiform *Saivodus striatus*, making this the youngest occurrence of this genus at MACA. Additional chondrichthyan fossils are known in situ but have not yet been identified.



Figure 173. Documenting chondrichthyan fossils from the Haney Formation at Cave #293. **A.** The entrance (background with Rick Toomey, Rick Olson, and Rich Boldon) and the stream that exits out of the cave (foreground with Kelli Tolleson). **B.** Partially exposed tooth of *Petalodus* sp. from within the cave. **C.** Tooth plate of *Psephodus* sp., found by Kelli Tolleson in the stream just outside the entrance of the cave (the only surface-collected chondrichthyan fossil at MACA to date). **D.** Euchondrocephalan (eugenodont?) symphysial tooth within the cave. Scale in millimeters. NPS / JP HODNETT & NPS

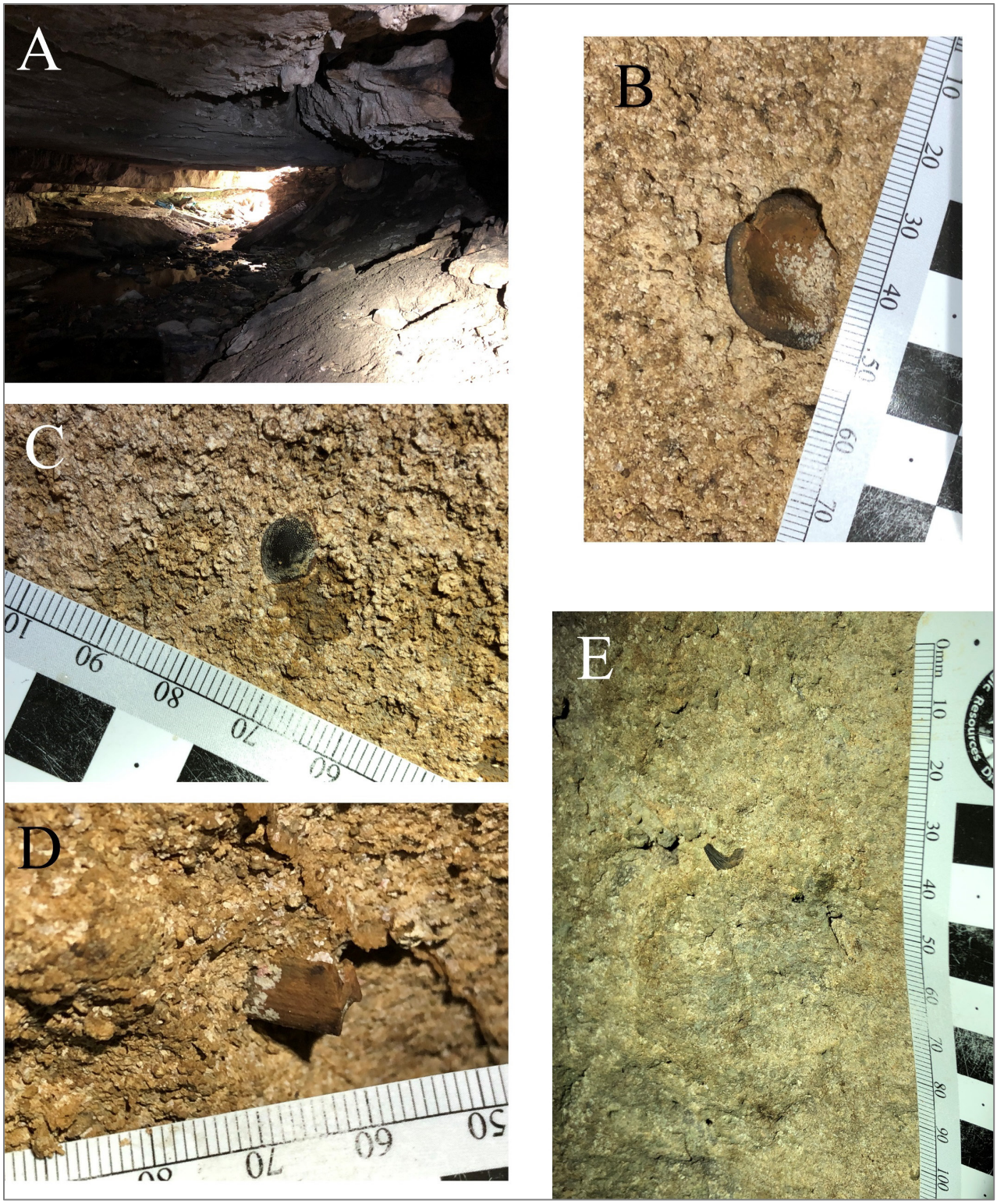


Figure 174. Documenting chondrichthyan fossils from the Haney Formation at Cave #203. **A.** View of the cave entrance from within the cave. **B.** Tooth plate of *Psephodus* sp. within the cave ceiling. **C.** Second smaller *Psephodus* sp. tooth plate in the cave ceiling. **D.** Indeterminate chondrichthyan dorsal fin spine fragment in the cave ceiling. **E.** Partial ctenacanth (cf. *Glikmanius* sp.) in the cave ceiling near the entrance. Scale for **B–E** in millimeters. NPS / JP HODNETT & NPS

Haney Formation Assemblage

At present only five chondrichthyan taxa representing four orders have been identified from the three cave sites described above (Table 13). The Haney Formation has not been divided into members and it is difficult to trace any of its beds between the different caves, so the assemblage is not divided stratigraphically.

Table 13. Chondrichthyan assemblage of the Haney Formation at MACA.

Higher Classification	Genus and Species	Cave #293	Cave #203	Salts Cave
Elasmobranchii: Ctenacanthiformes: "Tamiobatidae"	*Saivodus striatus*	–	–	Y
Elasmobranchii: Ctenacanthiformes: Heslerodidae	*Glikmanius careforum*	–	Y	–
Euchondrocephali	Indeterminate euchondrocephalan	Y	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalodontidae	*Petalodus* sp.	Y	–	–
Euchondrocephali: Holocephali: Cochliodontiformes: Psephodontidae	*Psephodus* sp.	Y	Y	–

Ctenacanthiformes—A single partial tooth of the ctenacanthiform chondrichthyan *Glikmanius careforum* was collected from the cave ceiling of Cave #203 (Hodnett et al. 2004a) (Figure 174E). Recently, a rather large tooth of *Saivodus striatus* was collected from rockfall in Salts Cave, extending the presence of this ctenacanthiform through much of the Mississippian sequence at MACA.

Euchondrocephali indeterminate—A bizarre mesiodistally symmetrical tooth was collected from Cave #293 (Figure 173D). The tooth is triangular with a prominent anterior cusp and a smaller posterior cuspid, with basolabial and orolingual depressions. From the uniform shape we surmise that this is a symphysial tooth either from a non-holocephalan, such as an unknown basal eugenodont, or one of the enigmatic taxa such as *Venustodus*.

Petalodontiformes—A single tooth of a small petalodont (Figure 173B) with some characteristics of the genus *Petalodus* was collected from Cave #293.

Holocephali—Tooth plates of *Psephodus* sp. were collected from both Cave #293 and Cave #203 (Figures 173C, 174B, and 174C).

Discussion and Recommendations

Regional and Global Context of the Mammoth Cave Mississippian Vertebrates

The Mississippian vertebrate assemblages identified from MACA have the potential to become a reference standard. At the regional level, the MACA assemblages can be compared with historical

collections made in the Illinois Basin that were not accurately described as assemblages, and also show changes in species diversity and abundance through a given stratigraphic section. For example, from our preliminary observations of the faunal assemblages of the St. Louis Formation and overlying Ste. Genevieve Formation, some orders such as the Petalodontiformes and Holocephali exhibit turnover at the species level. Taxa such as the petalodont *Petalorhynchus pseudosagittatus* occur only in the St. Louis Formation, while in the Ste. Genevieve Formation, *Petalorhynchus spatulatus* is observed. In contrast, other taxa such as the large ctenacanth *Saivodus striatus* and the holocephalan *Psephodus* show continuous distribution throughout the four primary Mississippian formations (St. Louis, Ste. Genevieve, Girkin, and Haney Formations) that form Mammoth Cave National Park, making these taxa the only chondrichthyans to be found in all of the stratigraphic formations at MACA that have produced Mississippian marine vertebrate material.

The Mammoth Cave vertebrate datum would also be a valuable resource for comparison with other Mississippian fish assemblages in North America, such as the Mississippian vertebrate fossil record at Grand Canyon National Park (Redwall Limestone and Surprise Canyon Formation; Hodnett and Elliott 2018; Hodnett et al. 2021b), the Monteagle Formation of Alabama (Stahl and Cicimurri 2005), the Fayetteville Shale of Arkansas (Pradel et al. 2014; Bronson et al. 2018), the Bear Gulch Limestone of Montana (Lund 1985), and the historic Mississippian localities from the Illinois Basin (St. John and Worthen 1875, 1883). Outside of North America, sites such as Glencartholm (Viséan) and Bearsden (Serpukhovian) in Scotland, both known for their well-preserved skeletal material of Mississippian marine vertebrates, have similar taxa (e.g., *Glencartius*, *Stethacanthus*, and *Deltoptychius*) to those seen at MACA (Moy-Thomas 1936; Dick et al. 1986). Comparison of these and other Mississippian global faunas with the Mammoth Cave Carboniferous vertebrate datum could provide insights on how these fishes were distributed worldwide and how those faunal assemblages reacted to the formation of Pangea over time.

Lastly, the Mammoth Cave Mississippian vertebrate datum could potentially help with historical issues. The datum may be useful to refine the stratigraphic distribution of taxa described originally in the late 1800s, many of which had vague geologic provenance. Also, Mammoth Cave vertebrate fossils could help refine the taxonomic standings of various species described in the late 1800s that have had little to no review since description. For example, a number of new samples of the petalodont *Petalodus linguifer* were collected from the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave. This taxon was originally described by Newberry and Worthen in 1866 and has never been reviewed and/or revised. Review and revision of the taxonomic groups found within the Illinois Basin would be critical for the faunal comparison work described above. Further research and field work would be necessary at Mammoth Cave to assist in the above review, revision, and comparison tasks, and would likely produce additional taxa and more discoveries of anatomically significant specimens.

Recommendations for Further Research

Within the three-year period since we began a concentrated effort to document the Mississippian marine vertebrates from the Mammoth Cave passages and some of the smaller caves found throughout the park, a great number of localities and geologic horizons have been identified that

demonstrate both the presence, and in some places, a rich diversity of vertebrate fossils in these Mississippian beds. Many of these passages and geologic horizons have extensive vertebrate assemblages with high specimen concentrations, while others demonstrate diversity but low specimen presence. These patterns can be analyzed in many ways, such as:

- Why are some taxa, such as the petalodontimorph *Chomatodus*, abundant in some horizons but rare in others?
- Is there a correlation between invertebrate species richness and vertebrate species richness at the various geologic horizons?
- What are the vertebrate community structures for these geologic horizons? Are some groups more common than others?

To facilitate answering these and other questions, the following suggestions for further field and lab research are proposed:

- Continue collecting specimen samples from geologic horizons with low specimen abundance (such as the Girkin and Haney Formations). However, for sites on public or staff teaching trails, leave such specimens in place for educational outreach.
- For sites that have a high abundance of vertebrate material, such as Fossil Avenue, concentrate on collecting identified uncommon and rare taxa to have sufficient sample sizes for description, and leave more common taxa in place, such as *Chomatodus* at Fossil Avenue.
- Continue surveying sites in the higher stratigraphic beds such as the Haney Formation, to identify new fossil resources.
- Identify sites with good natural fossil hash fall and procure quantities of sediment samples for further screen-washing.
- Begin scanning electron microscopy for small vertebrate materials to facilitate identification and description.

For the final product of the above research, we propose a monograph that covers the various geologic horizons and their vertebrate assemblages. This could be published through the Journal of Vertebrate Paleontology supplemental monograph series, through a special volume of the New Mexico Museum of Natural History and Science Bulletin Series, or another comparable publishing venue.

Recommendations for Public Outreach

Another important product of our current research efforts is generating materials for interpretive staff at the park to educate themselves and park visitors about the diverse assemblages of sharks and other fish that are found within the Mississippian rocks of MACA. Resources for interpretive staff could include but are not limited to:

- Interpretive cards with photos of in situ shark fossils on tour trails, along with images of the animals these fossils represent.

- Casts or 3D-printed copies of fossils produced for interpretive staff to show the public during tours or programs.
- A dedicated video production on the Mississippian marine world of MACA, to be played in the visitor center theater.

More static and self-guided educational outreach for visitors could include:

- Physical exhibits of fossils, casts, and models of the various shark species. These can include:
    - A life-size (7.6–8.5 m [25–28 ft]-long) model of *Saivodus striatus*.
    - A "paleo-aquarium", a snapshot reconstruction of the Mississippian sea floor with life-size models of invertebrates and vertebrates interacting within a large glass enclosure.
    - A display case or cases with fossils found during this research project.
    - Modular displays highlighting a few unique species, distributed throughout the park (e.g., outdoor trails, visitor center, etc.).

MACA should also take advantage of annual events such as "Shark Week" (summer, July/August) and National Fossil Day (fall, October) to showcase and celebrate their fossil resources as well.

Conclusions

As demonstrated above, MACA preserves one of the most extensive and diverse Mississippian marine vertebrate records in North America. The localities identified and the fossil information collected from them offer not only important scientific data for both regional and global paleoichthyology, but also provide exciting offerings to educate visitors to the park about the diverse and often weird creatures that called central Kentucky home 340 to 325 million years ago. MACA has an ancient life story that goes beyond the cave itself, but can only be told because of the formation of the cave and from exploration by dedicated adventurers and scientists who push ever deeper to find sharks in the dark.

Acknowledgments

We are greatly indebted to MACA Superintendent Barclay Trimble and head of the MACA Science and Resource Management unit, Timothy Pinion, for their support of our project. The success of our project is largely due to a dedicated group of staff and volunteers who have helped us locate new localities and spot new fossils within the passages of Mammoth Cave. Guide Rich Boldon was instrumental in finding a number of new fossil localities presented here. We also thank our fossil "spotters" Kailey Alessi, Bryce Belanger, Kristen Bobo, Max Bovis, Matt Cecil, Magnus Cleveland, Spike Crews, Joe Douglas, Amber Flowers, Chris Groves, Taylor Harlow, Mandolin Harris, Ed Jakaitis, Pat Kambesis, Nathaniel Leies, Mike May, Carolyn Mikowski, Rachel Saker, Marissa Schorr, Stacey South, Barclay Trimble, and Elizabeth Winkler. Thanks also to the Cave Research Foundation for their support of John Wood's photogrammetry work, shark fossil recovery efforts, and cartography and resource inventory of caves at MACA. Matt Friedman (University of Michigan)

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Appendix F: Overall Taxonomic Lists

Tables 14–16 provide overall taxonomic lists of the species observed in this study.

Table 14. Fossil acanthodian taxa from MACA.

Higher Classification	Genus and Species	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Acanthodiformes: Acanthodidae	cf. *Acanthodes* sp.	–	Y	–	–

Table 15. Fossil chondrichthyan taxa from MACA.

Higher Classification	Genus and Species	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Cladodontomorphi: Symmoriiformes: Stethacanthidae	*Stethacanthus* sp. 1 (5-cusped teeth)	–	Y	–	–
	Stethacanthus sp. 2 (3-cusped teeth)	–	Y	–	–
Cladodontomorphi: Symmoriiformes	"*Denaea*" sp. 1	–	Y	–	–
	"*Denaea*" sp. 2	–	Y	–	–
	Genus and species indet.	–	Y	–	–
Elasmobranchii: Phoebodontiformes: Thrinacodontidae	*Thrinacodus* cf. *T. dziki*	–	Y	–	–
Elasmobranchii: Phoebodontiformes	Genus and species indet.	–	Y	–	–
Elasmobranchii: Xenacanthimorpha: Bransonelliformes	*Bransonella lingulata*	–	Y	–	–
	Bransonella nebrascensis	–	Y	–	–
Elasmobranchii: Ctenacanthiformes: Ctenacanthidae	*Cladodus elegans*	Y	–	–	–
	Cladodus mirabilis	–	Y	–	–
	?*Cladodus* sp. (large form)	–	Y	–	–

Table 15 (continued). Fossil chondrichthyan taxa from MACA.

Higher Classification	Genus and Species	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Elasmobranchii: Ctenacanthiformes: Ctenacanthidae (continued)	cf. *Ctenacanthus venustus*	Y	–	–	–
	Troglocladodus trimblei	Y	Y	–	–
	Genus and species indet. 1	Y	Y	–	–
Elasmobranchii: Ctenacanthiformes: “Tamiobatidae”	*Saivodus striatus*	Y	Y	Y	Y
Elasmobranchii: Ctenacanthiformes: Heslerodidae	cf. *Bythiacanthus siderius*	Y	–	–	–
	Glencartius costellatus	Y	Y	–	–
	Glikmanius careforum	Y	Y	–	Y
	Genus and species indet.	–	Y	–	–
Elasmobranchii: Euselachii: Protacrodontiformes	Genus and species indet.	–	Y	–	–
Elasmobranchii: Euselachii: Hybodontiformes	Genus and species indet.	–	Y	–	–
Elasmobranchii: Euselachii: Neoselachii: Anachronistidae	cf. *Cooleyella* sp.	–	Y	–	–
Elasmobranchii: Euselachii: Neoselachii	*Amelacanthus* sp.	Y	Y	–	–
	?*Eunemacanthus* sp.	–	Y	–	–
Euchondrocephali	*Euglossodus* sp.	–	Y	–	–
	Venustodus sp. 1	–	Y	–	–
	Venustodus sp. 2	–	Y	–	–
	Genus and species indet. 1	–	Y	–	–
	Genus and species indet. 2	–	Y	–	–
	Indeterminate euchondrocephalan	–	–	–	Y

Table 15 (continued). Fossil chondrichthyan taxa from MACA.

Higher Classification	Genus and Species	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Euchondrocephali: Paraselachii: Gregoriidae	Genus and species indet.	–	Y	–	–
uchondrocephali: Paraselachii: Debeeriidae	*Heteropetalus* sp.	–	Y	–	–
	Genus and species indet.	–	Y	Y	–
Euchondrocephali: Paraselachii	Paraselachid indet. 1	Y	–	–	–
	Paraselachid indet. 2	Y	–	–	–
Euchondrocephali: Orodontiformes: Orodontidae	*Orodus* sp. 1 (*O. ramosus* type)	–	Y	–	–
	Orodus sp. 2 (*O. elongatus* type)	–	Y	–	–
Euchondrocephali: Orodontiformes: Leiodontidae	*Leiodus calcaratus*	Y	–	–	–
	Leiodus sp.	–	Y	–	–
Euchondrocephali: Orodontiformes	Genus and species indet.	Y	Y	–	–
Euchondrocephali: Eugenodontiformes	Genus and species indet.	–	Y	–	–
Euchondrocephali: Eugenodontiformes: Eugenodontidae	Genus and species indet.	–	–	Y	–
Euchondrocephali: Petalodontimorpha	*Chomatodus* sp. 1	Y	Y	–	–
	Chomatodus sp. 2	–	Y	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Janassidae	*Janassa* sp.	–	Y	–	–
	Strigilodus tollesonae	–	Y	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalodontidae	*Antilodus* sp.	–	Y	–	–
	Harpacodus sp.	–	Y	–	–
	?*Lisgodus* sp.	–	Y	–	–
	Petalodus hastingsii	–	Y	–	–

Table 15 (continued). Fossil chondrichthyan taxa from MACA.

Higher Classification	Genus and Species	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalodontidae (continued)	*Petalodus linguifer*	–	Y	–	–
	Petalodus sp. nov.	–	Y	–	–
	Petalodus sp.	–	–	–	Y
	?*Petalodus* sp.	–	Y	–	–
	Polyrhizodus concavus	Y	–	–	–
	Tanaodus pumilis	Y	–	–	–
	Genus and species indet.	–	–	Y	Y
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Petalorhynchidae	*Petalorhynchus pseudosagittatus*	Y	–	–	–
	Petalorhynchus cf. *P. beargulchensis*	–	Y	–	–
	Petalorhynchus cf. *P. spatulatus*	–	Y	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: “Obruchevodidae”	*Netsepoye* sp.	–	Y	–	–
	Genus et. species nov.	–	Y	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes: Belantseidae	cf. *Belantsea* sp.	–	Y	–	–
Euchondrocephali: Petalodontimorpha: Petalodontiformes	Genus and species indet. 1	–	Y	–	–
	Genus and species indet. 2	–	Y	–	–
Euchondrocephali: Holocephali	Indeterminate holocephalan	–	–	Y	–
Euchondrocephali: Holocephali: Chondrenchelyiformes: Chondrenchelyidae	Genus and species indet.	–	Y	–	–
Euchondrocephali: Holocephali: Helodontiformes: Helodontidae	*Helodus* sp.	Y	Y	Y	–

Table 15 (continued). Fossil chondrichthyan taxa from MACA.

Higher Classification	Genus and Species	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Euchondrocephali: Holocephali: Cochliodontiformes: Psephodontidae	*Psephodus* sp.	Y	Y	Y	Y
Euchondrocephali: Holocephali: Cochliodontiformes: Cochliodontidae	*Cochliodus* sp.	Y	Y	–	–
	?*Cochliodus* sp.	–	–	Y	–
	Deltodus cf. *D. sublaevis*	–	Y	–	–
	Deltodus sp.	Y	Y	–	–
	?*Deltodus* sp.	–	–	Y	–
	Poecilodus sp.	–	Y	–	–
	?*Poecilodus* sp.	Y	–	–	–
	Sandalodus sp.	Y	Y	–	–
Euchondrocephali: Holocephali: Psammodontiformes: Psammodontidae	*Psammodus* sp.	Y	Y	–	–
Euchondrocephali: Holocephali: Copodontiformes: Copodontidae	*Copodus cornutus*	Y	–	–	–
Euchondrocephali: Holocephali: Menaspiformes: Deltoptychiidae	*Deltoptychius* sp.	Y	Y	–	–
Euchondrocephali: Holocephali: Menaspiformes: Traquairiidae	cf. *Traquairius* sp.	Y	–	–	–

Table 16. Fossil osteichthyan taxa from MACA.

