Sharks in the dark: Paleontological resource inventory reveals multiple successive Mississippian Subperiod cartilaginous fish (Chondrichthyes) assemblages within Mammoth Cave National Park, Kentucky

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ABSTRACT

A focused search for ancient Mississippian Subperiod marine vertebrates during a paleontological resource inventory of Mammoth Cave National Park, Kentucky, has yielded a wealth of new fossil data, previously unrecognized at this park. To date, we have identified marine vertebrate fossils from four primary horizons at the park, two of which are the first records of marine vertebrate fossils occurring in those horizons. Mammoth Cave sites have produced more than 70 species of ancient fish, about 90% representing cartilaginous fishes (sharks and kin), including several new species. The paleontological resource inventory of Mammoth Cave demonstrates that this park is an important resource for providing data on how fish assemblages changed during the formation of the super-continent Pangea. The inventory data also can help correct antiquated information on fossil sharks found in the region (in some cases not updated since their publication in the late 19th century).

INTRODUCTION

Mammoth Cave National Park (MACA), in central Kentucky, is home to the longest cave system in the world (Palmer 1981). To date, more than 426 miles of passageways have been mapped within the 52,830 acres that form the park. In addition, there are over 500 smaller caves within the park boundary. These cave passages were formed through dissolution by underground rivers, streams, and other drainages that cut through a series of limestones, capped by a resistant sandstone, that date to the Middle and Late Mississippian Period, approximately 340 to 325 million years ago. These passages opened a unique view of these limestones, which are time capsules holding a wealth of information on the ancient marine environments of their deposition. Invertebrate fossils from these beds such as

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horn corals, fan-like bryozoans, brachiopods, gastropods, shelled cephalopods, and a diverse array of echinoderms have been found throughout the various formations that form the cave (Palmer 1981).

Some of the earliest fossil observations from Mammoth Cave date to 1832, when naturalist Constantine Samuel Rafinesque commented on the occurrences of corals (Rafinesque 1832). Pleistocene vertebrate fossils have also been well documented at MACA, which represent records of ancient animals entering or being transported into the cave after its formation (Colburn 2017; O'Connor Olson 2017). Extinct Pleistocene mammals such as mastodon, sabertoothed cat, giant short face bear, horse, tapir, peccary, and vampire bat have been found in many passages within MACA (Colburn 2005 and 2017). Concerning vertebrate fossils from the Mississippian Subperiod at MACA, early records are sparse. Communications in 1937 between W.W. Thompson, general manager of Mammoth Cave (before it became a national park in 1941), and University of Chicago geology professor J. Harlen Bretz established the presence of an isolated shark fin spine from an undisclosed section of Mammoth Cave. Bretz identified the spine as belonging to "*Ctenacanthus*," a common identification of shark spines found during the Mississippian. The fate of this spine is unclear, as it is not in the MACA museum collections. Other chondrichthyan (cartilaginous fishes) fossils from Mammoth Cave were known to park staff, including rare skeletal cartilage of chondrichthyans found in a few cave passages during the 1990s. In 2018, photos of these cartilages were sent to two of the authors of the present paper (VLS and JPH). They concluded that these shark fossils were of major significance and that a Paleontological Resource Inventory (PRI) was necessary to assess the extent of the record and support the identification of MACA's ancient sharks.

Consequently, the PRI began in 2019 and to this day continues identifying new occurrences of Mississippian Period chondrichthyans throughout the park, both in the main Mammoth Cave system and from smaller isolated caves. Our inventory focusing on fossil chondrichthyans at MACA has revealed a wealth of information, not only providing new data on previously known ancient sharks, but also records of new species and the evidence of faunal transitions over time within a small geographic region. Here we present a condensed summary of the PRI's results so far.

INVENTORY METHODS

Typical fieldwork in paleontology requires a variety of field tools (hammers, chisels, picks, etc.) and packing materials (collection bags, paper towels, small containers, etc.) appropriate to the geology and fossils, as well as water supplies, food, and miscellaneous items, all of which are carried in large field backpacks for long periods in open-air localities. However, cave paleontology has much different requirements for logistics. The closed environment of caves requires careful consideration and planning for traversing, putting tight limits on what can be carried as field gear and collecting supplies. The majority of the shark fossil sites at MACA are well away from public passageways (Figure 1). Many of these cave sites have low ceilings, requiring crawling for long distances on hands and knees, and at times, belly crawling. Some underground stream passages require inflatable kayaks and wetsuits that need to be carried down to the launch sites (Figures 1A and 1B). These kayaks are used to traverse long stretches of deep water to access fossil sites. Rappelling by rope can also be necessary to access cave passages, sometimes down long, narrow boreholes (Figure 1E). Field packs for cave paleontology tend to be smaller than for open-air collecting, with collecting tools usually limited to small hammers, chisels, and dental picks, and small portable battery-powered diamond-bladed rock saws (Figure 1D). At times gear will be split up between the field team to reduce weight and increase space in field bags.