Higher Classification	Genus and Species	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Actinopterygii: Palaeonisciformes	Genus and species indet. 1	–	Y	–	–
	Genus and species indet. 2	–	Y	–	–
	Genus and species indet. 3	–	Y	–	–
	Genus and species indet. 4	–	Y	–	–
	Genus and species indet. 5	–	Y	–	–
Actinopterygii: ?Eurynotiformes	Genus and species indet. 1	–	Y	–	–
	Genus and species indet. 2	–	Y	–	–
Actinopterygii?	Indeterminate actinopterygian?	–	–	Y	–

Chapter 8. Pleistocene and Holocene Paleontology of Mammoth Cave National Park

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Introduction

In 1994, Rick Olson contacted Rick Toomey, then at the Illinois State Museum (ISM), to help assess a bat bone bed in Bat Cave at MACA. This led to a ten-year relationship between the park and the ISM to inventory and document Quaternary vertebrate remains in the park. The project was directed first by Toomey and later by Mona Colburn, after Toomey left the ISM for Arizona. This project culminated in a report (Colburn 2005), Colburn's master's thesis (2006), and several smaller abstracts and reports. This chapter summarizes the major findings of that inventory as well as adds details and references concerning more recent additions to our knowledge of the Quaternary vertebrate paleontology of MACA. This chapter does not list every fossil or site that was found during the ISM work. Indeed, in that study 1,553 locations with noteworthy faunal remains were identified in the upper-level passages of the Historic section between the Historic Entrance and the Violet City Entrance of Mammoth Cave alone. For more detailed information on the individual remains and sites, Colburn (2005) should be referenced. Colburn (2005) as well as other studies examined paleontological remains in both the Mammoth Cave System and in other caves in the park. By local convention any cave that is not connected to the Mammoth Cave System may be referred to as a "lesser cave" or a "small cave." Both conventions are used interchangeably in this chapter. For ease of understanding which localities are from the Mammoth Cave System and which are not, we have included (MCS) in locality headings for sites in the Mammoth Cave System and (LC) for Lesser Caves. Paleontological resources in this chapter are listed by deposit types including primary cave stream deposits, Pleistocene/Holocene entrance facies, Pleistocene/Holocene bat roosts, and scattered surface finds in cave passages. (A geologic time scale is included as an appendix to this inventory, Appendix I.) For this reason, in some cases different remains from the same cave or cave area will be listed in separate accounts. All remains were found within MACA unless specifically noted.

The earliest potential report of Quaternary remains in what would become MACA was of a giant ground sloth or *Megalonyx* in White Cave, first mentioned in print in 1831 (Harlan 1831). However, after contradictory reports occurred on this material, it was established that the fossils actually came from Tennessee. Robert Montgomery Bird (1838) mentioned the tooth of a large rodent, such as a beaver, in Solitary Cave, a passage within Mammoth. The first person to do systematic work on Quaternary remains in park caves was park naturalist Claude Hibbard. He documented vertebrate bones in Cave #028 in June of 1935. He also found a bison tooth somewhere in the park in 1934 and accessioned it at his alma mater, the University of Kansas. See Figure 23 in Chapter 2 for a photo of

this significant find. Chapter 2 contains details on these and other Quaternary remains that were found prior to the establishment of the national park.

Primary Cave Stream Deposits

Primary cave stream deposits are materials that are deposited by cave streams as they form a cave or shortly after that time. They occur near the bottom level of the cave as it was configured at the time of deposition. They represent material that was either washed into the cave by flooding or back-flooded into the cave by the paleo-Green River, and date to relatively near the time the host cave passages were formed. The deposits range in age from at least 4 to 6 million years (mya) (Granger et al. 2001, as modified by Palmer 2019) to modern along active base level streams. Although deposits of this kind are found throughout the cave, we have only identified Quaternary fossil material in two places: Backsliders Alley and Sandy Avenue. Both of these deposits are in the upper levels of the cave.

Backsliders Alley (MCS)

Backsliders Alley, a side passage near the tour trail in Main Cave at Booth's Amphitheater, contains an exposure of sediments that were deposited by backflooding during the formation of the cave. The sediments are thinly bedded, fine-grained silts that were probably deposited by larger floods when the main flow through the cave was occurring in Blacksnake Avenue (Palmer Level C). Granger et al. (2001, as modified by Palmer 2019) dated the flow in Blacksnake Avenue to between 1.5 and 1.6 mya.

Within these sediments, Toomey, Colburn, and Olson located some white, chalky, fragmentary salamander bones. Because of its fragmentary nature, the material cannot be identified beyond cf. *Cryptobranchus*. However, it is consistent with *Cryptobranchus alleganiensis*. *C. alleganiensis* is known historically from the Green River in the park. Although the recovered material is limited, it does include two fragmentary atlas vertebrae. Therefore, at least two individuals are represented by the material. This material likely represents two hellbenders that probably were washed into the cave during a large paleoflood event (Colburn 2005).

This material is interesting in that it represents the only identifiable fossils that are contemporaneous with the primary dissolution of the main upper cave levels. All other materials date to later times when the cave was air-filled and would have come in via cave entrances.

Sandy Avenue (MCS)

A bank of silty, red sediment in Sandy Avenue contains the only other material that is firmly associated with the primary stream sediments that were deposited as the cave formed. Sandy Avenue in the Frozen Niagara section is a portion of Kentucky Avenue representing a sublevel in Palmer Level B. Its primary stream sediments were deposited between 3 and 6 mya (Granger et al. 2001, as modified by Palmer 2019). However, it would have been subject to additional deposition during large floods of Palmer Level C (as seen in the Backslider Alley deposits). It is not clear from the stratigraphy of the Sandy Avenue deposits whether the sediments of this locality represent primary stream sediments or later backflooding. The sediment bank is exposed due to sediment mining for

trail building. Two small fragments of very white bone were collected from this sediment but cannot be identified taxonomically (Colburn 2005). It is notable that these bones may be pre-Quaternary and potentially represent the oldest paleontological material identified from a post-cave-formation context.

Pleistocene/Holocene Entrance Facies

Frozen Niagara (MCS)

The paleontological site at the Frozen Niagara Entrance (Mammoth Cave System) is potentially one of the most significant Quaternary paleontological sites in the park. The deposits have only been studied preliminarily. The previous work is discussed in Colburn et al. (2000) and Colburn (2005, 2006).

The exposed fossil-bearing deposits consist of approximately 1.5 m (4.9 ft) of travertine shelves interbedded with pockets of sediment (Figure 175). The travertines include flowstones, carbonate crusts, and cave popcorn. The sediment pockets contain red sediment matrix with pebbles and small bones. The interbedded travertines and sediment represent deposits from an ancient cave entrance that was in the immediate area. The entrance changed size over time. Travertine layers likely represent times when the entrance was more restricted, and sediment may have washed in when it was more open. The bone in the deposit probably represents a mix of animals that lived in the cave and others that were washed in or brought in by predators.

The deposit was exposed in 1924 when George Morrison opened the Frozen Niagara Entrance and cut through the travertine and sediment wedge to allow people to walk into the cave. The bones in the deposit went unnoticed until 1999 when Toomey happened to notice them in the sediment while helping with a Cave Research Foundation (CRF) mapping trip in the area. The ISM team collected sediment and Colburn processed and identified the material (Colburn et al. 2000; Colburn 2005, 2006)

The taxa in the deposit are diverse, but in terms of specimens the deposit is dominated by rodent and bat bones. The deposit contains the following taxa († = extinct):

- Anura (frogs)
- Caudata (salamanders)
- Chelonia (turtles)
- Serpentes (snakes)
- Squamata (lizards)
- Aves (birds)
- *Dasypus bellus*† (beautiful armadillo)
- Chiroptera (bats)
- *Procyon lotor* (common raccoon)

- *Geomys* sp. (pocket gopher)
- *Neofiber leonardi*† (extinct muskrat)
- *Platygonus* sp.† (extinct peccary)
- *Odocoileus virginianus* (white-tailed deer)
- *Equus* sp.† (extinct horse)

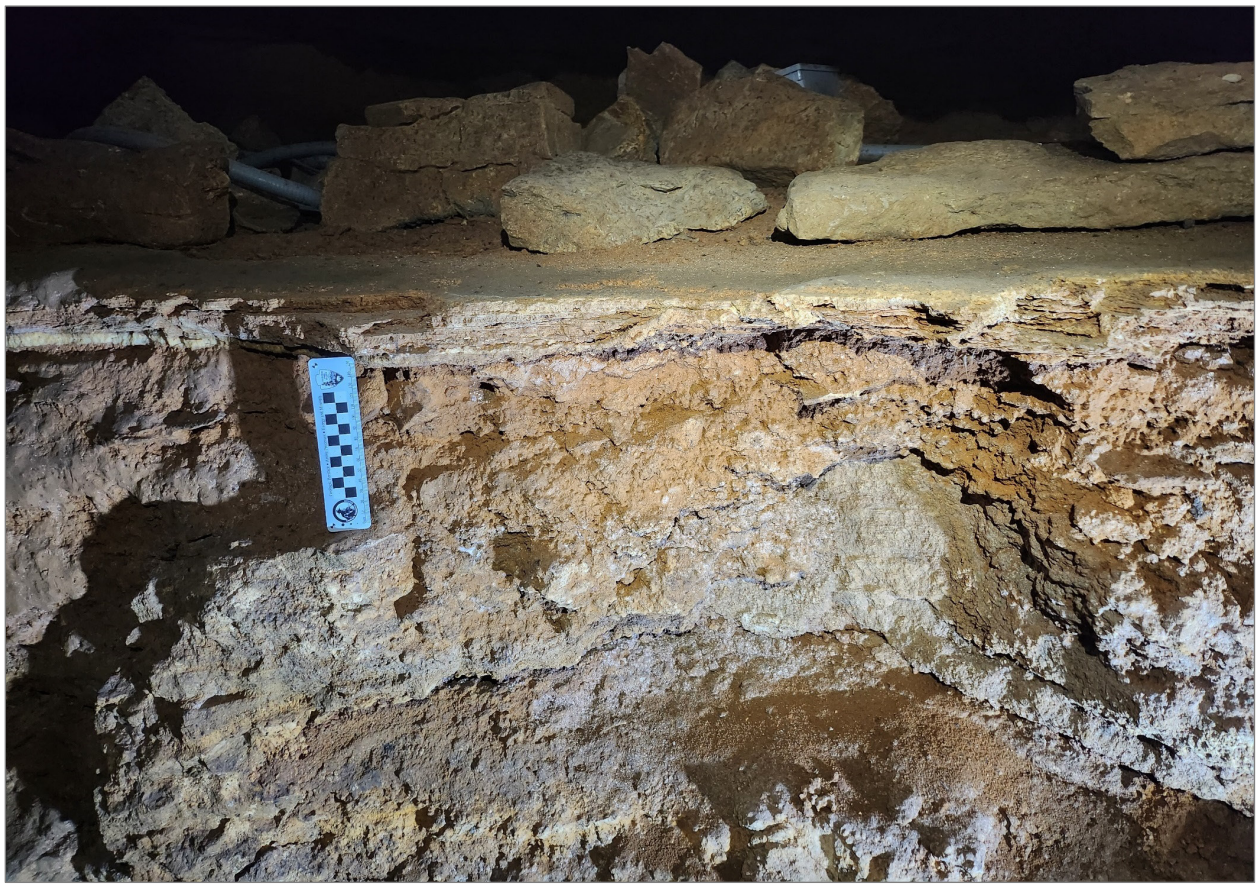


Figure 175. Interglacial interbedded travertine and bone-bearing sediments near the Frozen Niagara Entrance. NPS

Samples of the travertine were taken to attempt to determine the age of the deposit. Jeff Dorale was able to date samples of the thick travertine overlying the deposit at the University of Minnesota. That travertine dated 126,000–125,000 years before present. Because of that date, Colburn et al. (2000) interpreted the site as representing a fauna from the Sangamon interglacial. However, as Colburn (2005, 2006) noted, the capping date merely establishes a youngest possible date. It is quite possible that the fossil assemblage could represent a significantly older time, potentially even Irvingtonian (approximately 1.9–0.25 mya). The presence of *Dasypus*† and an extinct species of *Neofiber* suggests that the fauna represents an interstadial or interglacial interval.

The presence of extralimital pocket gophers (*Geomys* sp.) suggests the presence of significant open areas (such as prairie) in the neighborhood of the former entrance. This is significantly different than the existing forest in the area.

Because this area is along a tour trail, it is of significant management concern to the park. During recent tour trail reconstruction, the park required the contractor to place protection against the walls in this area, so that the deposit would not be impacted by construction activity in the area.

Proctor Cave, Frost Avenue Terminal Breakdown and Stream Deposits in that Area (MCS)

Deposits associated with a sinkhole that terminates Frost Avenue in the Proctor section of the Mammoth Cave System contain a significant assemblage of Pleistocene fossils. This area was studied by both Ron Wilson and the ISM team (Wilson 1981, 1985; Colburn 2005, 2006). During a survey of Proctor Cave in the late 1970s, cavers found several bones. They reported these to Ron Wilson, who went into the cave to evaluate and collect them. Toomey, Colburn, Blaine Schubert, and Olson revisited these sites on several occasions between 1996 and 2001. The ISM confirmed and expanded on the Wilson finds. The material collected in the 1980s by Ron Wilson is curated at the Carnegie Museum of Natural History (CMNH) (Wilson 1980). The ISM-collected material is curated at the ISM. In addition to the collections, both Toomey and Colburn visited the CMNH and evaluated the material from the earlier collections.

Bones in this area occur in two different contexts. At the end of Frost Avenue (at survey station X-118), there is a talus cone related to a sinkhole or valley wall collapse. This cone contains mud, sandstone cobbles and blocks, and a scattering of bone. The bone in this area is wet, mushy, leached of organics and often coated with a black coating (probably manganese) (Figure 176). This talus represents a now mostly closed entrance to the cave that allowed bone to wash in and potentially animals to enter and exit the cave. The second context for bone finds is a pair of crawlways, one with a small stream. These are beside and below the terminal breakdown at X-118. Bone was found as surface finds washed into the stream amongst the cobbles and also included bones and bone fragments cemented to the channel floor/walls. We interpret these bones as likely coming from the terminal breakdown at X118 or related nearby sinks. For this reason, we are currently treating the assemblage as related.

Taxa recovered from the primary sinkhole fill at X-118 include the following:

- Caudata (salamanders)
- Serpentes (snakes)
- Indet. large Mammalia
- *Blarina* sp. (short-tailed shrew)
- Indet. Chiroptera (bats)
- *Perimyotis subflavus* (tricolored bat)
- Mouse-sized rodent

- *Procyon lotor* (common raccoon)
- Indet. Proboscidea† (extinct member of group including elephants, mammoths, mastodons, etc.)
- *Mammut americanum*† (American mastodon)



Figure 176. Scattered bone and tusk fragments from talus at end of Frost Avenue. NPS / RICK TOOMEY

This list includes both CRF-collected material in the CMNH (Wilson 1980, 1981) and materials collected or observed by the ISM team (Colburn 2005, 2006).

Near the end of the X survey (but not quite to the sinkhole termination) several connected crawlways take off: the Y and Z surveys. These crawlways are about 10 m (33 ft) lower than the X survey and contain streams. Bones were first noted by the CRF team surveying the Y-survey on 24 April 1976. The team even sketched the *Arctodus*† jaw in enough detail for Ron Wilson to identify it as a tremarctine bear (Figure 177; see also Figure 23 in Chapter 2). Several years later, Wilson and CRF teams collected both Pleistocene and Holocene bone from these streams (Wilson 1980, 1981, 1985). The ISM crew also recovered both Pleistocene and Holocene bones from the stream in the Y-survey crawl (Colburn 2005, 2006). Neither Wilson nor the ISM team could find the source where either the Pleistocene or the Holocene bones were weathering out. However, Toomey thinks that a portion of

the sinkhole fill or valley termination observed at X-118 is the likely source of the Pleistocene remains. The Holocene remains probably are coming in via either an unmapped modern dome off these crawlways or a section of the closed sinkhole fill that has reopened. Because the bones are being recovered from an active stream channel, they tend to be larger bones from larger animals. Taxa that have been recovered in the Y and Z crawlways include the following:

- Indet. large Mammalia
- *Didelphis virginiana* (Virginia opossum)
- Indet. Chiroptera (bats)
- *Perimyotis subflavus* (tricolored bat)
- cf. *Sylvilagus floridanus* (eastern cottontail)
- Mouse-sized rodent
- *Neotoma* sp. (woodrat)
- *Procyon lotor* (common raccoon)
- *Lynx rufus* (bobcat)
- *Smilodon* sp.† (saber-toothed cat)
- *Arctodus simus*† (short-faced bear)
- Indet. Proboscidea† (extinct member of group including elephants, mammoths, mastodons, etc.)
- *Mammut americanum*† (American mastodon)
- *Equus* sp.†? (horse)
- *Platygonus compressus*† (flat-headed peccary)
- cf. *Platygonus* sp.† (extinct peccary)
- *Sus scrofa* (domestic pig)
- *Bos taurus* (domestic cow)



Figure 177. *Arctodus*† jaw from crawlway off Frost Avenue. NPS / RICK TOOMEY

Because this area of the cave is reached via a long (3–4 hour) trip including traversing a 300-m (980-ft)-long crawlway and a complex set of narrow canyons, there has been limited research on the deposits in this area. Although further study is warranted, it will take enthusiastic caving paleontologists to do so.

Pleistocene/Holocene Bat Roosts

Paleo bat roosts are some of the earliest recognized and most studied vertebrate fossil deposits at MACA. They represent places where colonial bats roosted in caves in the past. Evidence of them include bat bones, guano deposits (or their degraded remains), and ceiling and wall staining produced by roosting bats. In some roosts, there are also signs of predation associated with the bat roosts (raccoon feces or scratches). Only roosts of colonial bats (such as *Tadarida*, some *Myotis* species, and *Corynorhinus rafinesquii*) generally provide enough local impact to be visible in the fossil record; solitary roosting bats leave only isolated mummies or bones. The roosts can represent either hibernacula (winter use) or maternity or bachelor roosts (summer use). These can sometimes be distinguished by guano types (presence of insect remains or not) or bat species (cave hibernators or not). Roosts are usually associated with fairly large cave passages, since most local colonial bats utilize passages at least 1.5 m (4.9 ft) tall for roosting. In the case of the Bat Cave deposits, the deposits are in a crawlway, but they represent roosts in larger cave passages.

Paleo bat roosts in MACA caves vary in age from unknown Pleistocene age to roosts that were abandoned in historic times (since the 1800s). Some of the younger ones are well-dated. However, since only a few of the roosts are historic or have finite radiocarbon dates, most roosts have only general age constraints.

The earliest documentation of a Mammoth Cave paleo bat roost was a fossil *Myotis* roost in New Discovery (Dearolf 1941, 1942). In 1959, Davies and Chao reported on desiccated guano deposits in Chief City (Historic section). They even dated guano from that deposit (>38,000 radiocarbon years before present [RCYBP; 1950 is used as "present" for "before present"], W-712, Rubin and Alexander 1960) that is also the first radiocarbon date completed from MACA. This deposit is discussed below in the discussion of fossil *Tadarida* roosts in the Historic section. In the early 1960s, Thomas Jegla and John S. Hall furthered documentation of not only the New Discovery and Chief City deposits, but also completed an initial study of the Bat Cave deposits (Jegla 1961, 1963; Jegla and Hall 1962).

Historic Section of Mammoth Cave (MCS)

The Historic section of Mammoth Cave has been used by bats (at least intermittently if not continuously) since an indeterminant time in the Pleistocene. Use has continued late into historic times and continues at a lesser level today. This use has been detailed in numerous papers: Davies and Chao (1959), Jegla (1961), Jegla and Hall (1962), Colburn (2005, 2006), Widga and Colburn (2015), and Thomas and Toomey (2017). This summary will not detail all bat remains that have been found in the Historic section. See individual papers for more specifics on the materials documented. For the purposes of this discussion, the Historic section of Mammoth Cave consists of the upper-level passages between the Historic and Violet City Entrances (including Gothic Avenue, Backsliders Alley, Blue Spring Branch, Blackall Avenue, Wrights Rotunda, and Black Chambers). It also includes Audubon Avenue (including Little Bat Avenue, Rafinesque Hall [including Lookout Mountain], and Vespertilio Hall), and two breakdown-choked stopes that provided access to lower levels (The Corkscrew and the Vanderbilt Hall Breakdown). This broad locality represents approximately 6,650 m (21,800 ft) of cave passage. Some individual sites mentioned below represent a single locality or only portions of this area; others represent large portions of the area.

Pleistocene Vampire Bat

The oldest bat specimens from the cave are probably a partial femur from the extinct vampire bat *Desmodus stocki*† (Figure 178) and a fragment of a radius of *Tadarida* sp. that were recovered in the area where Backsliders Alley comes off Booths Amphitheater in the Historic section of Mammoth Cave (Colburn 2005, 2006). Although these bones were not found in place, based on the color of the bones and sediment and bone preservation, both are thought to have weathered out of the finely laminated, silty cave sediments that were deposited by flooding when Palmer Level C was the actively eroding level in cave formation. The sediments that these two bones likely came from are slightly higher in the local sediment column than the *Cryptobranchus* remains described earlier in this chapter. Dating of active deposition in Palmer Level C would suggest an age of about 1.5 mya (Granger et al. 2001 as modified by Palmer 2019). The *Desmodus stocki*† femur represents one of the northernmost records of this vampire bat species (Ray et al. 1988).



Figure 178. *Desmodus stocki*† partial femur from Backsliders Alley (bottom) with modern *Desmodus rotundus* femur (top) for comparison. PHOTO BY GARY ANDRASHKO FOR NPS

Interglacial *Tadarida*

While studying the surface and cave sediments at MACA during the 1950s, Davies and Chao (1959: 16) identified a deposit of "dark brown dust derived from the desiccation of bat guano" in Chief City along the tour trail in Mammoth Cave. They analyzed the chemistry of the sediments and had the material radiocarbon dated (>38,000 RCYBP, W-712, Rubin and Alexander 1960).

Jegla and Hall (1962) studied bat remains associated with the guano Davies and Chao identified in Chief City and two nearby areas (Settles Gorge and Ste. Catherines City). They identified skeletal remains of *Tadarida* associated with the guano deposits. Based on comparing measurements with modern subspecies, they identified the Mammoth Cave remains as *Tadarida brasiliensis cynocephala*. They also identified *Peromyscus* and *Myotis* in the deposits, but *Tadarida* dominated. They also further characterized some of the desiccated guano deposits. They concluded that the deposits were not glacial, and were probably from the Sangamon interglacial stage, although they did not indicate how they ruled out earlier interglacials.

The ISM team examined the upper Historic section of Mammoth Cave and identified guano deposits attributed to *Tadarida* over an area of about 1,800 m (5,900 ft) of passage, including the area from Wrights Rotunda to Anzer Hall and parts of the side passages of Blue Springs Branch and Blackall Avenue. In many areas *Tadarida* skeletal remains associated with the guano were identified, but some areas of guano were attributed to *Tadarida* based on the similarity of the guano deposits to ones with skeletal remains. The guano deposits are not distributed evenly or throughout the entire passages. Instead, they are preserved and visible locally and are especially concentrated in large rooms and under heightened ceiling features called breakout domes (for example Chief City [Figure

179], Wrights Rotunda, Waldach Dome, and Hains Dome). Specific areas and remains are detailed in Colburn (2005, 2006). Two radiocarbon dates were completed on verified and presumed *Tadarida* guano during the ISM work. A date of 42,440 ± 720 RCYBP (CAMS-63092) was returned from a deposit in Wrights Rotunda. A sample of pellets from a deposit in Settles Gorge was dated at >54,000 RCYBP (CAMS-63093). During this work, similar degraded guano deposits were located in Gothic Avenue. However, because no *Tadarida* remains were found associated with these deposits and because they were significantly farther from the known deposits, these deposits were not attributed to *Tadarida* in the ISM work (Colburn 2005, 2006). The paleontological inventory work served to greatly expand our understanding of the extent of the *Tadarida* roost. The work also highlighted the fact that the existing tour trail (and any potential new trail work) impacts these significant paleontological materials.



Figure 179. *Tadarida* guano exposed under large breakdown block in Chief City. NPS / RICK TOOMEY

The next work on the *Tadarida* roosts in the Historic section was undertaken during a combined archeological and paleontological survey of tour trails to support an Environmental Assessment of potential projects to upgrade tour trail infrastructure. From December 2007 through July 2008, crews from the University of Kentucky Program for Archaeological Research excavated sites along the Historic, Lantern, Gothic, Grand Avenue, and Great Onyx Tour routes to evaluate archeological and paleontological potential for trail renovation planning purposes. The archeological faunal remains and paleontological remains were analyzed by the ISM team and are reported in Widga and Colburn

(in Ahler 2012) and Widga and Colburn (2015). Their recovery of *Tadarida* in excavation units in Gothic Avenue and Giant's Coffin expand the area in which it has been found. However, Widga and Colburn (2015) question whether the find at Giant's Coffin is in primary context. The find in Gothic is from an excavation unit but is not associated with guano deposits in that passage. The excavations also recovered occasional remains of juvenile *Tadarida*, which confirmed the previous supposition that this roost represented a maternity roost for *Tadarida*.

Widga and Colburn (2015) report six additional radiocarbon dates on bulk guano and bone associated with *Tadarida*, from excavations in Chief City and Haines Dome (Table 17).

Table 17. Radiocarbon dates on bat guano and bone associated with *Tadarida* (Widga and Colburn 2015). See discussion below on which dates are considered valid.

Location	Date (RCYBP)	Lab Number	Comments
Haines Dome	18,560 ± 210	UCIAMS76219	Rejected by authors
Chief City	32,420 ± 1090	UCIAMS76222	Rejected by authors
Chief City	33,090 ± 360	UCIAMS76223	Rejected by authors
Chief City	30,580 ± 300	UCIAMS76220	Rejected by authors
Chief City	13,735 ± 45	UCIAMS76212	Rejected by authors
Chief City	>48,000	Aeon 826	Accepted by authors

They also submitted a number of samples with different treatments that failed to date (Widga and Colburn 2015). In addition to the radiocarbon analyses, Widga and Colburn analyzed percent organics (via Loss on Ignition), $\delta^{15}N$, $\delta^{13}C$, percent nitrogen, percent carbon, and carbon/nitrogen ratio (C/N) on *Tadarida* guano samples, including the dated samples (see Table 17). These parameters, notably C/N, provide information on alteration of the guano. The only dated sample that has a C/N classified as representing fresh guano was Aeon 826 (>48,000 RCYBP). Because of these apparent issues with chitin diagenesis and potential for Holocene archeological charcoal contamination in the other samples, Widga and Colburn reject the finite dates and suggest that the *Tadarida* guano was deposited in a previous interglacial, possibly the Sangamon interglacial (~110–120 kya), the warm period from 170–220 kya, or potentially earlier.

In addition to *Tadarida*, Widga and Colburn identified a number of other taxa associated with the *Tadarida* roosts. Additional bats included *Eptesicus fuscus*, *Lasiurus borealis*, *Lasiurus cinereus*, *Lasiurus* sp., *Corynorhinus* sp., *Perimyotis subflavus*, *Myotis grisescens*, *Myotis leibii*, *Myotis* spp., and indet. Chiroptera. Non-bat remains from these contexts included unidentified Mammalia, unidentified Rodentia, *Neotoma* sp., *Peromyscus* sp., and *Mustela* sp. All of these taxa are still found in the park, and none provide additional information on the age of the deposits.

Widga and Colburn (2015) performed two additional analyses to determine the paleoenvironment associated with these deposits. They examined stable carbon and nitrogen ratios of the guano. This analysis suggested that the *Tadarida* were feeding on insects that were foraging in a deciduous forest.

Using wing morphometrics of the recovered bat species, they concluded that the interglacial deposits were dominated by fast-flying, open-space taxa (notably *Tadarida*). They noted that the results of the isotopic study and the ecomorphometric study are not in accord and suggested that either the ancient *Tadarida* occupy a somewhat different niche than modern ones or that the landscape had no modern analogue (with C3 deciduous plants but open spaces).

Interstadial—Gothic Avenue

During the archeological and paleontological testing for future trail work, Widga and Colburn (2015) also confirmed a younger roost in Gothic Avenue. They dated guano and got a date of 23,910 ± 490 RCYBP (UCIAMS76221; 27,200–29,000 calibrated years before present, BP). They examined this sample and found no disseminated charcoal, and concluded that this date was valid and represented bat use of Gothic Avenue during the Farmdalian Interstadial. Most of the bones associated with this roost came from Chiroptera, but could not be further identified, except one *Eptesicus* bone, one *Myotis grisescens* bone, and one bone that could be identified to *Myotis* sp. Therefore, it is not possible to assess what species of bat roosted in Gothic Avenue during this interval. A mass of degraded guano suggests that *Myotis grisescens* may have been the species, but other species (such as *Tadarida*) could have been present as well. Colburn (2017) also noted that bats utilized Gothic Avenue around 12,600 years ago during the Bølling–Allerød interstadial.

Holocene to Protohistoric Bat Roost

The upper Historic area of Mammoth Cave housed major bat roosts that were used either continuously (supposition) or episodically (strictly supported by dates) during the Holocene through to the modern era. Radiocarbon dates on surface bat bones, mummified bats, bat guano, and raccoon scat containing bat bones from the Historic section in Mammoth Cave range in age from modern to greater than 10,000 years old (Colburn 2005), not including *Tadarida* guano deposits. These roosts are represented by scattered guano, surface finds of mummified bats (Figure 180), articulated and non-articulated bat bone, raccoon scat, raccoon scratchings, staining from bat use on the ceilings and walls, and bone recovered in archeological and paleontological tests. Toomey et al. (2002), Colburn (2005, 2006), Widga and Colburn (2015), and Thomas and Toomey (2017) document these roosts. Most of these roosts are interpreted as winter use of the cave as hibernacula or transient spring, summer, or fall use. Most of the dispersed guano consists of isolated, unaltered, intact feces. Some of these feces have insect parts visible when examined under a hand lens; however, the vast majority lack any evidence of chitin when examined with a hand lens. We interpret the absence of visible chitin as evidence for guano representing fat metabolism rather than active feeding. Because this is the majority of guano at these sites, we interpret them as being primarily winter (hibernation) roosts. The most pervasive and widespread remains are guano pellets and scattered bat bones. Raccoon scratchings and scat are concentrated near the Historic Entrance in areas thought to be extensive hibernacula of at least *Myotis sodalis* and *Myotis lucifugus*. Ceiling and wall staining is also concentrated in these areas. However, staining can also be found in other isolated areas where clustering bats roosted. Mummified remains are scattered throughout the Historic area but are not generally very concentrated.



Figure 180. Mummified *Myotis* carcass from the Historic section. NPS / RICK TOOMEY

One of the areas with the most intensive bat use in the Historic section was Vespertilio Hall. Historically, there were so many bats hibernating in this location between Bunker Hill and Olive's Bower that it was given the name Vespertilio Hall around the turn of the 19th century (Hovey 1912: 26–27). There is a ceiling pocket with the heaviest bat staining of any place in Mammoth Cave, and the site was used by Indiana bats for hibernation at least until the early 1900s. Bat species noted in Colburn (2005: 77) as mummified remains include *Corynorhinus* sp., *Myotis grisescens*, *M. sodalis*, and *Perimyotis subflavus*. In the same report, bats identified from bones included *Eptesicus fuscus*, *Myotis austroriparius*, *M. grisescens*, *M. sodalis*, and *Perimyotis subflavus*. Additional species noted included *Procyon lotor*, *Peromyscus* sp., *Neotoma* sp., and *Sylvilagus*, among others.

Another area with particularly heavy prehistoric and early historic bat use in this area was Little Bat Avenue. Although it was heavily modified due to saltpeter mining and early tourism, bat and raccoon scat remains can be found in many small alcoves along this passage. In addition, very heavy and extensive ceiling stain can be found in it. Bats represent the majority of material recovered from Little Bat Avenue, although most cannot be identified to species. *Myotis* sp. and medium-sized *Myotis* sp. were most common. Materials that could be identified to species included *Myotis sodalis*, *Myotis lucifugus*, *Myotis* cf. *M. leibii*, *Myotis* cf. *M. grisescens*, and *Eptesicus fuscus*. Non-bat remains include *Procyon lotor* (scat), *Neotoma* sp. (scat and nests/larders), mouse-sized rodents, *Odocoileus virginianus*, and the domestic chicken *Gallus gallus*. The chicken bones almost certainly represent the remains of chicken dinners brought into the cave and consumed. Other trash from those meals is also found in the cave.

One near-historic colonial summer bat roost has also been identified. In Rafinesque Hall, there is a mass of compressed guano that is about 2 m long × 0.6 m wide × 0.4 m deep (7 ft × 2 ft × 1 ft) along the right wall. This guano is unusual in Historic Mammoth Cave in that it has abundant insect parts, indicating summer use of that area. Two radiocarbon dates were run on the deposit and dated to 200 ± 60 (CAMS-24124) and 280 ± 60 (CAMS-27966) RCYBP; however, they were in reverse stratigraphic order. This may indicate that the bed is disturbed, or it may simply be due to the deposit representing a short period of deposition near the time the cave was developed for saltpeter and tours. This roost is interpreted to be a *Myotis grisescens* roost that was probably a bachelor roost (Toomey et al. 2002; Colburn 2005).

On the left side at the intersection of Audubon Avenue and Rafinesque Hall the walls are comprised of large amounts of shattered rock. This shattered rock is interpreted as occurring due to freeze-thaw action and frost shatter. It is likely this frost shatter occurred at some time in the past when an entrance was open at the end of Lookout Mountain. With an entrance there, extreme cold air would easily penetrate to the corner and cause frost shatter. Paleontological remains in this corner support this interpretation. Bones in sediment at the base of the wall and in cracks in the wall are of *Eptesicus fuscus* and *Myotis leibii* bats. Both of those species utilize cold, windy areas during the winter. They occur in Houchin's Narrows in the winter today. For this area to support these species an entrance had to be close by. Unfortunately, we have not been able to date these remains, so we do not know when this entrance was open.

Gratz Avenue, Lee's Cistern, Unknown Age Deposit

A deposit of reworked bat bones can be found in the small room overlooking Lee's Cistern off Gratz Avenue. This deposit consists of a thin (about 2 cm) layer of mud that contains very abundant bat bones and some bat bones scattered on this mud. The bones appear to be transported to the area, probably by the stream draining Annetta's Dome. Most of the visible material consists of wing bones. The age, species composition, and original site of the bat roost that is the source of the bones has not been identified. This deposit needs further study.

Proctor Trunk (MCS)

In the main trunk passage of Proctor Cave (part of the Mammoth Cave System) there is a surface bone deposit that represents past bat use (Colburn 2005, 2006). In the area between survey stations X56 and 61, there is abundant bat bone on the surface of the cave floor's sediments. In addition, drip holes indicate that the bone extends into the sediments. There is also a dark band in the superficial sediment layer that is interpreted as degraded bat guano. On the ceiling over this area, there is faded brown staining that is interpreted as bat roost staining. Skull elements and mandibles indicate that the majority of the identifiable material is *Myotis grisescens*. In addition, a few medium-sized *Myotis* elements (possibly *M. sodalis*, *M. lucifugus*, or *M. austroriparius*) are present. One dentary of *Eptesicus fuscus* was also identified. This area is interpreted as a large gray bat roost. Since gray bats utilize caves in both the summer and winter, it is not certain whether this was a hibernaculum or a summer roost. However, degraded guano deposits are more likely from a summer roost. The age of the roost is unknown. It is far from any current entrance. The nearest area that is identified as a likely

past entrance is the terminal breakdown of Frost Avenue at X-118. The fossils associated with this former entrance area are Pleistocene and are described elsewhere in this chapter.

In addition to the bat material, a skull of a *Sorex fumeus* was recovered from a drip hole within the bat roost area. This taxon is still found in the park. Also, near this roost, several bones of a *Martes americana* were recovered from the sediment surface (Figure 181). This taxon is a boreomontane species that today occurs significantly north of the park. Its presence is consistent with a Pleistocene opening that would have allowed the bats and other animals into this part of the cave.



Figure 181. *Martes americana* skull on surface in Proctor Trunk. NPS / RICK OLSON

New Discovery, Fossil Avenue (MCS)

Fossil Avenue, in the New Discovery section of Mammoth Cave, has been identified as a Quaternary vertebrate site for most of the time it has been known. The area was discovered in 1938 by Carl Hanson, Leo Hunt, Pete Hanson, and Claude Hunt. It was noted for its beautiful gypsum formations and was targeted for development to show the public. In 1939 Frederick Vosburgh of the National Geographic Society visited the area (Vosburgh n.d.). He noted “millions of bats’ bones” that had

been “carried by a stream of water.” In addition, he identified raccoon scratches on the walls in Fossil Avenue. He also indicated that C. [Charles] Gilmore (Smithsonian Institution) had identified raccoon bones and the ulna of a large bear (Vosburgh n.d.: 24) from Fossil Avenue.

Shortly after the Civilian Conservation Corps opened the New Discovery Entrance in 1940, Kenneth Dearolf conducted a biological reconnaissance in the Fossil Avenue area of New Discovery (Dearolf 1941). During this reconnaissance he too found a variety of fossil bones. These bones were located in a large series of small (~2–3 cm [~1 in] high), dry rimstone dams located along the floor of Fossil Avenue (see Figures 16 and 18 in Chapter 2). He specifically noted the presence of skull, wing, and leg bones that he identified as *Myotis lucifugus* in the rimstones. He noted that these bats must have entered the area through an entrance that had not yet been found, a closed entrance, or through the Historic Entrance (although he did not discuss how they might have gotten to this area from the Historic Entrance). He also noted scratches on the wall that he attributed to *Procyon lotor*. He proposed that the bats were killed by a flooding event. He noted that the bones were likely deposited in the rimstone pools by water, so that they were transported (at least slightly) from the roosting area. Dearolf also identified other taxa associated with the bat roost assemblages. They included *Martes americana*, *Lynx rufus*, and *Neotoma* sp.

Jegla (1961, 1963) also examined the deposit in New Discovery. He measured skulls from the deposit and confirmed Dearolf’s *M. lucifugus* identification. He indicated that because of the elevation of Fossil Avenue, Green River flooding would not have been the reason the bats were killed. He proposed that the bats were killed in a flooding event in a nearby dome-pit. He did not identify any candidate localities, but there is a tall dome nearby in Fossil Avenue. However, this dome is configured such that it would be impossible to trap bats in it via flooding; the top of the dome is simply higher than any reasonable flood level. He cites the presence of whole skulls as evidence that the bats were probably transported to the site intact and disarticulated after being deposited. He specifically considered the deposits to represent a Holocene (Recent in his papers) bat roost.

The results of the ISM team’s study of the Fossil Avenue deposits confirmed some of the previous work and added information and interpretations (Colburn 2005). The ISM work confirmed that the bat remains are primarily *M. lucifugus*. However, they also recovered other species. Of the 141 whole or partial skulls identified by the ISM team, 85% were *Myotis lucifugus*. *Myotis sodalis* represented 7% of the identified skulls and *Perimyotis subflavu*s represented 4%. The remaining 4% could not be identified below *Myotis*. In addition, one humerus was found that was tentatively identified as *M. grisescens*. So, the analysis confirms that the deposit represents a bat roost dominated by *M. lucifugus*. The mix of species suggests that the roost was probably a hibernaculum. This interpretation is bolstered by the presence of the raccoon scratches, a relatively common feature of *Myotis* hibernacula.

The ISM team found a number of additional taxa as well as the bats. They are as follows:

- *Spilogale putorius* (eastern spotted skunk)

- *Mustela nivalis* (least weasel)
- *Procyon lotor* (common raccoon)
- *Peromyscus* sp. (deer mouse)
- *Neotoma* sp. (woodrat)
- Indeterminate mouse
- Medium-sized mammal

Neither *Mustela nivalis* from the ISM work or the *Martes americana* found by Dearolf are found in this area now. Both are associated with more northern climates, in the case of *Martes americana* mainly boreomontane habitats. These animals suggest the possibility that the deposits do not represent a Holocene assemblage. Instead, the bones from Fossil Avenue may represent a Pleistocene deposit, since both taxa are known from Pleistocene deposits in Kentucky or further south (Colburn 2005). The lack of preserved organic material (tissue or significant guano) also supports the possibility that the deposit is not very recent.

Although both Dearolf (1941) and Jegla (1961, 1963) interpreted the deposits as an assemblage of roosting bats killed in a flooding event, the potential that the bones represent an attritional assemblage that formed as bats and other animals died over a longer stretch of time and accumulated should also be considered.

None of the scientists who have studied the Fossil Avenue deposit have located a past closed entrance that would have served as the entry for the animals found in the deposit. Jegla (1961, 1963) noted that he did not think the material was transported very violently or far. Toomey agrees with this assessment based on both the preservation of the bones and because of the raccoon scratches going up the wall. Based on observations in modern *Myotis* hibernacula, he suspects that the raccoon scratches represent animals climbing the walls to prey upon bats while they are in torpor. Although bats may fly several miles into caves for their hibernation roosts, the presence of the bones of other animals may indicate that the closed entrance was not particularly distant from Fossil Avenue.

Unknown Cave, Dead Bat Avenue (MCS)

Dead Bat Avenue is an approximately 300-m (980 ft)-long, low, wide crawl off Turner Avenue in the Unknown Cave section of the Mammoth Cave System. It is accessed from the Austin Entrance. Roger Brucker noted mummified bats when the passage was originally surveyed in 1960, hence the passage name. Toomey and Colburn inventoried the passage with a CRF re-survey team in January 1998. The inventory only included material within reach of the narrow path through the passage. Colburn (2005) summarizes the results of the inventory. The passage contains several types of remains. There are 10 mummified bats; approximately five bats are represented by skeletal material. Mummified bats include eight *Perimyotis subflavus*, one *Myotis lucifugus*, and one *Myotis septentrionalis*. Skeletal bat remains include one *Perimyotis subflavus* and one *Myotis leibii*. Three *Neotoma magister* (two skeletal and one partially mummified, partially skeletonized), two subadult, were also identified in the passage. The entrance that these animals used to get into this area has not

been identified and the age of the material has not been determined. However, the passage dead-ends into a sink near the head of Three Sisters Hollow. It is possible that this sink was once open to allow bats and woodrats to enter.

Bat Cave (LC)

Bat Cave is a lesser cave on the north side of the Green River. Its mapped length is about 1.6 km (1.0 mi), and it houses a modern Indiana bat and little brown bat hibernaculum. A significant bat bone deposit in a crawlway in the cave (Figure 182) has been noted several times since 1960 (Hall 1960; Jegla 1961; MacGregor 1993). At the urging of Rick Olson, Rick Toomey, Mona Colburn, and Blaine Schubert studied the site during the ISM paleontological inventory project in 1999 (Colburn 2005). The deposit was originally interpreted as a single catastrophic deposit potentially caused by a large Green River flood killing bats during hibernation. Although none of Hall, Jegla, or MacGregor suggested an age for the flooding, park management staff had interpreted the flooding as having been during the 20th century, perhaps the 1937 flood. Olson's doubts that the deposit was as young as it was being interpreted led to the ISM paleontological inventory in the 1990s.

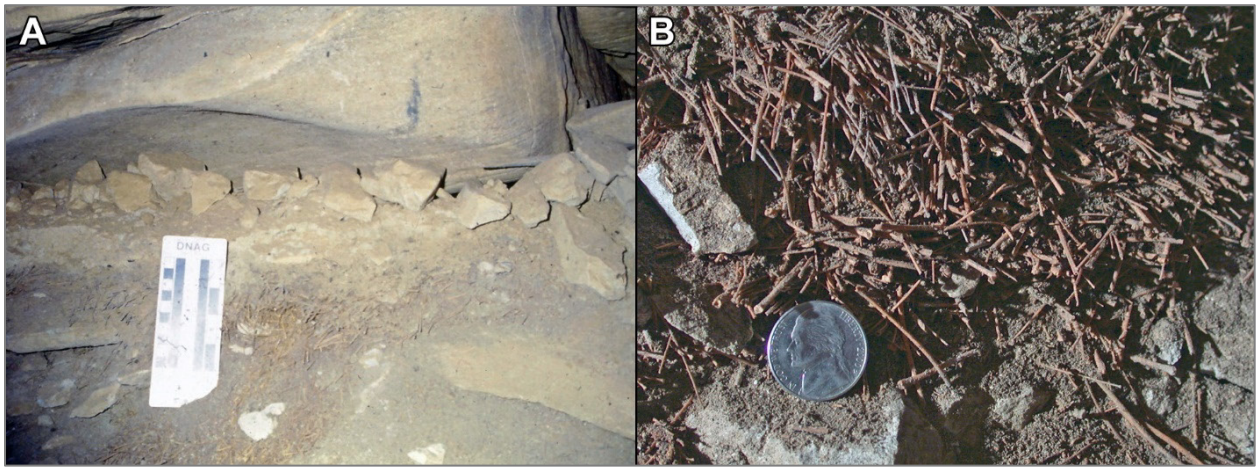


Figure 182. Wider (**A**) and close-up (**B**) view of Holocene bat bones deposit exposed in Bat Cave crawlway. **A:** NPS / RICK TOOMEY; **B:** NPS / RICK OLSON

Detailed excavation and radiocarbon dating has indicated that the bone deposit consists of at least 11 deposition events (Colburn et al. 2015). The oldest dated event (at the base of the deposit as exposed in the crawlway) is 9510 ± 640 BP (NZA32585; 10,610–10,880 cal BP). The youngest date (from Level 2 of the deposit) is 2250 ± 625 BP (NZA32583; 2160–2340 cal BP). Therefore, the deposit spans most of the Holocene.

The deposits are now interpreted to represent one, or both, of two deposition scenarios. It is possible that the bones in the deposit represent bats killed in large Green River floods. The other scenario is that the individual deposition events contain bones accumulated in the cave by normal attrition between flood events. These bones were then washed to the low spot where the deposit is located during large flooding events. It is also possible that both scenarios may be true or that different depositional events may represent different balances of these two possibilities (Colburn et al. 2015).

The vast majority of the bones identifiable below family in the deposit represent bones of *Myotis* bats (Hall 1960; Jegla 1961; MacGregor 1993; Colburn 2005; Jansky 2013; Colburn et al. 2015; Jansky et al. 2016). Hall (1960) identified skulls in the deposit as representing *M. sodalis*. However, he only tried to differentiate *M. sodalis* and *M. lucifugus*. Based on a sampling of humeri and an estimated volume of the deposit he calculated that the deposit contained bones from 300,000 individual bats. Colburn et al. (2015) identified the following taxa from the bone deposits:

- Fish
- Plethodontid salamander
- Indet. bird or mammal
- Vespertilionidae (vesper bats)
- *Myotis* spp.
- Medium *Myotis*
- *Myotis leibii* (eastern small-footed bat)
- *Myotis lucifugus* (little brown bat)
- *Myotis sodalis* (Indiana bat)
- *Corynorhinus* sp. (big-eared bat)
- *Eptesicus fuscus* (big brown bat)
- Rat-sized rodent
- Mouse-sized rodent
- Medium mammal
- *Procyon lotor* (common raccoon)
- *Odocoileus virginianus* (white-tailed deer)

They noted that the majority of the materials could not be identified below Vespertilionidae, and most of material that could be identified to at least genus was *Myotis* spp. They did not note variation in the fauna through the levels. Jansky (2013) and Jansky et al. (2016) used morphometric analysis to attempt to better identify the *Myotis* material and determined that *Myotis austroriparius* and *M. sodalis* dominate the assemblage. In addition, they found small numbers of *M. leibii* and *M. grisescens*. All species from this deposit are extant and all have been recovered in or near Bat Cave historically.

Dixon Cave (LC)

Dixon Cave is a lesser cave that is separated from the Mammoth Cave System by the collapse sink that formed the Historic Entrance. It is approximately 300 m (980 ft) long, 12 m (39 ft) wide, and almost 20 m (66 ft) high, and has a large, walk-in entrance located about 400 m (1,300 ft) from the Historic Entrance to Mammoth Cave. It was extensively mined for saltpeter in the early 1800s. This

has left the cave surface deposits very disturbed. It is a modern *Myotis* bat roost with *M. sodalis*, *M. lucifugus*, and *M. grisescens* using it for a hibernaculum. It also houses a small *M. grisescens* summer colony. Numerous other bat species utilize the cave at times, especially during fall swarming. Recent and modern bat use of Dixon Cave is discussed in Colburn (2005, 2006) and Thomas and Toomey (2017). The entrance also sometimes serves as a nesting area for a pair of *Coragyps atratus* as well as several *Sayornis phoebe*.

During the summers of 2000 and 2001, Colburn and the ISM team mapped and collected bones and surface sediment samples from 324 individual points throughout Dixon Cave. The sediment samples were screened and sorted. Guano and ceiling stain from bat roosts were also prevalent throughout the cave, as might be expected in a major modern bat roost. Their effort led to the identification of 32 different taxa of vertebrates from the surface and surficial sediment deposits of Dixon Cave. Table 18 lists the taxa and their relative ubiquity from this cave (from Colburn 2006).

Table 18. Vertebrate remains found in Dixon Cave. Percent ubiquity based on 324 data points. Modified from Colburn (2005, 2006) to update some taxonomy.

Group	Scientific Name	Common Name	# Data Points	% Ubiquity
Fish	Osteichthyes	Unidentified fish	2	0.6
Amphibians	Salamandridae	Unidentified salamander	3	0.9
	Bufo sp.	Toad	2	0.6
	Anura	Frog or toad	8	2.5
Reptiles	*Terrapene* sp.	Box turtle	3	0.9
	Testudines	Unidentified turtle	2	0.6
	Sauria	Unidentified lizard	1	0.3
	Colubridae	Coluber-type snake	1	0.3
	Serpentes	Unidentified snake	1	0.3
Birds	*Gallus gallus*	Chicken	1	0.3
	Strigiformes	Owl	1	0.3
	Aves	Small to medium-sized bird	1	0.3
Mammals	*Didelphis virginiana*	Opossum	2	0.6
	Blarina brevicauda	Short-tailed shrew	2	0.6
	Sorex sp.	Indeterminate shrew	1	0.3
	Corynorhinus sp.	Big-eared bat	2	0.6
	Eptesicus fuscus	Big brown bat	47	14.5
	cf. *E. fuscus*	Possible big brown bat	2	0.6
	Myotis cf. *M. austroriparius*	Possible southeastern myotis	1	0.3
	Myotis grisescens	Gray bat	5	1.5
	Myotis cf. *M. grisescens*	Myotis, possibly gray bat	3	0.9
	Myotis leibii	Small-footed bat	30	9.3

Table 18 (continued). Vertebrate remains found in Dixon Cave. Percent ubiquity based on 324 data points. Modified from Colburn (2005, 2006) to update some taxonomy.

Group	Scientific Name	Common Name	# Data Points	% Ubiquity
Mammals (continued)	*Myotis* cf. *M. leibii*	Myotis, possibly small-footed bat	2	0.6
	Myotis lucifugus	Little brown bat	12	3.7
	Myotis cf. *M. lucifugus*	Myotis, possibly little brown bat	3	0.9
	Myotis sodalis	Indiana bat	38	11.7
	Myotis cf. *M. sodalis*	Myotis, possibly Indiana bat	15	4.6
	Medium-sized *Myotis* sp.	Indeterminate medium-sized Myotis	84	25.9
	Myotis sp.	Indeterminate Myotis	38	11.7
	cf. *Myotis*	Possible mouse-eared bat	5	1.5
	Perimyotis subflavus	Tricolored bat	24	7.4
	Vespertilionidae	Indeterminate vespertilionid bat	206	63.6
	Canis sp.	Dog or coyote	1	0.3
	Procyon lotor	Raccoon	82	25.3
	cf. *P. lotor*	Possible raccoon	1	0.3
	cf. *Mephitis mephitis*	Possible striped skunk	1	0.3
	Lynx cf. *rufus*	Bobcat	1	0.3
	Carnivora	Indeterminate carnivore	1	0.3
	Sus scrofa	Domestic pig	1	0.3
	Odocoileus virginianus	White-tailed deer	2	0.6
	O. virginianus or *Sus scrofa*	Artiodactyl, likely deer or pig	1	0.3
	Glaucomys volans	Flying squirrel	1	0.3
	Marmota monax	Woodchuck	2	0.6
	Peromyscus sp.	White-tailed or deer mouse	9	2.8
	Microtus ochrogaster (& *Microtus* sp.)	Prairie vole (& vole)	1	0.3
	Rodentia (small taxa)	Mouse-sized rodent	10	3.1
	Neotoma floridana or *N. magister*	Eastern or Alleghany woodrat	49	15.1
	cf. *Neotoma floridana* or *N. magister*	Possible eastern or Alleghany woodrat	1	0.3
	Sylvilagus floridanus	Eastern cottontail rabbit	2	0.6
	Mammalia, medium-sized	Indeterminate medium-sized mammal	2	0.6
	Mammalia, large-sized	Indeterminate large mammal	1	0.3

As is evident in Table 18, bats are by far the most ubiquitous group represented in the cave. They are represented by numerous bones as well as guano deposits. Among the bats, the medium-sized *Myotis* (including both *M. lucifugus* and *M. sodalis*), *Myotis leibii*, *Perimyotis subflavus*, and *Eptesicus fuscus* dominate. Following the bats, *Procyon lotor* and *Neotoma* sp. are the most frequently encountered remains. In most cases, *Procyon lotor* is represented by feces. This represents raccoons entering the cave and eating hibernating bats. Most of the feces contain bat bones as the primary constituent. These finds represent an expected assemblage for a large *Myotis* hibernaculum.

The non-bat taxa found in the Dixon Cave assemblage all represent taxa that are present in the modern fauna of the park. Two of the taxa (*Sus scrofa* and *Gallus gallus*) represent domestic animals that must be historic in age; they could represent meals of people working in the cave. Two radiocarbon dates were completed on raccoon feces with bat bones and provided ages of 470 ± 60 RCYBP (GX-27147) and 1380 ± 70 RCYBP (GX-27145). Although both are prehistoric, the fauna and dates show no evidence that deposits extend beyond the Holocene.

Lee Cave, Marshall Ave (LC)

Lee Cave is a lesser cave located on the south side of the Green River and is about 11 km (6.8 mi) long. It is probably most notable as an archeological site (Freeman et al. 1973; Watson 1997). However, it is also notable as both a modern bat roost and as an older one; whether the roosting has been continuous has not been determined. The evidence of past bat use was first noticed by archeologists in the early 1970s, who observed lumps of dark organic matter. They originally interpreted these as being human paleofeces, but when they examined the lumps more closely, they determined that these were not of human origin (Kennedy and Watson 1996; Watson 1997). When Olson, Colburn and Toomey examined Lee Cave for paleontological remains in 1998, they noted not only the lumps of dark organic matter, but also lenticular masses of the same organic matter with lumps breaking off at the edge. With careful examination, they identified those masses as ancient, compressed masses of bat guano. They submitted a chunk of the guano for dating, and it was found to have an age of 1639 ± 40 RCYBP (CAMS-63101) (Colburn 2005). These masses of compressed older guano are near (and in some places under) existing gray bat summer bachelor roosts. Therefore Olson, Toomey, and Colburn have interpreted these fossil bat guano masses as representing past summer use of the area by *Myotis grisescens* (probably bachelor colonies like current use). In addition to the guano, they found bat bones. The identifiable bones were dominated by *Myotis grisescens*. Two *Myotis grisescens* humeri were submitted for dating, but both samples failed to date.

Marshall Avenue also had some other paleontological remains. Several mummified *Perimyotis subflavus*, a mummified *Myotis lucifugus*, and probable *Eptesicus fuscus* humerus were found. Non-bat remains were limited to a single rodent-gnawed *Odocoileus virginianus* bone in a woodrat larder near the terminal breakdown. A mummified woodrat was identified by a CRF team (Freeman et al. 1973), but it was not relocated by the ISM crew (Colburn 2005).

Cave #056 (LC)

Cave #056 is an 8.9-km (5.5 mi)-long lesser cave on the north side of the Green River. It is a current *Myotis* hibernaculum (*M. sodalis* and M. *lucifugus*), although populations have been decimated by

white nose syndrome. Hall (1960) reported 550 *M. sodalis* in Cave #056 in the winter of 1957–1958. Paleontological reconnaissance of Cave #056 occurred in 1996–1997 (Toomey) and 1999 (Colburn and Olson). The most common remains that were encountered in Cave #056 were bat bones and bat guano. Bat staining was also widespread in the Historic section of the cave. Abundant bat bones (although relatively few skulls for species-level identification) were noted in the D-crawl. In addition to unidentified vespertilionid remains, skulls or mandibles of *Perimyotis subflavus*, *Myotis sodalis*, *Myotis lucifugus*, and *Myotis* sp. were identified from the cave. From a mix of woodrat debris and powdery, organic sediment near survey station FSB2981 C17, Toomey recorded *Procyon lotor* scat, *Neotoma* feces, plant debris, and bones from *Rana* sp., *Terrapene* sp., *Microtus* sp., *Myotis* sp., and indeterminate chiropterans. This area is interpreted as material that sifted down from an overlying *Neotoma* larder. Colburn (2005) summarized the reconnaissance of Cave #056. The station for the sediment deposit was listed as W18 (FSB698 W18) in the original report and Colburn (2005). However, that survey has been replaced and Dave West (Cave Research Foundation, pers. comm., 2023) indicates that the modern survey designation in that area would be C17. Karen Willmes led a CRF trip in February 1995 to survey a side lead off DD35. At FSB 3241 DD35 the team found a limb bone identified as larger than a bat, probably a rodent. They left the bone at the DD35 station marker cairn.

Long Cave (LC)

Long Cave is a lesser cave on the South Side of the Green River, with a length of 2,130 m (7,000 ft). It houses the largest hibernating bat colony in the park; there were more than 310,000 gray bats wintering in it as of 2019. However, most of those bats have moved into the cave since 2003 when airflow to the entrance was restored by removing a large concrete sill. Colburn (2017) indicated that Long Cave contains significant bat remains and stain (Figure 183) representing large former bat roosts. She identified the following species of bats: *Eptesicus fuscus*, *Lasiurus borealis*, *Myotis grisescens*, possible *M. austroriparius*, *M. leibii*, *M. lucifugus*, *M. sodalis*, *Perimyotis subflavus*, and *Corynorhinus* sp. All of these species occur at MACA, and most have been recovered live in Long Cave at least once. In addition to bats, *Procyon lotor* scat filled with bat bones and claw scratches on the wall indicate that the cave housed a large winter bat roost. Colburn also reported *Neotoma* sp. and *Peromyscus* remains in Long Cave. She interpreted the material from Long Cave as representing relatively recent use of the cave, as opposed to Pleistocene or early Holocene use.



Figure 183. Mona Colburn (ISM) examining bat staining on the wall and ceiling of Long Cave.
NPS / RICK OLSON

Scattered Surface Finds

The most widely distributed type of paleontological remains in MACA caves are surface finds. These are generally isolated finds that occur on the surface of passage floors and ledges. The finds range from single bones or teeth to articulated or partially articulated skeletons. Sometimes these are in current intermittent or permanent streams; sometimes they are in either older dry stream beds or away from streams. Most finds were probably washed into the area where they were found, but some could represent animals that came into the cave and died. In most cases, it is not clear where the material entered the cave, although sometimes it is possible to generally determine where a past opening might have been. Most of these findings are undated. Some represent extinct or extralimital species that would have occurred in the Pleistocene, although their current location may represent redeposition.

Historic Section of Mammoth Cave (MCS)

The long-term, large, diverse, and important bat roost that existed in the Historic section of Mammoth Cave was discussed earlier in this chapter. As a reminder, for this report the Historic section of Mammoth Cave consists of the upper-level passages between the Historic and Violet City

Entrances (including Gothic Avenue, Backsliders Alley, Blue Spring Branch, Blackall Avenue, Wrights Rotunda, and Black Chambers). It also includes Audubon Avenue (including Little Bat Avenue, Rafinesque Hall, Watson Trace, Lookout Mountain, and Vespertilio Hall), and two breakdown-choked stopes that provided access to lower levels (The Corkscrew and the Vanderbilt Hall Breakdown). This broad locality represents approximately 6,650 m (21,800 ft) of cave passage.

In addition to the remains from the bat roosts, this area contains large numbers of remains (mostly bones, but also scat and mummified remains) of other animals (Figure 184, raccoon bones and woodrat skull). Many of these remains are located on the surface of the passage floor or on ledges along the passage walls. These remains are treated in detail in Colburn (2005). Some of the remains are in sediment deposits associated with bat guano or archeological deposits. Although some materials from sediments were discussed in Colburn (2005), more were recovered and analyzed during the combined archeological and paleontological survey of tour trails to support an Environmental Assessment of potential projects to upgrade tour trail infrastructure. From December 2007 through July 2008 crews from the University of Kentucky Program for Archaeological Research excavated sites along the Historic, Lantern, Gothic, Grand Avenue, and Great Onyx Tour routes to evaluate archeological and paleontological potential for trail renovation planning purposes. The archeological faunal remains and paleontological remains were analyzed by the Illinois State Museum team and are reported in Ahler (2012) and Widga and Colburn (2015).

The paleontological materials with the best chronological control are those that were excavated during the survey of archeological and paleontological potential of the cave trails. The non-bat results of that survey (Widga and Colburn 2015) are summarized in Table 19.

The ISM team (Colburn 2005) identified a large variety of vertebrate remains at 1,553 data points in the Historic section. These remains included isolated bones, partial and whole skeletons, partial and whole mummified animals, in situ deposits of bones, bat guano pellets, masses of in situ guano, woodrat feces, raccoon scats, and trace fossils (scratchings, footprints, trails, and staining). Some of these, such as the *Cryptobranchus* remains, the *Desmodus* femur, and the various bats roost remains have been discussed in detail in other sections of this chapter. Table 20 contains a summary of the taxa recovered at these 1,553 points. With the exception of *Desmodus* and *Tadarida*, all of the taxa occur at MACA in modern times. The remains also include several domesticated taxa that represent historic cave use. Details of specific taxa and where they were found can be found in Colburn (2005).



Figure 184. Scattered *Procyon lotor* bones (**A**) in Watson Trace and a *Neotoma* skull and dung (**B**) in Vespertilio Hall. NPS

Table 19. Taxa recovered during University of Kentucky Program for Archaeological Research combined archeological and paleontological survey of tour trails (Ahler 2012; Widga and Colburn 2015). Number represents the number of individual specimens of each taxon.

Taxon	Historic	Late Holocene	Interglacial
Meleagris gallopavo	1	–	–
cf. *Gallus gallus*	20	5	–
Unidentified Aves (medium)	1	13	–
Mustela sp.	–	–	2
Odocoileus virginianus	2	–	–
Peromyscus sp.	–	–	13
Neotoma sp.	–	1	7
Unidentified Rodentia	2	57	80
Unidentified Mammalia	–	7	10
Unidentified Chelonia	–	1	–
Unidentified Squamata	–	1	–

Table 20. Taxa recovered during ISM paleontological survey of Historic tour area (Colburn 2005).

Group	Scientific Name	Common Name
Fish	*Moxostoma* sp.	Redhorse
	Catostomidae or Carp	Sucker family or carp
	Ictaluridae	Catfish family
	Centrarchidae	Sunfish family
Amphibians	cf. *Cryptobranchus*	Hellbender
	Caudata	Salamander
	Bufo sp.	Toad
	cf. *Rana* sp.	Frog
	Anura	Frog or toad
	Herptile	Amphibian or reptile
Reptiles	Testudines	Turtle
	Colubridae	Colubrid snakes
	Crotalus sp.	Rattlesnake
	Serpentes	Snake
Birds	*Gallus gallus*	Chicken
	Meleagris gallopavo	Turkey
	Phasianidae	Pheasant, grouse, quail family
	Asio otus	Screech owl
	Colaptes auratus	Northern flicker

Table 20 (continued). Taxa recovered during ISM paleontological survey of Historic tour area (Colburn 2005).

Group	Scientific Name	Common Name
Birds (continued)	Passeriformes	Perching bird
Mammals	*Scalopus aquaticus*	Eastern mole
	Desmodus stocki	Extinct vampire bat
	Eptesicus fuscus	Big brown bat
	Lasiurus borealis	Red bat
	Myotis austroriparius	Southeastern bat
	Myotis grisescens	Gray bat
	Myotis leibii	Small-footed myotis
	Myotis lucifugus	Little brown bat
	Myotis sodalis	Indiana bat
	Myotis lucifugus or *M. sodalis*	Little brown or Indiana bat
	Myotis septentrionalis	Northern long-eared myotis
	Myotis sp., small-sized	Small myotis
	Myotis sp., medium-sized	Medium myotis
	Myotis sp.	Indeterminate species of myotis
	Nycticeius humeralis	Evening bat
	Perimyotis subflavus	Tricolored bat
	Corynorhinus sp.	Big-eared bat
	Vespertilionidae	Indeterminate vespertilionid bat
	Tadarida sp.	Free-tailed bat
	Chiroptera	Bat
	Canis sp.	Dog/coyote
	Procyon lotor	Raccoon
	Mephitis mephitis	Skunk
	Carnivora	Indeterminate carnivore
	Sus scrofa	Domestic pig
	Bos taurus or *Sus scrofa*	Cow or pig
	Odocoileus virginianus	White-tailed deer
	Artiodactyla	Indeterminate ungulate
	Marmota monax	Woodchuck
	Sciurus sp.	Tree squirrel
	Tamias sp.	Chipmunk
	Neotoma floridana or *N. magister*	Eastern or Alleghany Woodrat
	cf. *Neotoma*	Probably woodrat (but a few remains could be old world rat)

Table 20 (continued). Taxa recovered during ISM paleontological survey of Historic tour area (Colburn 2005).

Group	Scientific Name	Common Name
Mammals (continued)	*Rattus* sp.	Old world rat
	Mus musculus	House mouse
	Peromyscus sp.	Deer or white-footed mouse
	Microtus pinetorum	Woodland vole
	Rodentia	Rodent
	Sylvilagus sp.	Cottontail rabbit
	Homo sapiens	Human
	Vertebrata	Vertebrate
	Indeterminate Vertebrata	Unknown vertebrate

Mammoth Cave, Fox Avenue (MCS)

Sometime in 1919 or the early 1920s, skeletal remains were found by explorers in a lower-level passage in the Frozen Niagara vicinity. These were thought to be the remains of foxes and the passage was so named (Morrison 1929: 47). Others subsequently realized that the remains were actually those of raccoons (*Procyon lotor*). In 2000, guide Chuck DeCroix led paleontologists to Fox Avenue to make observations. One skeleton was obvious in the trail, but another partial skull was found by Mona Colburn. The only other remains were a scatter of indeterminate bat bones and, interestingly, skeletal parts of at least three frogs (Colburn 2005: 241). More information about this area can be found in Chapter 2.

Mammoth Cave, Sophy's Avenue and Kennedy Domes (MCS)

In December 1978 and February 1979 paleontologists visited Sophy's Avenue and Kennedy Domes in the Mammoth Cave System. Bones of medium size *Myotis*, *Sciurus*, *Neotoma*, and *Peromyscus* were recovered in the domes. More exciting was the find of a black bear (*Ursus americana*) tibia during the 1978 visit near survey station Z20 in Sophy's Avenue (Wilson 1980). In March of 2001, Rick Olson accompanied Rick Toomey and Mona Colburn to Sophy's Avenue. Little was found until Olson went a short distance down the N survey crawl off the Z and found a bone that proved to be a left black bear tibia. The tibia from 1978 had been identified as a right tibia, but to Colburn it did not look like that in the photograph from collections at Carnegie Museum of Natural History in Pittsburgh, Pennsylvania (Colburn 2005: 250). So, she visited and determined that both are left tibias. Therefore, either there was a bear with two left legs, or we have remains from two separate bears.

Proctor Cave, Proctor Crawl (MCS)

In 1978, Ron Wilson found a tapir tooth in the Proctor Crawl near survey station N17 (Wilson 1980, 1981, 1985). The crawl is a long, winding connector between the entrance area of Proctor Cave and Proctor Trunk. The tooth is a lower fourth premolar from the extinct Pleistocene tapir *Tapirus* cf. *T. veroensis*. It is not known how the tooth got into this upper-level crawl.

Cave #353 (LC)

On 2 May 2021, during a trip to check several lesser caves for shark remains, guide Kelli Tolleson found a partial lower molar or premolar of a tapir, likely *Tapirus veroensis*, in Cave #353. This is a lesser cave north of Green River. The tooth was found just inside the entrance on the floor of the cave with no other large vertebrate remains present. However, a woodrat humerus was found nearby.

Mammoth Cave, Logsdon River (MCS)

An elk (*Cervus elaphus*) tooth was found by Rick Olson on 29 November 1980, in a rimstone dam in a level above Logsdon River near survey station B13. The tooth was given to paleontologist Ron Wilson for curation at Carnegie Museum of Natural History but unfortunately it was lost (CRF Trip Report 1980). The stream was given as Hawkins River in the report, but this section is now designated as Logsdon River.

On 17 April 2021, during a trip to recover a shark braincase in the ceiling, guide Kelli Tolleson found a partial horse (*Equus* sp.) tooth in Logsdon River near Banana Pass (near station FSB 2452 N28). The tooth was under flowing water, and the floor was black chert. It is unclear whether the tooth is from a Pleistocene horse or a modern one. This stream floods frequently and has many modern stream inputs from the surface. However, the tooth does have a manganese coating on it, which could indicate that it is older.

Mammoth Cave, New Discovery (MCS)

In 1979 during CRF surveying in New Discovery, Tom Brucker and Tom Gracinin collected several bones from the C survey in the far northwestern area of New Discovery. These were a *Procyon lotor* radius, a large mammal rib, and a partial bird femur. Ron Wilson deposited these bones with other fossils from MACA at the Carnegie Museum. These finds were in or along a dry stream channel near where the passage fills and becomes impassable. This termination is near a sinkhole off Bruce Hollow which could be the source of the bones. This area is intriguing because bone is washing in, but the poor preservation makes it impossible to determine its significance. This area is several kilometers or miles away from the New Discovery bat roost discussed above and the finds are not related to those from the bat roost.

Mammoth Cave, River Acheron (MCS)

In a tributary to River Styx called River Acheron, Rick Toomey found a horse (*Equus* sp.) tooth cemented into fill at survey station PQ8 on 27 November 2009. On the same trip, Rick Olson found two black bear (*Ursus americanus*) vertebrae jammed in a bedrock fissure next to the stream at station PQ36. River Acheron is a tributary of River Styx in the Historic section of Mammoth Cave. In addition to the bones and tooth, the site also contains trash washed in from the campground at Mammoth Cave. It is likely that the material came in through Mammoth Dome sink, and it is clear that material has come in relatively recently. Unfortunately, neither horse nor bear provide any good temporal control. The material could be Pleistocene (horse and/or bear), Holocene (bear), or Historic (bear and/or horse) in age. If the material is Pleistocene, it is likely reworked from an older deposit, because the stream is too dynamic to allow material to remain in it for an extended time.

Mammoth Cave, Bransford Avenue (MCS)

During an orientation trip to Bransford Avenue in August 2017 for guide Jerry Bransford, a partial horse (*Equus* sp.) tooth was found by fellow guide Lauren Bly. The tooth was on the floor amid breakdown near survey station FSB2721 S58. The tooth was water-worn and clearly had to have been transported to its resting place by floodwaters. It is not clear where it might have entered the cave. The tooth could be Pleistocene or Historic. The context does not provide additional information.

On a CRF trip in January 1984 led by George Wood, Jeff Arp found the pelvis of a small mammal in a shaft drain of a side pit to Pit T68.5 in West Bransford Avenue. The bone was not collected.

Mammoth Cave, Mammoth Dome (MCS)

On 11 July 2021, guide Rich Boldon found a horse (*Equus* sp.) tooth in Mammoth Dome about 20 feet above the bottom near survey station FBS 3115 DA1. He found this tooth while examining Mammoth Dome for shark teeth. Mammoth Dome is an active dome that drains the developed area near the Hotel and its parking lot, including a large historic dump. It is unknown whether the tooth represents an extinct horse and washed out of an older deposit in a sinkhole or a modern horse tooth that washed in from the surface, the historic dump, or a sink.

Mammoth Cave, Cathedral Domes Area (MCS)

In October 1977 a CRF team led by Tom Brucker observed nuts, an old *Neotoma* nest, *Neotoma* feces, and a moderate sized rib bone (10 cm [4 in] long and 0.953 cm [0.375 in] wide) in a roomy canyon beyond survey station FSB1365 F18 above Cathedral Domes. The material was left in place.

Unknown Cave, Malott Avenue (MCS)

In August 1963 a CRF team led by Earl Geil surveyed in Malott Avenue (also written “Mallott” and “Mallett”) in Unknown Cave, a portion of the Mammoth Cave System. Their trip report (associated with FSB 0152) indicated the following: “NOTE: A bone was collected 20 feet [6 m] past station 6 and deposited in the CRF headquarters for later identification.” The whereabouts and identification of this bone are not known.

Unknown Cave, Ralph Stone Hall (MCS)

In April 2020 a CRF team led by Tom Brucker surveyed to a side room off FSB 2037 C14 at Ralph Stone Hall. Their trip report (associated with FSB 3561) indicated the following: “Above C14 we surveyed to the side room and found a significant bat bone deposit.” The bones are located between FSB3561 DC10 and DC11. This deposit of bones has not been evaluated further.

Unknown Cave, Candlelight River (MCS)

In July 2005 a CRF team led by Spike Crews was resurveying Upstream Candlelight River. Their trip report (associated with FSB 3939) indicated the following: “Near U49 Andy [Free] discovered a rather large fragment of bone that appears to be a piece of femur; perhaps of a bear. It was photographed.” We have not seen the photograph and the bone has not been evaluated further.

Crystal Cave, Thomas Avenue (MCS)

In July 1994, a CRF team led by Paul Rubin observed two bone fragments placed on a rock near survey station FSB260 T27 beyond Scotchman's Trap near the end of Thomas Avenue. They tentatively identified one of the bones as part of a deer leg bone. The description of the other suggests a proximal femur (or possibly humerus) of a small mammal. They also noted a bat bone sticking out of sediment in a small pit near T27. The area has been resurveyed and T27 is now FSB4707 DD117.

Salts Cave, Beneath Vestibule (MCS)

On an August 1996 CRF trip (associated with FSB 3305) into the area beneath the Salts Cave vestibule, Mick Sutton reported the following paleontological finds:

> *Paleontological: We noticed three large bones or fragments in the SA survey: 1) piece of long bone about 8.5 cm [3.3 in] long with a maximum width of 3.5 cm [1.4 in] at SA9; 2) large vertebra, 5 cm [2 in] long by 7 cm [3 in] wide near SA5; 3) fragment of partly mineralised [sic] long bone (?) at SA 3 10 cm [4 in] long, 1–3 cm [0.4–1 in] wide.*

These finds were left in place and have not been further evaluated.

Salts Cave, South Trunk (Moonwalk Blvd.) (MCS)

During a November 2000 CRF trip (associated with FSB 3604) into South Trunk of Salts Cave, Mick Sutton reported the following paleontological finds:

> *At around R50 there were patches of polish on the rocks reminiscent of woodrat activity. In the undercut at RA1, there was an area of impressive (old?) mud cracks, and in the same area were bits of squirrel bone, along with bat bones.*

Toomey was on the survey trip and helped identify the material. These finds were left in place and have not been further evaluated.

Colossal Cave, Lee Pit Area (MCS)

A CRF survey trip led by Fred Benington in August 1961 (FSB 0076) reported a bone within a circle inscribed in a mud floor in a side lead off U29-31.

Cave #053 (LC)

On 26 March 2022, Rich Boldon found a deer tooth in Cave #053, a lesser cave south of Green River. Cave #053 has both prehistoric and historic cultural resources in it. The tooth could have washed out of an archeological context. However, deer are quite common in the woods around Cave #053, so it may represent a more recent tooth that washed into the cave or was brought in by a woodrat.

Running Branch Cave (LC)

On 12 March 1983, Ron Wilson led a CRF party to Running Branch Cave to identify a skeleton that had been previously reported by a survey team. Running Branch Cave is a cave on the north side of the Green River which is about 1,460 m (4,790 ft) long. Although a CRF report on the resources of Running Branch Cave (CRF 1995) indicated a lack of Quaternary paleontological remains, it does

note that Ron Wilson identified a raccoon skeleton in the Formation Passage. Wilson's original trip report (1983) indicates that it was partially buried in gypsum sand between survey stations D7 and D8.

Cave #325 (LC)

Cave #325 is an approximately 15-m (49-ft)-deep pit on the park boundary. It is on the south side of the Green River. Colburn (2005) discusses it in more detail. The pit was a trap that contained a variety of animal remains including *Bufo* sp., unidentified anurans, a *Sciurus carolinensis* skeleton, *Peromyscus* sp., and parts of at least two *Equus* sp. individuals. Side passages at and near the bottom of the pit contained remains of additional anurans, *Acris* sp., a passerine bird, *Perimyotis subflavus*, unidentified bats, *Odocoileus virginianus*, *Equus* sp., *Sylvilagus floridanus*, *Peromyscus* sp., *Reithrodontomys* sp., *Neotoma* sp., and a ground squirrel. Colburn also identified a skull of *Sorex fumeus* from the site. We suspect the bones represent a recent accumulation. Assuming the *Equus* remains represent *Equus caballus*, all of the taxa that have been recovered in Cave #325 are currently found in or around the park.

Cave #081 (LC)

Cave #081 is a small cave on the north side of the Green River. The cave was dug open, probably in the 1920s, for tours. Several *Corynorhinus* cf. *C. rafinesquii* skeletons were collected from the site. The site has an approximately 12-m (39-ft)-pit at the end of the right-hand branch. Bones from anurans, chiropterans, *Sylvilagus floridanus*, *Neotoma* sp., and *Peromyscus* sp. were recovered in the pit. All of the remains are thought to be recent in age (Colburn 2005).

Cave #100 (LC)

Cave #100 is a small cave on the south side of the Green River. Its total surveyed length is about 17 m (56 ft), and is notable for bones of *Terrapene carolina*. Colburn, Olson, and Toomey noted *Procyon lotor* bones and two mouse carcasses. Colburn (2005) concluded that the remains were likely recent.

Cave #381 (LC)

Cave #381 is a small cave on the north side of the Green River. In May 2000 Colburn, Olson, and Toomey checked it for paleontological remains (Colburn 2005). They found bones of *Acris* sp., *Terrapene carolina*, *Scalopus aquaticus*, and bat wing bones on the entrance talus of the cave. They also noted bat staining on several areas of ceiling.

Cave #028 (LC)

Cave #028 is an approximately 40-m (130-ft)-long cave on the north side of the Green River. The cave is a canyon passage. The site is an archeological and paleontological site. It contains a small, modern *Corynorhinus rafinesquii* winter roost. Claude Hibbard visited the site in 1935 while a naturalist at MACA. He reported (Hibbard 1935) bones of frogs, reptiles, small birds, mammals, and *Odocoileus virginianus*. He (Hibbard 1935: 60) made the following comment: "Probably bones of new extinct forms in the park may be found in this cave since a deer tooth was observed in the cave." The Illinois State Museum team also inventoried the cave. They identified *Bufo* sp., Colubridae, Aves (small), *Didelphis virginiana*, *Neotoma* sp., *Microtus* sp., and *Odocoileus virginianus* (Colburn

2005). All taxa that have been identified from the site are extant and occur in the area, so Hibbard's prediction has yet to be borne out.

Cave #102 (LC)

Cave #102 is a section of large collapsed passage. During a CRF trip to assess archeological and paleontological potential of several sites in November 1994, Toomey observed modern and older *Neotoma* feces in the cave. In addition, a possible *Lynx rufus* track was observed in mud at the top of the breakdown in the cave. This track is probably modern, but with the woodrat feces demonstrates use of this cave by animals. This suggests at least the potential that older material may be present.

Cave #200 (LC)

In November 1994, Toomey and Dr. Crothers (University of Kentucky) were evaluating archeological and paleontological potential of several caves. In their trip report they evaluated an unnamed cave with the number Cave #349, but this cave number does not occur in the area they were working. Consultation with the CRF small caves lead (Bill Copeland) suggests that the cave they were in was Cave #200. The cave was evaluated as follows:

> *Very small cave with not much material. but there is a ledge along the back of the cave with an older bank of sediment perched along the ledge. Numerous small bones exposed in this sediment (deer mouse, cotton tail rabbit, frog or toad, nonpoisonous snake, wood rat and possible fish or amphibian unidentified element). This sediment appears to have some antiquity but is probably Holocene in age.*

The cave has not been further evaluated. It appears that further evaluation would require excavation of the sediment bank.

Cave #084 and Cave #294 (LC)

Although Colburn (2005) reports that Cave #084 lacks paleontological remains, later finds complicate that conclusion. Cave #294 is the upper end of the same cave system. Although no paleontological material has been found in the lower section (Cave #084), a CRF trip led by Toomey in January 2009 (FSB 4284) located scattered bone on the floors of the first two pits in the Cave #294 section. Taxa found included *Didelphis virginiana*, *Procyon lotor*, *Neotoma* sp., and probably *Odocoileus virginianus*.

Cave #300 (LC)

Cave #300 is a small cave on the north side of the Green River. During a CRF survey trip in January 1999, the team observed bat bones, gastropods, an old rat nest, abundant walnut and hickory shells, a unionid, a turtle shell fragment, a cow or horse tooth, a deer bone, and other animal bones. The material was left in the cave and has not been further evaluated.

Cave #251 (LC)

Cave #251 is an approximately 12-m (39-ft)-long cave on the north side of the Green River. During a CRF survey trip in November 2000, the team observed a limb bone of a medium-sized mammal.

They conjectured that it might have been from a raccoon. Old *Neotoma* sp. feces were also observed in the cave. The material was left in the cave and has not been further evaluated.

Cave #337 (LC)

Cave #337 is an approximately 250-m (820-ft)-long cave on the south side of the Green River. It has a pit entrance and several small internal pits. During a CRF survey trip and paleontological inventory in February 2001 (FSB 3621), Toomey observed that the cave has very abundant bone and that it appears to act as a natural trap collecting remains of a diverse set of vertebrates. Bone was reported to be abundant on both the upper and main levels. Taxa observed included *Terrapene* sp., Colubridae, *Didelphis virginianus*, Chiroptera, *Procyon lotor*, and *Odocoileus virginianus*. However, the trip report states that little effort was made to individually inventory bones and Toomey recommended further paleontological evaluation. The site has not received a full paleontological evaluation.

Cave #493 (LC)

Cave #493 is an approximately 100-m (330-ft)-long cave on the north side of the Green River. It is a *Corynorhinus rafinesquii* maternity site. During a CRF survey trip in January 2016, the survey team observed a bone fragment. The material was left in the cave and has not been further evaluated. Toomey has also observed bat bones in this cave.

Cave #034 (LC)

In July 1980, Keith Poulson took Gail Wagner on a CRF trip to check a possible human bone at Cave #034. Dr. Wagner identified the bone as *Odocoileus virginianus* rather than human and suggested that Ron Wilson should be consulted. We are unaware of whether Ron Wilson ever checked the bone. As far as we can tell, this find has not been evaluated further.

Other Caves (LC)

Further investigation is expected to uncover additional accumulations of note. Some lesser caves have been investigated and found to be barren of paleontological remains. Colburn (2005) discusses several lesser caves that were checked during the Illinois State Museum paleontological inventory which were not found to have paleontological remains. These included Cave #118 and Cave #042. During CRF trips in the 1990s, Toomey also checked several other lesser caves for paleontological potential. He specifically noted the following caves as not having Quaternary paleontological remains or potential: Cave #020, Cave #057, and Cave #231.

Conclusions

Quaternary remains at MACA are as varied as one would expect to see in any large cave system or set of small caves. They range from isolated bones or skeletons of animals that may have been using the cave for shelter, such as bats, bears, and raccoons, to complex stratified deposits associated with deposition at a cave entrance or in a bat roost over time. Most of the remains that have been identified are surface finds. Many of these remains represent material lying at or near where it was originally deposited. Most of the bat roosts and materials associated with bat roosts fall into this category. However, another large group of surface remains were found in sites that indicate they were transported to the area (usually by water). These include both isolated finds, such as isolated

teeth found in several caves and cave passages, and groups of mixed age bones such as those found in the crawlways of the end of Frost Avenue in Proctor Cave. Much less common, but very important, are the sites which contain Quaternary bone in a stratigraphic context. Prominent among these are the Frozen Niagara interglacial deposits, some of the *Tadarida* roost guano deposits, and the Bat Cave deposits.

The fossils and deposits at MACA are interpreted as spanning much of the Quaternary. The oldest identifiable Quaternary fossils are the *Cryptobranchus* bones that represent individuals that washed into the cave in a flood as the cave was forming. The youngest materials are historic. They represent bats and other animals that were utilizing the cave even while people were mining saltpeter and touring the cave. Unfortunately, many of the deposits at MACA remain undated. Many sites would benefit from additional radiocarbon dating. Prominent among those sites would be the New Discovery bat remains, and the bat roost in Proctor Trunk.

The fossil deposits in the cave are significant for a variety of reasons. They provide a glimpse of what environmental conditions were like during interglacial (Frozen Niagara, *Tadarida* roosts) and glacial (Proctor Trunk and New Discovery) conditions. The more recent remains, such as historic bat roosts, have provided the park with information on past entrances and environmental targets for restoration of past conditions due to modification of entrances for tourism. The historic bat roosts also provide data for understanding the population collapse of species such as the Indiana bat which is now federally endangered.

Another significance of the Mammoth Cave fossil deposits is that they contain remains of extinct species as well as extralimital species no longer present in the Mammoth Cave area. Lists of these two groups are provided below.

Extinct species represented by Quaternary fossils at MACA:

- *Dasypus bellus* (beautiful armadillo)
- *Neofiber leonardi* (extinct muskrat)
- *Desmodus stocki* (Stock's vampire bat)
- *Smilodon* sp. (saber-toothed cat)
- *Arctodus simus* (short-faced bear)
- Indet. Proboscidea (extinct member of group including elephants, mammoths, mastodons, etc.)
- *Mammut americanum* (American mastodon)
- *Equus* sp. (extinct horse)
- *Tapirus* cf. *veroensis* (extinct tapir)
- *Platygonus* sp. (extinct peccary)
- *Platygonus compressus* (flat-headed peccary)

- cf. *Platygonus* sp. (extinct peccary)

Extralimital species represented by Quaternary fossils at MACA:

- *Geomys* sp. (pocket gopher)
- *Tadarida* sp. (free-tailed bat)
- *Martes americana* (American marten)
- *Mustela nivalis* (least weasel)
- *Cervus canadensis* (American elk)
- *Bison* sp. (bison)

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Chapter 9. Mammoth Cave National Park Paleontological Resources Management and Protection

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Introduction: National Park Service Policy

Paleontological resources are non-renewable remains of past life preserved in a geologic context. At present, there are 433 official units of the National Park System, plus national rivers, national trails, and affiliated units that are not included in the official number. Of these, 287 are known to have some form of paleontological resources, and paleontological resources are mentioned in the enabling legislation of 18 units. Fossils possess scientific and educational value and are of great interest to the public; therefore, it is exceedingly important that appropriate management attention be placed on protecting, monitoring, collecting, and curating these non-renewable paleontological specimens from federal lands. In March 2009, the Paleontological Resources Preservation Act (PRPA) was signed into law as part of the Omnibus Public Land Management Act of 2009. The new paleontology-focused legislation includes provisions related to inventory, monitoring, public education, research and collecting permits, curation, and criminal/civil prosecution associated with fossils from designated Department of Interior (DOI) lands. More information on laws, policies, and authorities governing NPS management of paleontological resources is detailed in Appendix G. Paleontological resource protection training is available for NPS staff through the NPS Paleontology Program. The Paleontology Program is also available to provide support in investigations involving paleontological resource theft or vandalism.

Between 2009 and 2022 an interagency coordination team including representatives from the Bureau of Land Management (BLM), Bureau of Reclamation (BOR), National Park Service (NPS) and U.S. Fish & Wildlife Service (FWS) developed the DOI final regulations for PRPA. The draft DOI regulations were published in the Federal Register in December 2016 and were available for 60 days to allow for public comment. The interagency team has reviewed public comments provided for the draft regulation and have incorporated these into the final regulation. The final regulation was surnamed by the DOI Solicitor's Office and each of the four bureau directors. On August 2, 2022, the DOI Paleontological Resources Preservation Act final regulation was published in the Federal Register. After 30 days the Office of Management and Budget approved the final DOI PRPA regulation, which is available at the following website: https://www.federalregister.gov/documents/2022/08/02/2022-16405/paleontological-resources-

preservation. For more information regarding this act, visit https://www.nps.gov/subjects/fossils/fossil-protection.htm.

2006 National Park Service Management Policies (section 4.8.2.1) state

> *... Paleontological resources, including both organic and mineralized remains in body or trace form, will be protected, preserved, and managed for public education, interpretation, and scientific research. The Service will study and manage paleontological resources in their paleoecological context (that is, in terms of the geologic data associated with a particular fossil that provides information about the ancient environment).*
>
> *Superintendents will establish programs to inventory paleontological resources and systematically monitor for newly exposed fossils, especially in areas of rapid erosion. Scientifically significant resources will be protected by collection or by on-site protection and stabilization. The Service will encourage and help the academic community to conduct paleontological field research in accordance with the terms of a scientific research and collecting permit. Fossil localities and associated geologic data will be adequately documented when specimens are collected. Paleontological resources found in an archeological context are also subject to the policies for archeological resources. Paleontological specimens that are to be retained permanently are subject to the policies for museum objects.*
>
> *The Service will take appropriate action to prevent damage to and unauthorized collection of fossils. To protect paleontological resources from harm, theft, or destruction, the Service will ensure, where necessary, that information about the nature and specific location of these resources remains confidential, in accordance with the National Parks Omnibus Management Act of 1998.*
>
> *All NPS construction projects in areas with potential paleontological resources must be preceded by a preconstruction surface assessment prior to disturbance. For any occurrences noted, or when the site may yield paleontological resources, the site will be avoided or the resources will, if necessary, be collected and properly cared for before construction begins. Areas with potential paleontological resources must also be monitored during construction projects.*

Fossils have scientific, aesthetic, cultural, educational, and tourism value, and impacts to any of these values impairs their usefulness. Effective paleontological resource management protects fossil resources by implementing strategies that mitigate, reduce, or eliminate loss of fossilized materials and their relevant data. Because fossils are representatives of adaptation, evolution, and diversity of life through deep time, they have intrinsic scientific value beyond just the physical objects themselves. Their geological and geospatial contexts provide additional critical data concerning paleoenvironmental, paleogeographic, paleoecologic, and a number of other conditions that together allow for a more complete interpretation of the physical and biological history of the earth.

Therefore, paleontological resource management must act to protect not only the fossils themselves, but to collect and maintain other contextual data as well.

In general, losses of paleontological resources result from naturally occurring physical processes, by direct or indirect human activities, or by a combination of both. These processes or activities influence the stability and condition of in situ paleontological resources (Santucci and Koch 2003; Santucci et al. 2009). The greatest loss of associated contextual data occurs when fossils are removed from their original geological context without appropriate documentation. Thus, when a fossil weathers and erodes from its surrounding sediments and geologic context, it begins to lose significant ancillary data until, at some point, it becomes more a scientific curiosity than a useful piece of scientific data. A piece of loose fossil "float" can still be of scientific value. However, when a fossil has been completely removed from its original context, such as an unlabeled personal souvenir or a specimen with no provenance information in a collection, it is of very limited scientific utility. Similarly, inadvertent exhumation of fossils during roadway construction or a building excavation may result in the loss or impairment of the scientific and educational values associated with those fossils. It is not necessary to list here all of the natural and anthropogenic factors that can lead to the loss of paleontological resources; rather it is sufficient to acknowledge that anything that disturbs native sediment or original bedrock has potential to result in the loss of the paleontological resources that occur there, or the loss of associated paleontological resource data.

Cave localities, such as abound at Mammoth Cave National Park (MACA), are in a distinct class for management due to the close connection with archeological resources and unique issues affecting cave resources. See Santucci et al. (2001) for additional discussion of paleontological resources in cave settings.

Management strategies to address any of these conditions and factors can also incorporate the assistance of qualified specialists to collect and document resources rather than relying solely on staff to accomplish such a large task. Active recruitment of paleontological research scientists should also be used as a management strategy.

MACA Paleontological Resource Inventory

Paleontological resource inventories compile baseline paleontological resource information and data on the scope, significance, distribution (both geospatial and temporal), and management issues associated with fossils. Paleontological resource inventories are specifically identified within the Paleontological Resource Preservation Act (2009). The MACA paleontological resource inventory was initiated in October 2019 as a collaboration between the park and the NPS Paleontology Program under a technical assistance request (TAR 12143). Previously, Quaternary paleontological resource inventories were undertaken at MACA by Mona Colburn (Illinois State Museum) and Rick Toomey (Colburn et al. 2000, 2015; Colburn 2005, 2006, 2017; Toomey et al. 1998, 2000). In 2009 a paleontological resource inventory for MACA and the other parks of the Cumberland Piedmont Inventory and Monitoring Network was published (Hunt-Foster et al. 2009). This network-based inventory was based primarily on a comprehensive literature review, museum collections inventory,

consultation with geologists and paleontologists who have worked in network parks, and review of park and NPS archives.

The paleontological resource inventory for MACA that was initiated in 2019 involved extensive field work, largely examining fossiliferous exposures within cave passages. The field team consisted of several park staff and volunteers who were experienced cavers, along with the staff of the NPS Paleontology Program. Paleontologist JP Hodnett (Maryland National Capital Parks and Planning Commission) was recruited to join the MACA paleontological resource inventory team given his specialization in Paleozoic chondrichthyans. Hodnett was instrumental is the discovery, collection, and identification of 82 different Mississippian chondrichthyans which were previously undocumented from MACA (see Chapter 7 for more information). Collectively the diversity of Mississippian sharks and related forms from MACA represent one of the richest assemblages documented from the Paleozoic of North America. To date, three new species of Mississippian sharks have been described and named from MACA (Hodnett et al. 2023, 2024a, 2024b). At least two potentially new species of sharks are being studied and manuscripts developed for future publication. Other specialists were recruited as new topics of interest were identified: paleobotanist Michael Donovan (Field Museum of Natural History) documented the Carboniferous plants (Chapter 4) and fossil echinoderm specialist William Ausich (The Ohio State University) did likewise for the blastoids, crinoids, and echinoids found in the Mississippian rocks (Chapter 6). Finally, long-time Mammoth Cave geology experts Arthur and Margaret Palmer contributed a geological description of the bedrock (Chapter 3).

The MACA paleontological resource inventory has spanned nearly five years with extensive inventory work in multiple caves and on the surface, rewarding the team with a wide variety of important and sometimes well-preserved fossil specimens from numerous locations (Figure 185). A large number of fossils were collected during this inventory and professionally cataloged by the park curator Terry Langford to support future research and public education.

The MACA paleontological resource inventory has captured considerable media and public attention with hundreds of articles published online. The new discoveries have been translated into new art by artists Julius Csotonyi and Benji Paysnoe to interpret the Mississippian fauna to enhance opportunities for public education by the park. A new exhibit featuring the paintings and fossil specimens was premiered at the Mammoth Cave Visitor Center on October 23, 2023, for National Fossil Day 2023.

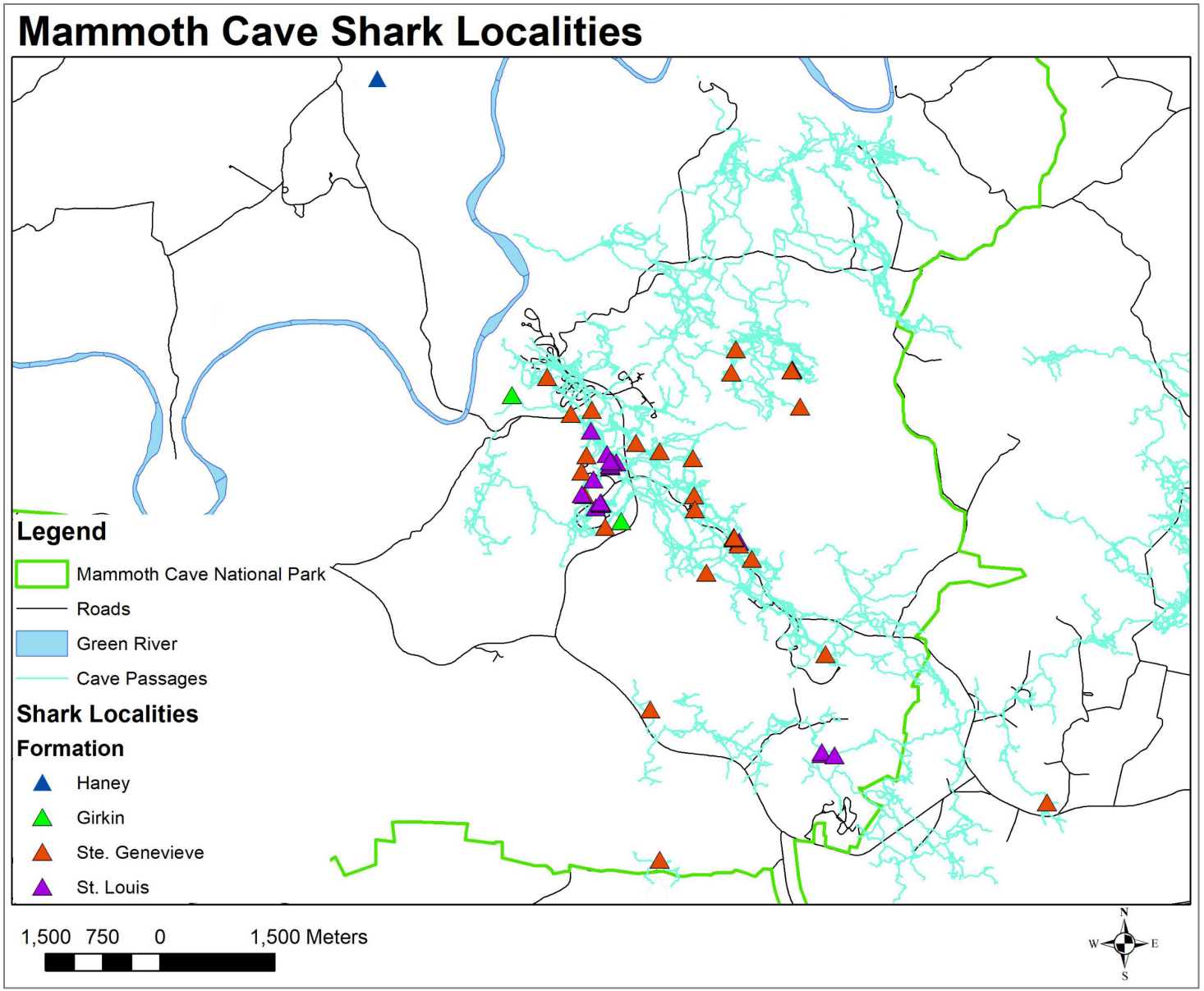


Figure 185. A map of fossil shark localities in MACA, with symbol colors indicating stratigraphy. NPS

MACA Paleontological Resource Monitoring

Paleontological resource monitoring is an important resource management tool for assessing the condition and stability of in situ fossils which are subjected to natural processes and human activities (Santucci and Koch 2003; Santucci et al. 2009). Paleontological resource monitoring is specifically identified within the Paleontological Resources Preservation Act (2009). Based on the rich and diverse paleontological resources documented during the recent MACA paleontological resource inventory, the park may consider developing a paleontological resource monitoring strategy. This planning can be accomplished through the support of the NPS Paleontology Program.

MACA Paleontological Resource Protection

No incidents of unauthorized fossil collection or paleontological resource crimes have been reported at MACA. However, the increased public awareness that has resulted from the recent media and scientific reporting on the new fossil discoveries at MACA may lead to new resource protection challenges for the park. The park may consider presenting paleontological resource protection training to the MACA law enforcement rangers to familiarize them with fossil crime activities and investigations.

MACA Paleontological Resource Research and Permits

Research Permits

Since the early 1990s, 25 permits have been issued for projects at MACA that were either paleontological in focus, or were a geological project with paleontological implications. They are listed below in chronological order by project. The permits issued in the 1990s may be over-counted or incomplete, as the research permitting system was different.

- MACA1991ABOP, principal investigator Arthur Palmer of State University College, project "*Geology of Mammoth Cave*", issued for 1991; this project was continued in 1992 under MACA1992ADAK (under similar title "*Geology of the Mammoth Cave System*"), 1994 under MACA1994AKVM, 1996 under MACA1996AQSQ, 1997 under MACA1997ATYB, 1998 under MACA1998PALM, 1999–2000 under MACA1999palmer, 2001 under MACA-2001-palmer, 2002–2003 under MACA-N-105, 2003–2008 under MACA-2003-SCI-0001, 2009–2014 under MACA-2009-SCI-0008, and 2015–2018 under MACA-2015-SCI-0023.
- MACA1994AKVR, principal investigator Patty Watson of Washington University, project "*Cave Research Foundation Archeological Project: Paleofeces Research Group*", issued for 1994; this project was archeological in intent, but may provide information on Holocene paleoecology of the MACA area.
- MACA1995ANJU, principal investigator Phillip Statler (Southeast Missouri State University), project "*Unusually Large Mississippian Burrow Structures In Mammoth Cave National Park: Enlargement By Chertification Or Preservation Of Original Size*", issued for 1995; this project was continued in 1996 under MACA1996AQST (under title "*A Possible New Genus of Paleozoic Large Burrow Traces in Mammoth Cave National Park: Evidence For Paleozoic Large-Burrow Diversity*").

- MACA1997ATXW, principal investigator Darryl Granger of Purdue University, project "*Age and Evolution of the Mammoth Cave System*", issued for 1997; this project was continued in 1998 under MACA1998GRAN and 1999 under MACA1999GRAN.
- MACA-1997-SCI-0001, principal investigator Rickard Toomey of the Illinois State Museum, project "*Conservation of Threatened Vertebrate Paleontological Resources at Mammoth Cave National Park*", issued for 1997–2001; this project was continued or done concurrently with MACA-2003-SCI-0009, principal investigator Mona Colburn of the Illinois State Museum, same title, issued for 1997–2004.
- MACA-2014-SCI-0015, principal investigator George Crothers of the University of Kentucky, project "*Radiocarbon determination of charcoal samples recovered during the 1960-1970s Salts Cave Vestibule excavations, Mammoth Cave National Park*", issued for 2014–2015.
- MACA-2018-SCI-0007, principal investigator Chris Smart of the University of Western Ontario, project "*Sedimentology and stratigraphy: Mammoth Cave*", issued for 2018.
- MACA-2019-SCI-0017, principal investigator John-Paul Hodnett of the Maryland-National Capital Park and Planning Commission, Department of Parks and Recreation, project "*Late Mississippian Chondrichthyans from Mammoth Cave National Park*", issued for 2019–2020; this project was continued 2021–2022 under MACA-2021-SCI-0003 and 2023–2025 under MACA-2023-SCI-0013.

MACA Paleontological Resource Curation and Museum Collections

Scope of Paleontological Collections

The MACA paleontology collections have grown considerably since the beginning of the recent paleontological resource inventory at the park in 2019. As of July 2024, the MACA museum collections include 1,015 records and 3,064 specimens pertaining to paleontology (Terry Langford, MACA, pers. comm., 2024). Fossil specimens in the MACA collections include a diversity of Carboniferous invertebrates, vertebrates, and plants, along with Quaternary vertebrates (Figures 186 to 188). Other fossil specimens from MACA are curated by at least six outside museum repositories; see below for a list. The park also has a small interpretive collection of fossils that are not formally cataloged.



Figure 186. A tray of fossils from MACA collections. NPS



Figure 187. Fossils collected during the MACA paleontological inventory. NPS



Figure 188. JP Hodnett examining MACA fossils. NPS

Holotype Fossil Specimens from MACA

As of July 2024, there are three fossil species named from specimens known to have been discovered within MACA (Table 21). Each species is a chondrichthyan and is based on material discovered during the field paleontological resource inventories at MACA that began in 2019. There are potentially two additional new fossil chondrichthyan species from MACA that are currently being studied for description.

There is also a holotype that potentially came from MACA before the park was established, but the locality information is too vague to be certain (Table 22). The rugose coral *Lithodrumus veryi* Greene (1904) is based on a specimen from the "St. Louis Group, (sub-carboniferous) four miles south-east of Mammoth Cave, Kentucky" (Greene 1904: 169). Based on the locality description the specimen may have been collected from a site now within the park, but this cannot be confirmed without additional information. Further complicating matters, the holotype has apparently been lost since at least the early 1940s per Easton (1943), which reported that it could not be located in the Greene

collection at the American Museum of Natural History (AMNH). The American Museum of Natural History is not the only place it could be, if it is still extant; Lane (1987) reports that the Greene collection, except for holotypes, was never catalogued by the AMNH and was donated to the National Museum of Natural History (USNM) in 1960, so if the *L. veryi* type had not been recognized as a type specimen, it may be at the USNM instead. Alternatively, Greene traded or sold specimens to other collectors (Lane 1987), so it is possible that this was the fate of the *L. veryi* type. Fortunately, Greene's description includes a photo of the type that should allow it to be recognized if it is ever located (see Figure 82 in Chapter 5). The photo shows it to be a distinctive "bouquet of horn corals" form that is abundant in the Beaver Bend Member of the Girkin Formation.

Table 21. Fossil taxa named from specimens found within MACA.

Taxon	Citation	Age, Formation	Type Specimen	Notes
Glikmanius careforum	Hodnett et al. 2024a	Mississippian, Ste. Genevieve	MACA 64335	Ctenacanthiform chondrichthyan
Strigilodus tollesonae	Hodnett et al. 2023	Mississippian, Ste. Genevieve	MACA 62166	Petalodont chondrichthyan
Troglocladodus trimblei	Hodnett et al. 2024a	Mississippian, Ste. Genevieve	MACA 62062	Ctenacanthiform chondrichthyan

Table 22. Fossil taxa named from specimens possibly found within MACA.

Taxon	Citation	Age, Formation	Type Specimen	Notes
Lithodrumus veryi	Greene 1904	Mississippian, Girkin	Lost (Easton 1943)	Rugose coral

Notable Contributors to Paleontological Collections

MACA has historically benefited from several paleontologists either working on staff or working closely with staff, resulting in important fossil collections from cave passages and surface exposures. In 1935 Dr. Erwin Robert Pohl was hired through the Civilian Conservation Corps to serve as a geologist at Mammoth Cave, and his fieldwork is captured in a handful of Weekly Activity Reports dating from July 15 to November 9, 1935 (Pohl 1935, 1970) (other reports have been lost). A large collection of Mississippian marine invertebrates and terrestrial plant fossils were collected by Pohl, including specimens of corals, bryozoans, brachiopods, trilobites, and echinoderms. Pohl produced a geologic map for the park and recognized the occurrence and utility of both marine and terrestrial fossils in the biostratigraphy of park strata. Zoologist and vertebrate paleontologist Claude Hibbard worked as a park naturalist in the run-up to the establishment of MACA, and park archives preserve a log of his activities between June 1, 1934 and August 22, 1935 (Hibbard 1935). Hibbard documented fossils and other natural history observations in his log, but only is known to have collected one fossil specimen in his work at Mammoth Cave, a bison tooth (KUVP 255) that he gave to the Museum of Natural History at his alma mater, the University of Kansas (see Figure 13 in Chapter 2). Paleontologist Ron Wilson from the University of Louisville worked in the park from 1978–1980 and collected many fossils from Mammoth Cave, Bedquilt Cave, Great Onyx Cave, and Proctor Cave. These fossil collections were reposited at the Carnegie Museum of Natural History (Wilson 1980). Vertebrate paleontologist Rick Toomey began working at MACA as a researcher in 1994, joined the park through a cooperative agreement in 2005, and was hired as a park employee in 2013. Rick has served as the long-term advocate for MACA paleontology and has helped to coordinate the paleontological resource inventory at MACA that began in 2019.

The Cave Research Foundation (CRF) has supported paleontological (and other research) at Mammoth Cave since 1957. Although exploration and survey of the cave are primary missions of CRF, they also carefully document fossils that are observed, provide support for teams working on paleontological studies (especially important for paleontologists who are not familiar with caves, or at least Mammoth Cave), and create maps that can be used to document paleontological finds. Paleontological work by Ron Wilson, Walter Johnson, Rick Toomey, Mona Colburn, and Tammy Eifert was notably assisted by CRF support. Both Ron Wilson and Rick Toomey went on to become presidents of CRF. Numerous significant fossils were first identified and documented during CRF survey work. One of these is the partial *Glikmanius* skull exposed beneath Marion Avenue that Walter Johnson noted on a survey trip in 1991 (see Figure 155 in Chapter 7). Another example is the *Arctodus* jaw found by a survey team in Proctor Cave in 1976 and collected by Ron Wilson with a CRF team in 1979 (see Figure 23 in Chapter 2 and Figure 177 in Chapter 8). In addition, Toomey and Colburn utilized both CRF teams and CRF base maps to make detailed maps of Quaternary vertebrate remains (Colburn 2005). The CRF trip report database contains numerous fossil observations. Hodnett et al. (2024a) named the shark *Glikmanius careforum* to honor CRF's contributions to paleontology at MACA.

Paleontological Collections in Outside Repositories

Fossils from MACA are confirmed to be reposited at six outside museum repositories: Carnegie Museum of Natural History (CM or CMNH; Pittsburgh, Pennsylvania); Cincinnati Museum Center

(CMC; Cincinnati, Ohio); Illinois State Museum (ISM; Springfield, Illinois); the Smithsonian's National Museum of Natural History (USNM; Washington, D.C.); University of Kansas Museum of Natural History (KU; Lawrence, Kansas); and Yale Peabody Museum of Natural History (YPM; New Haven, Connecticut). See Appendix H for external repository contact information. The most extensive fossil collections outside of the park museum are maintained at the CMNH and ISM, which host the Quaternary fossils recovered over the past few decades. KU is only known to hold the bison tooth mentioned above. The CMC, USNM, and YPM are only known to hold small numbers of invertebrate specimens. CMC collections include unidentified invertebrate specimens IP3166 and IP3167 from entrances to Mammoth Cave, as well as a former University of Minnesota specimen now on display and cataloged as CMC IP80689 that may have come from the park. USNM collections include USNM PAL 380837, an unusually complete and well-preserved specimen of the echinoid *Melonechinus indianensis* (see Figure 139C in Chapter 6). YPM collections from Mammoth Cave include an undetermined echinoderm (YPM IP 424686), an undetermined rugose coral (YPM 424702), and two *Pentremites* sp. blastoids (YPM IP 424703 and 424704).

MACA Paleontology Archives

The comprehensive paleontological resource inventory and associated research has significantly contributed to the discovery and organization of the MACA paleontology archives, such as field notes and maps from researchers early in park history and historic photographs. These digital and hardcopy records will be maintained both at the park and within the NPS Paleontology Archives and Library maintained by the NPS Paleontology Program.

MACA Paleontological Resource Interpretation, Education, and Outreach

The paleontological resource inventory at MACA has significantly expanded the park's understanding of the scope, significance, distribution (both geospatial and temporal), and the management issues associated with the park's fossils.

Current Long Range Interpretive Plan

MACA has a current Long-Range Interpretive Plan, but it does not address fossils or paleontology.

Current Paleontological Interpretive Programs

Ranger-Led Programs

Currently there is one ranger at MACA who presents an evening program on fossils. Occasionally a ranger will talk about fossils during a porch talk outside the MACA visitor center. Some of the park staff may talk about fossils during their cave tours. All paleontology programs developed by park rangers should instruct visitors on how to be paleontologically aware while in the park. The following topics should be highlighted when mentioning fossils in interpretive programs:

- When paleontologists survey for fossils, a geologic map is a vitally important tool. Paleontological resources are more common in certain geologic units, so knowing where those units are exposed is important for a successful survey. Other field paleontology tools include small picks and brushes, appropriate glues and consolidants, GPS, camera, topographic maps, and appropriate First Aid and safety equipment. It might be helpful to provide examples of these items for visitors during interpretive talks, if available.

- If a fossil is found in the park by a visitor, they should photograph it, note the location (by geospatial coordinates if possible), and notify a ranger of where the resource was found, but most importantly they should leave the fossil where they found it. It is extremely important for scientific and resource management purposes for original location information to be preserved. Visitors should be informed that park fossils are non-renewable resources that are protected by federal law (Paleontological Resources Preservation Act 2009).

Curriculum-Based Programs

MACA staff provide curriculum-based programs specifically tied to fossils and paleontology. As of July 2024, the park has provided 1,166 classroom visits working with more than 32,400 students this fiscal year. The topics of fossils and/or paleontology were the focus of presentations to 1,220 classroom students during 2024 (Jennifer Shackelford, MACA, pers. comm., July 2024). The park would like to obtain additional copies of the Junior Paleontologist activity booklets and badges for distribution to MACA visitors in the future.

Interpretive Signs and Exhibits

Permanent Signs and Exhibits

MACA currently has a number of wayside exhibits throughout the park that present interpretative information about park fossils. One of the most notable fossils on public exhibit is a fossil scale bark tree (*Lepidodendron*) specimen on display in the park's visitor center (Figure 189). This specimen is believed to have been discovered during the 1850s, and its history can be followed in various historic photos. A stereopair of photographs was produced for this specimen by Charles Waldack in 1866 (see Figure 5 in Chapter 2). The caption on the reverse of the stereopair photo reads "Curious Sand-stone Rock. Excavated near the cave about 15 years since, and now to be seen in the Hotel yard." Photos from the early years of the park show the *Lepidodendron* specimen on display in an outside exhibit (e.g., Figure 190 and Figure 6 in Chapter 2).



Figure 189. Detail of the Carboniferous *Lepidodendron* scale tree impression (MACA 2040) displayed in the park visitor center. NPS



Figure 190. The *Lepidodendron* block displayed on the park grounds, with a moveable informational placard. Caption on placard reads, "Natural impression of an ancient tree trunk. Eons ago forest trees of different types than those of to-day flourished in this district. One of those here represented toppling over was covered with sand making the mold(?) which has been preserved as the sand became rock. The imprint is that of a portion of the bark of a tree called Lepidodendron, a lycopod, and lived during Cypress time of the Mississippian period." NPS

New Fossil Artwork

Several original paintings depicting the Mississippian fauna discovered and documented at MACA were produced during the paleontological resource inventory to support interpretation and outreach, and for use in exhibits and media. Artist Julius Csotonyi created a painting that includes the diverse marine invertebrates and chondrichthyans that have been documented from MACA's Mississippian strata; a version has been annotated with taxonomic identifications to be used on a park website (https://www.nps.gov/subjects/fossils/paleontological-discoveries-at-mammoth-cave.htm) (Figure 191; see the cover of this document for the unannotated version). Artist Benji Paysnoe created two paintings depicting three new sharks discovered, described, and named from MACA. The first painting features a Mississippian petalodont shark (*Strigilodus tollesonae*) from the Joppa Member of the Ste. Genevieve Formation named in honor of Kelli Tolleson, MACA park guide and cave explorer who helped locate new fossil shark localities in Mammoth Cave (Hodnett et al. 2023) (Figure 192). The second painting by Paysnoe features two new ctenacanthiform sharks from the Joppa Member: *Glikmanius careforum*, named in honor of the Cave Research Foundation; and

Troglocladodus trimblei, named in honor of MACA superintendent Barclay Trimble, who discovered the holotype specimen (Hodnett et al. 2024a) (Figure 193).

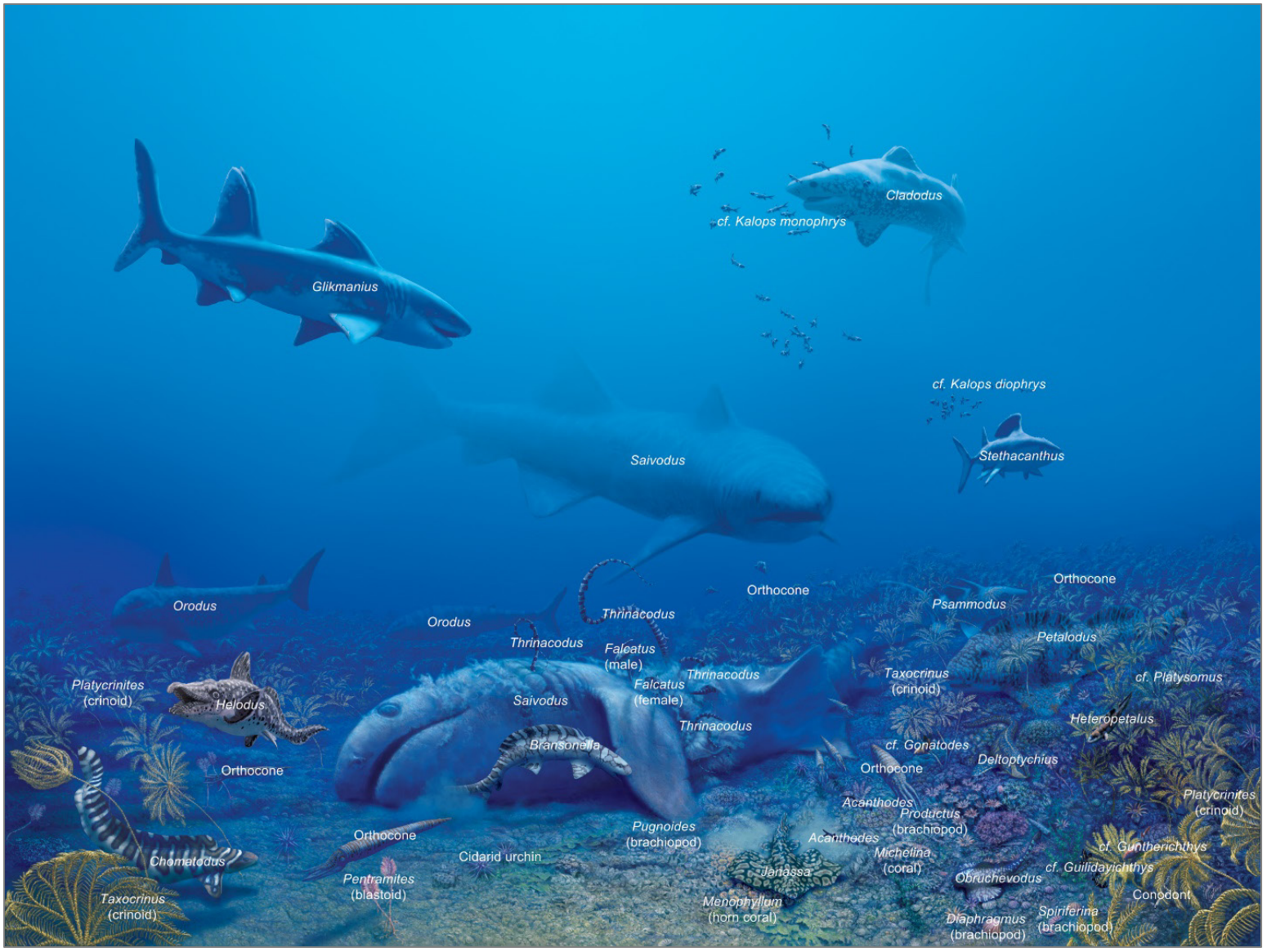


Figure 191. Painting depicting Mississippian marine fauna from Mammoth Cave National Park, Kentucky, with taxonomic identifications added (some identifications may have changed since the annotations were made). NPS / JULIUS CSOTONYI



Figure 192. Painting of the petalodont shark *Strigilodus tollesonae* based on specimens discovered at MACA. NPS / BENJI PAYSNOE



Figure 193. Painting of the ctenacanth sharks *Glikmanius careforum* (foreground) and *Troglocladodus trimblei* (background) based on specimens discovered at MACA. NPS / BENJI PAYSNOE

Interpretive Handouts, Site Bulletins, Brochures, and Websites

The park has a handout on the geology of Mammoth Cave to share with interested visitors that includes basic information on fossils. Park staff have recently updated the park's website to include information on the fossil discoveries made during the MACA paleontological resource inventory. The website address is: https://www.nps.gov/maca/learn/nature/fossils.htm.

The Prehistoric Life in the National Parks Coloring Book (https://www.nps.gov/subjects/fossils/coloring-book.htm; https://irma.nps.gov/DataStore/Reference/Profile/2279035), produced by the NPS Paleontology Program in 2020, features an illustration of the Mississippian shark *Saivodus striatus* from MACA that was prepared by artist Benji Paysnoe (Figure 194).

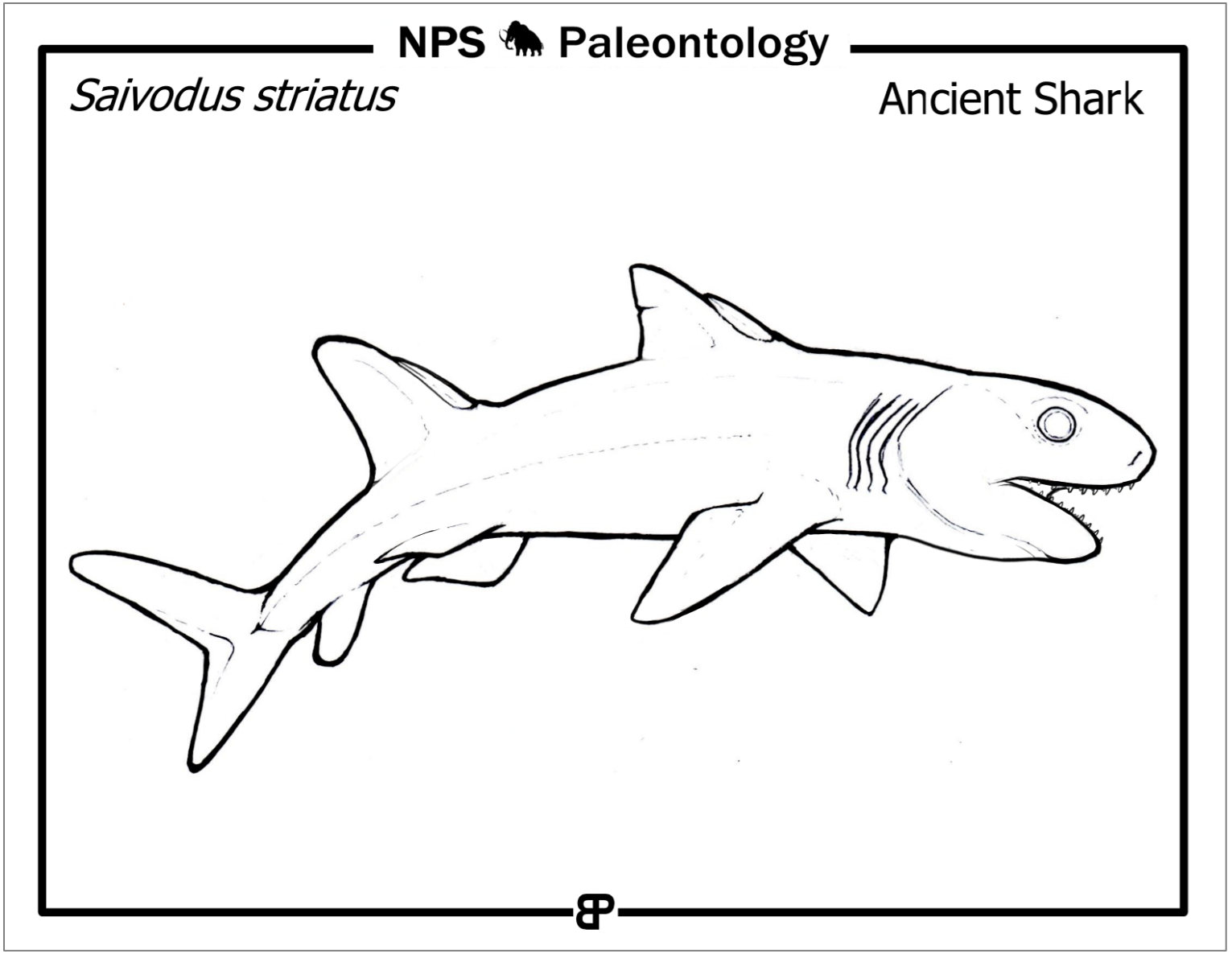


Figure 194. Coloring book illustration of Mississippian shark *Saivodus striatus*, based on MACA specimens. NPS / BENJI PAYSNOE

Interpretive Fossil Collection

The park maintains a small interpretive fossil collection used for public education and outreach. This collection was donated to the park from Western Kentucky University and is not formally cataloged into the MACA museum collection.

Interpretive Staff Training and Resources

Paleontological Resource Training

MACA does not currently provide any formal staff training in paleontology. However, there has been increased communication about paleontological resources among park staff due to the increased awareness and interest associated with the fossil discoveries that have been documented through the park's paleontological resource inventory.

National Fossil Day Event

National Fossil Day is an annual event that takes place nationwide on the Wednesday of the second full week in October, and is scheduled as part of Earth Science Week. The NPS Geologic Resources Division assists parks with planning and coordination for National Fossil Day activities and provides Junior Paleontologist Activity Program supplies including activity booklets, badges, posters, and other fossil-related educational resources. Contact Vincent Santucci for more details (vincent_santucci@nps.gov).

MACA hosted its first National Fossil Day event in 2021. The 2023 National Fossil Day logo featured Mississippian marine fossils from MACA (Figure 195). The park hosted a public event for National Fossil Day on October 23, 2023. Park visitors were provided opportunities to meet with park rangers and paleontologists to discuss and view fossils from MACA. Several porch talks were presented on various topics related to the fossil record from MACA (Figures 196 and 197). At the 2023 National Fossil Day event at MACA, a new exhibit was dedicated featuring some of the recently discovered fossils and the new artwork produced by Julius Csotonyi (Figure 198).

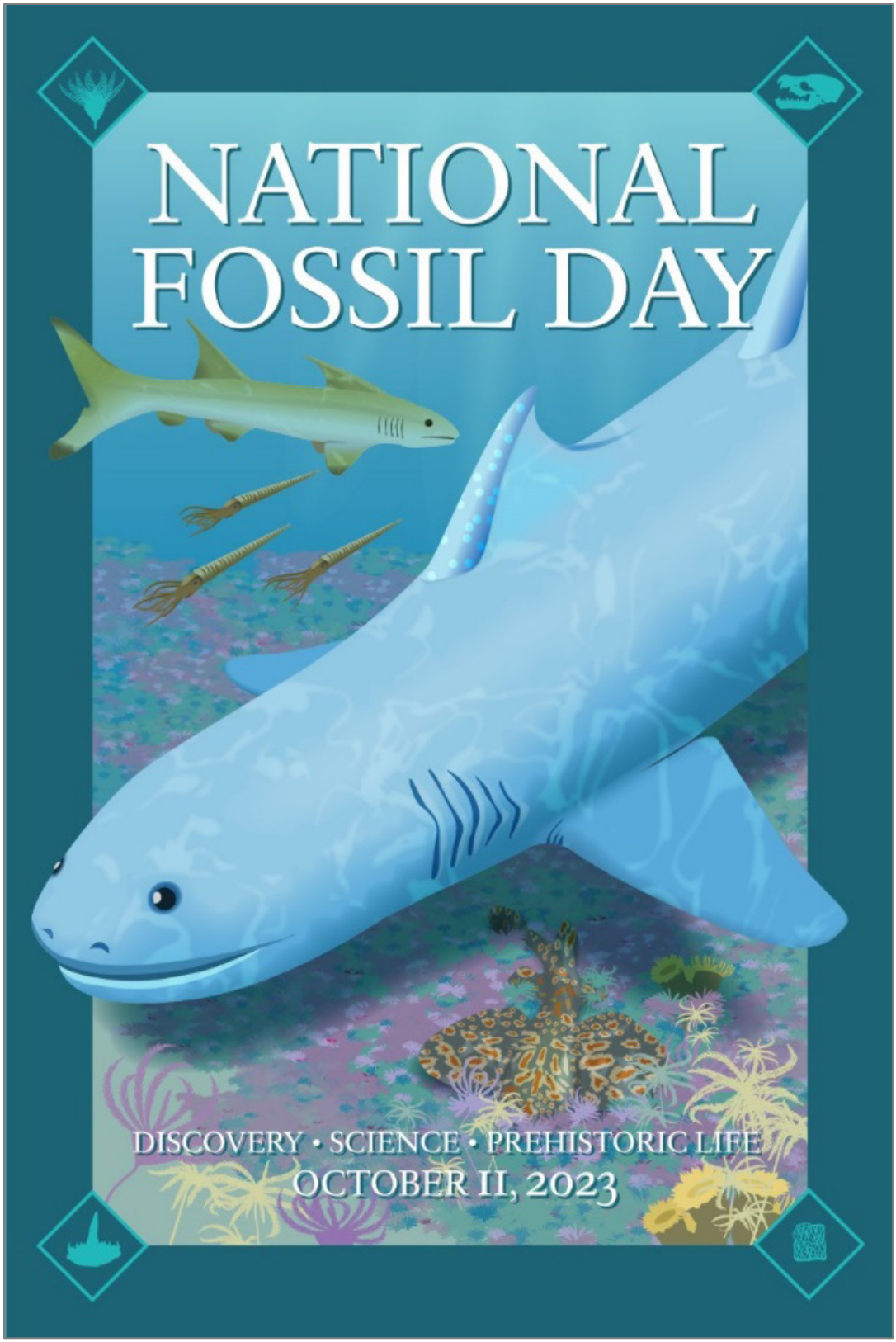


Figure 195. 2023 National Fossil Day annual logo artwork featuring Mississippian marine fauna from Mammoth Cave National Park, Kentucky. NPS / STUDIO 105



Figure 196. MACA cave resource specialist and paleontologist Rickard Toomey III presenting to the public during the 2023 National Fossil Day event hosted at MACA on October 23, 2023. NPS



Figure 197. Paleontologist JP Hodnett presenting to the public during the 2023 National Fossil Day event hosted at MACA on October 23, 2023. NPS

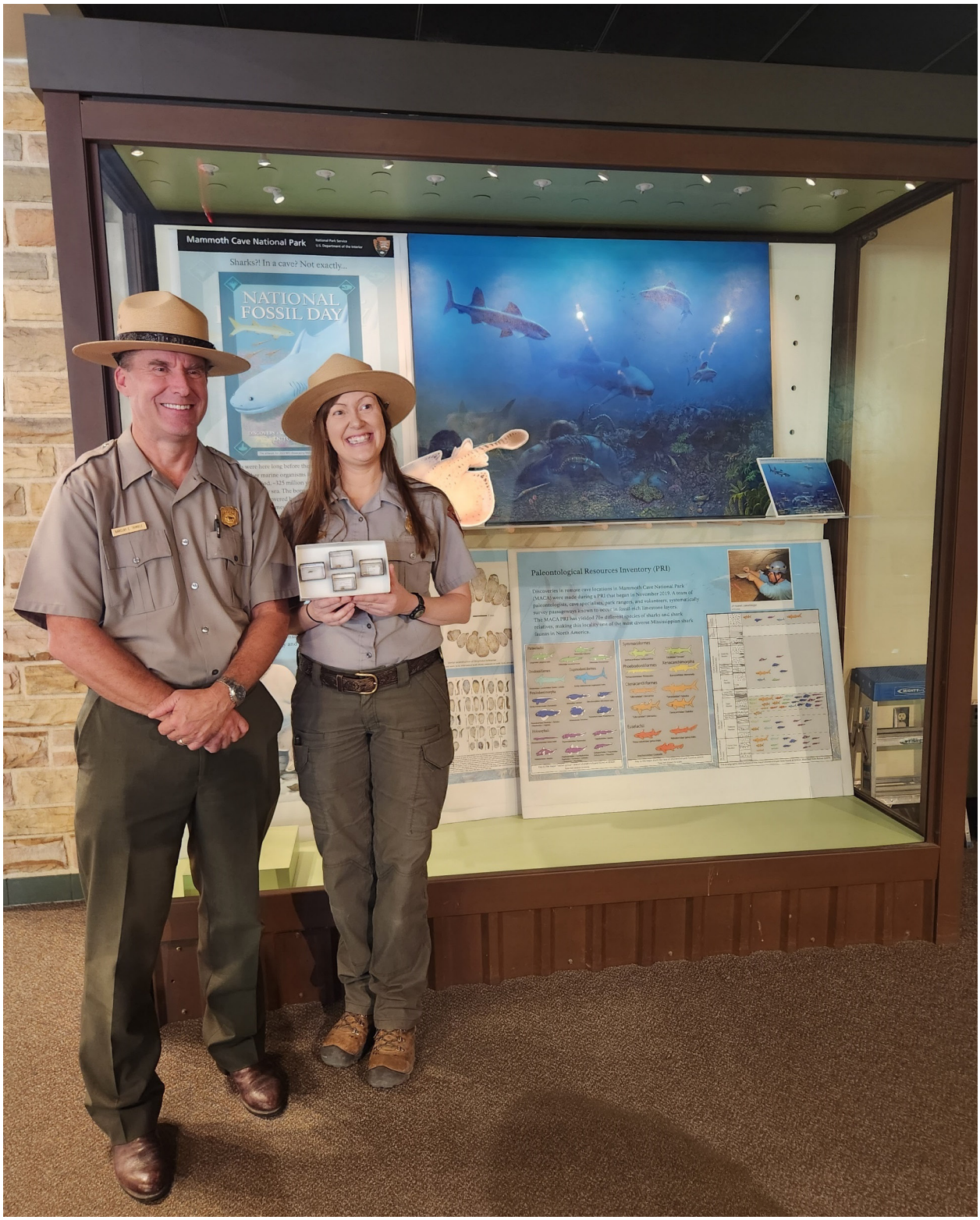


Figure 198. MACA superintendent Barclay Trimble and MACA park ranger Kelli Tolleson, honored in new species named from the park, show fossils in front of the new park paleontology exhibit at the 2023 National Fossil Day event. NPS

MACA Paleontological Resource Data Management

The Paleontological Resources Preservation Act (PRPA) mandates the management of fossils and associated data using scientific principles and expertise. MACA has facilitated paleontological research even before its designation as a National Park more than 80 years ago, leading to a wealth of data and resources that need to be properly managed. Information regarding paleontological resources at MACA, such as field notes, publications, and paleontology locality datasheets, are managed in the park's internal network. Field data collected at paleontological sites and localities are maintained within a geospatial database. The NPS Paleontology Program's archives have a copy of all of these MACA paleontological resource archives, records, and files. These databases and archives have been fully updated as part of the 2019 Paleontology Inventory.

MACA Paleontology Archives

MACA maintains a paleontology archive and library to organize all documents related to paleontology resources at the park. Items such as field notes, publications, historic photos, maps, research permits, and museum collection documents can be found within the archives.

Due to the sensitive nature of paleontological resources, paleontology archives are restricted access only. To request access to information within the archives, contact Rick Toomey (rick_toomey@nps.gov).

NPS Paleontology Program Archives (WASO)

The National Park Service Paleontology Program (WASO) maintains a copy of all digital and hardcopy field notes, sketches, photographs, maps, reports, publications, and lists of archived fossil specimens at MACA. This redundancy ensures the safety of paleontological resource data in the event either MACA or WASO archives are lost. To request access to materials in the WASO Paleontology Archives contact Vincent Santucci (vincent_santucci@nps.gov) or Justin Tweet (justin_tweet@nps.gov). See Santucci et al. (2018) for more information on the Paleontology Program's archives.

E&R Files

E&R files (from "Examination and Report on Referred Fossils") are unpublished internal USGS documents. For more than a century, USGS paleontologists identified and prepared informal reports on fossils sent to the survey by other geologists, for example to establish the relative age of a formation or to help correlate beds. The system was eventually formalized as a two-part process including a form sent by the transmitting geologist and a reply by the survey geologist. Sometimes the fossil identifications were incorporated into publications, but in many cases this information is unpublished. These E&R files include documentation of numerous fossil localities within current NPS areas, usually predating the establishment of the NPS unit in question and frequently unpublished or previously unrecognized. Extensive access to the original files was granted to the NPS by the USGS beginning in 2014 (Santucci et al. 2014). No E&R files are known for MACA at this time.

Conclusions

As illustrated in the chapters of this paleontological resource inventory report, MACA preserves a diverse and scientifically important fossil record. The establishment of comprehensive baseline data enhances opportunities for paleontological resource stewardship and science at MACA. Collectively, the paleontology-focused projects undertaken and accomplishments achieved at MACA represent the largest effort for paleontology in the park's history. This unprecedented work will help guide and inform future paleontological resource planning and activities for not only MACA, but other NPS areas. The MACA paleontological resource inventory provides the essential foundation for current and future park leaders to ensure that the non-renewable paleontological resources at MACA will continue to be monitored, conserved, and protected into the future.

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Appendix G: Paleontological Resource Law and Policy

The following material is reproduced in large part from Henkel et al. (2015); see also Kottkamp et al. (2020).

In March 2009, the Paleontological Resources Preservation Act (PRPA) (16 USC 460aaa) was signed into law (Public Law 111–11). This act defines paleontological resources as

> *…any fossilized remains, traces, or imprints of organisms, preserved in or on the [E]arth's crust, that are of paleontological interest and that provide information about the history of life on [E]arth.*

The law stipulates that the Secretary of the Interior should manage and protect paleontological resources using scientific principles. The Secretary should also develop plans for

> *…inventory, monitoring, and deriving the scientific and educational use of paleontological resources.*

Paleontological resources are considered park resources and values that are subject to the "no impairment" standard in the National Park Service Organic Act (1916). In addition to the Organic Act, PRPA will serve as a primary authority for the management, protection, and interpretation of paleontological resources. The proper management and preservation of these non-renewable resources should be considered by park resource managers whether or not fossil resources are specifically identified in the park's enabling legislation.

The Paleontological Resources Management section of NPS Reference Manual 77 provides guidance on the implementation and continuation of paleontological resource management programs. Administrative options include those listed below and a park management program will probably incorporate multiple options depending on specific circumstances:

- **No action**—no action would be taken to collect the fossils as they erode from the strata. The fossils would be left to erode naturally and over time crumble away, or possibly be vandalized by visitors, either intentionally or unintentionally. This is the least preferable plan of action of those listed here.
- **Surveys**—will be set up to document potential fossil localities. All sites will be documented with the use of GPS and will be entered into the park GIS database. Associated stratigraphic and depositional environment information will be collected for each locality. A preliminary fossil list will be developed. Any evidence of poaching activity will be recorded. Rates of erosion will be estimated for the site and a monitoring schedule will be developed based upon this information. An NPS Paleontological Locality Database Form will also be completed for each locality. A standard version of this form will be provided by the Paleontology Program of the Geologic Resources Division upon request and can be modified to account for local conditions and needs.
- **Monitoring**—fossil-rich areas would be examined periodically to determine if conditions have changed to such an extent that additional management actions are warranted. Photographic records should be kept so that changes can be more easily ascertained.
- **Cyclic prospecting**—areas of high erosion which also have a high potential for producing significant specimens would be examined periodically for new sites. The periodicity of such cyclic prospecting will depend on locality-specific characteristics such as rates of sediment erosion, abundance or rarity of fossils, and proximity to visitor use areas.

- **Stabilization and reburial**—significant specimens which cannot be immediately collected may be stabilized using appropriate consolidants and reburied. Reburial slows down but does not stop the destruction of a fossil by erosion. Therefore, this method would be used only as an interim and temporary stop-gap measure. In some situations, stabilization of a locality may require the consideration of vegetation. For example, roots can destroy in situ fossils, but can also protect against slope erosion, while plant growth can effectively obscure localities, which can be positive or negative depending on how park staff want to manage a locality.
- **Shelter construction**—it may be appropriate to exhibit certain fossil sites or specimens in situ, which would require the construction of protective shelters to protect them from the natural forces of weathering and erosion. The use of shelters draws attention to the fossils and increases the risk of vandalism or theft, but also provides opportunities for interpretation and education.
- **Excavation**—partial or complete removal of any or all fossils present on the surface and potentially the removal of specimens still beneath the surface which have not been exposed by erosion.
- **Closure**—the area containing fossils may be temporarily or permanently closed to the public to protect the fossil resources. Fossil-rich areas may be closed to the public unless accompanied by an interpretive ranger on a guided hike.
- **Patrols**—may be increased in areas of known fossil resources. Patrols can prevent and/or reduce theft and vandalism. The scientific community and the public expect the NPS to protect its paleontological resources from vandalism and theft. In some situations, a volunteer site stewardship program may be appropriate (for example the "Paleo Protectors" at Chesapeake & Ohio Canal National Historical Park).
- **Alarm systems/electronic surveillance**—seismic monitoring systems can be installed to alert rangers of disturbances to sensitive paleontological sites. Once the alarm is engaged, a ranger can be dispatched to investigate. Motion-activated cameras may also be mounted to visually document human activity in areas of vulnerable paleontological sites.

National Park Service Management Policies (2006; Section 4.8.2.1) also require that paleontological resources, including both organic and mineralized remains in body or trace form, will be protected, preserved, and managed for public education, interpretation, and scientific research. In 2010, the National Park Service established National Fossil Day as a celebration and partnership organized to promote public awareness and stewardship of fossils, as well as to foster a greater appreciation of their scientific and educational value (https://www.nps.gov/subjects/fossilday/index.htm). National Fossil Day occurs annually on Wednesday during the second full week in October in conjunction with Earth Science Week.

Related Laws, Legislation, and Management Guidelines

National Park Service Organic Act
The NPS Organic Act directs the NPS to manage units

> *…to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner as will leave them unimpaired for the enjoyment of future generations. (16 U.S.C. § 1).*

Congress reiterated this mandate in the Redwood National Park Expansion Act of 1978 by stating that the NPS must conduct its actions in a manner that will ensure no

> *…derogation of the values and purposes for which these various areas have been established, except as may have been or shall be directly and specifically provided by Congress. (16 U.S.C. § 1 a-1).*

The Organic Act prohibits actions that permanently impair park resources unless a law directly and specifically allows for the acts. An action constitutes an impairment when its impacts

> *…harm the integrity of park resources or values, including the opportunities that otherwise would be present for the enjoyment of those resources and values. (Management Policies 2006 1.4.3).*

Paleontological Resources Protection Act (P.L. 111-011, Omnibus Public Land Management Act of 2009, Subtitle D)
Section 6302 states

> *The Secretary (of the Interior) shall manage and protect paleontological resources on Federal land using scientific principles and expertise. The Secretary shall develop appropriate plans for inventory, monitoring, and the scientific and educational use of paleontological resources, in accordance with applicable agency laws, regulations, and policies. These plans shall emphasize interagency coordination and collaborative efforts where possible with non-Federal partners, the scientific community, and the general public.*

Federal Cave Resources Protection Act of 1988 (16 USC 4301)
This law provides a legal authority for the protection of all cave resources on NPS and other federal lands. The definition for "Cave Resource" in Section 4302 states

> *Cave resources include any material or substance occurring naturally in caves on Federal lands, such as animal life, plant life, paleontological deposits, sediments, minerals, speleogens, and speleothems.*

NPS Management Policies 2006
NPS Management Policies 2006 include direction for preserving and protecting cultural resources, natural resources, processes, systems, and values (National Park Service 2006). It is the goal of the

NPS to avoid or minimize potential impacts to resources to the greatest extent practicable consistent with the management policies. The following is taken from section 4.8.2.1 of the NPS Management Policies 2006, "Paleontological Resources and their contexts":

> *Paleontological resources, including both organic and mineralized remains in body or trace form, will be protected, preserved, and managed for public education, interpretation, and scientific research. The Service will study and manage paleontological resources in their paleoecological context (that is, in terms of the geologic data associated with a particular fossil that provides information about the ancient environment).*
>
> *Superintendents will establish programs to inventory paleontological resources and systematically monitor for newly exposed fossils, especially in areas of rapid erosion. Scientifically significant resources will be protected by collection or by on-site protection and stabilization. The Service will encourage and help the academic community to conduct paleontological field research in accordance with the terms of a scientific research and collecting permit. Fossil localities and associated geologic data will be adequately documented when specimens are collected. Paleontological resources found in an archeological context are also subject to the policies for archeological resources. Paleontological specimens that are to be retained permanently are subject to the policies for museum objects.*
>
> *The Service will take appropriate action to prevent damage to and unauthorized collection of fossils. To protect paleontological resources from harm, theft, or destruction, the Service will ensure, where necessary, that information about the nature and specific location of these resources remains confidential, in accordance with the National Parks Omnibus Management Act of 1998.*
>
> *Parks will exchange fossil specimens only with other museums and public institutions that are dedicated to the preservation and interpretation of natural heritage and qualified to manage museum collections. Fossils to be deaccessioned in an exchange must fall outside the park's scope of collection statement. Systematically collected fossils in an NPS museum collection in compliance with 36 CFR 2.5 cannot be outside the scope of the collection statement. Exchanges must follow deaccession procedures in the Museum Handbook, Part II, chapter 6.*
>
> *The sale of original paleontological specimens is prohibited in parks.*
>
> *The Service generally will avoid purchasing fossil specimens. Casts or replicas should be acquired instead. A park may purchase fossil specimens for the park museum collection only after making a written determination that*
>
> - *The specimens are scientifically significant and accompanied by detailed locality data and pertinent contextual data;*

- *The specimens were legally removed from their site of origin, and all transfers of ownership have been legal;*
- *The preparation of the specimens meets professional standards;*
- *The alternatives for making these specimens available to science and the public are unlikely;*
- *Acquisition is consistent with the park's enabling legislation and scope of collection statement, and acquisition will ensure the specimens' availability in perpetuity for public education and scientific research.*

All NPS construction projects in areas with potential paleontological resources must be preceded by a preconstruction surface assessment prior to disturbance. For any occurrences noted, or when the site may yield paleontological resources, the site will be avoided or the resources will, if necessary, be collected and properly cared for before construction begins. Areas with potential paleontological resources must also be monitored during construction projects.

(See Natural Resource Information 4.1.2; Studies and Collections 4.2; Independent Research 5.1.2; and Artifacts and Specimens 10.2.4.6 in NPS 2006, available here. Also see 36 CFR 2.5.)

NPS Director's Order-77, Paleontological Resources Management

DO-77 describes fossils as non-renewable resources and identifies the two major types, body fossils and trace fossils. It describes the need for managers to identify potential paleontological resources using literature and collection surveys, identify areas with potential for significant paleontological resources, and conduct paleontological surveys (inventory). It also describes appropriate actions for managing paleontological resources including: no action, monitoring, cyclic prospecting, stabilization and reburial, construction of protective structures, excavation, area closures, patrols, and the need to maintain confidentiality of sensitive location information.

Excerpt from Clites and Santucci (2012):

Monitoring

An important aspect of paleontological resource management is establishing a long-term paleontological resource monitoring program. National Park Service paleontological resource monitoring strategies were developed by Santucci et al. (2009). The park's monitoring program should incorporate the measurement and evaluation of the factors stated below.

Climatological Data Assessments

These assessments include measurements of factors such as annual and storm precipitation, freeze/thaw index (number of 24-hour periods per year where temperature fluctuates above and below 32 degrees Fahrenheit), relative humidity, and peak hourly wind speeds.

Rates of Erosion Studies

These studies require evaluation of lithology, slope degree, percent vegetation cover, and rates of denudation around established benchmarks. If a park does not have this information, there may be opportunities to set up joint projects, because erosion affects more than just paleontological resources.

Assessment of Human Activities, Behaviors, and Other Variables
These assessments involve determining access/proximity of paleontological resources to visitor use areas, annual visitor use, documented cases of theft/vandalism, commercial market value of the fossils, and amount of published material on the fossils.

Condition Assessment and Cyclic Prospecting
These monitoring methods entail visits to the locality to observe physical changes in the rocks and fossils, including the number of specimens lost and gained at the surface exposure. Paleontological prospecting would be especially beneficial during construction projects or road repair.

Periodic Photographic Monitoring
Maintaining photographic archives and continuing to photo-document fossil localities from established photo-points enables visual comparison of long-term changes in site variables.

Appendix H: Repository Contact Information

Contact information for institutions known to have collections from MACA is included below. Addresses, links, and email addresses to departments are included as available. This information is subject to change, particularly hyperlinks.

CARNEGIE MUSEUM OF NATURAL HISTORY
4400 Forbes Ave.
Pittsburgh, PA 15213
(412) 622-3131
https://carnegiemnh.org/

CINCINNATI MUSEUM CENTER
1301 Western Ave.
Cincinnati, OH 45203
(513) 287-7000
https://www.cincymuseum.org/
information@cincymuseum.org

ILLINOIS STATE MUSEUM
502 S. Spring St.
Springfield, IL 62706
(217) 782-0979
https://www.illinoisstatemuseum.org/

PEABODY MUSEUM OF NATURAL HISTORY AT YALE UNIVERSITY
P.O. Box 208118
170 Whitney Ave.
New Haven, CT 06520
(203) 432-5050
https://peabody.yale.edu/
peabody.collections@yale.edu

SMITHSONIAN INSTITUTION, NATIONAL MUSEUM OF NATURAL HISTORY
Department of Paleobiology
P.O. Box 37012
NHB MRC 121
Washington, D.C. 20013
https://naturalhistory.si.edu/research/paleobiology
paleodept@si.edu

UNIVERSITY OF KANSAS
KU Biodiversity Institute & Natural History Museum
1345 Jayhawk Blvd.
Lawrence, KS 66045
https://biodiversity.ku.edu/
biodiversity@ku.edu

Appendix I: Geologic Time Scale

A geologic time scale (Figure 199) is provided below for reference.

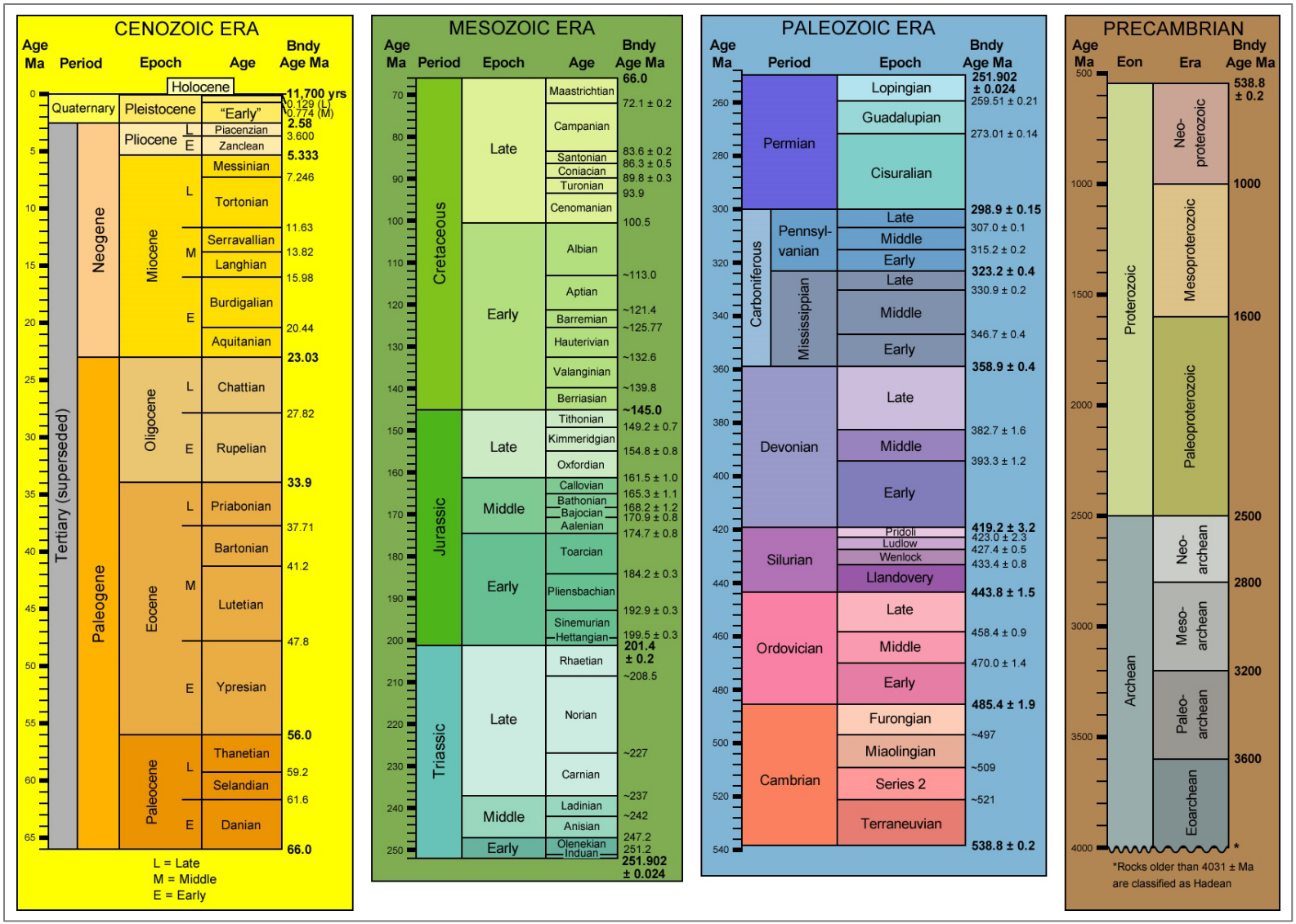


Figure 199. Geologic time scale**. Ma**=Millions of years old. **Bndy Age**=Boundary Age. Layout after 1999 Geological Society of America Time Scale (https://rock.geosociety.org/net/documents/gsa/timescale/timescl-1999.pdf). Dates after International Commission on Stratigraphy version 2023/09. NPS / JUSTIN TWEET

National Park Service
U.S. Department of the Interior

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