To protect the fossils for the return to the surface, each one is wrapped in a soft material (such as paper towels or toilet paper) and placed 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

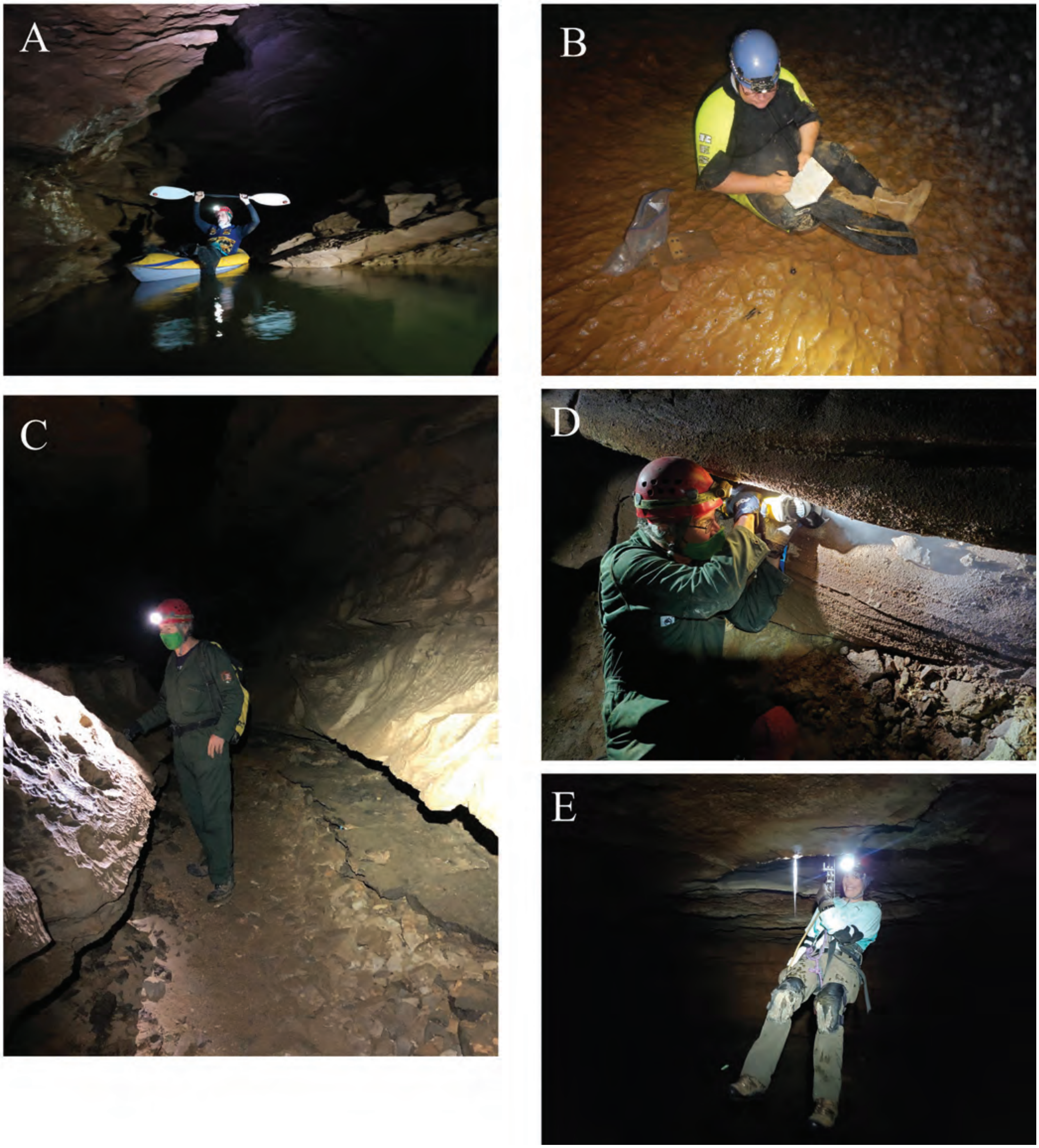


FIGURE 1. Paleontological fieldwork within Mammoth Cave National Park, Kentucky. (A) Rick Olson using a kayak to traverse underground rivers to document and collect chondrichthyan fossils from the St. Louis Formation. (B) JP Hodnett collecting data of chondrichthyan fossils on a cave floor in the St. Louis Formation. (C) Rick Toomey checking along cave passages for exposed fossils. (D) Rick Toomey using a portable diamond-bladed saw to extract a chondrichthyan tooth in the Ste. Genevieve Formation. (E) Kelly Tolleson descending by rope through a drill borehole to access a passage in the St. Louis Formation.

all but one cotton ball, carefully tease the fossil from the cave surface (often from the cave ceiling) 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 sampling of micro-vertebrate fossils, cave floor sediments are at times collected to search for specimens. These sediments are run through a stack of graded sieves and flushed with flowing water until the heavier concentrations are left behind. These graded concentrations are then picked through using a stereo microscope.

Cleaning of fossils for study 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 fitted with a carbide needle. Fossils from river passages can be cleaned with a simple solution of diluted acetic acid (white vinegar) and water to remove mud and silt.

For the large and fragile skeletal cartilages of chondrichthyans we encountered, we decided that collecting was not an option. This decision was initially based on the difficulty in reaching locations for the cartilaginous fossils. The logistics of cutting slabs with power tools within in the tight confines of the cave rendered collecting completely moot. Additionally, traditional casting methods with latex-based compounds might be deleterious to these large specimens, so we decided against this as well. Instead, we turned to photogrammetry. 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 to make computer models that can be three-dimensionally printed. This is crucial, as these skeletal cartilages are important specimens that cannot be safely removed from the cave, and/or are difficult to access by visiting researchers. Using the 3D data from photogrammetry, a printed voucher specimen created from rapid prototyping technologies can be placed in the Mammoth Cave National Park Museum collections for description and review purposes. Thus, photogrammetry solves the two issues for these fragile specimens: access, and providing information to researchers needing detail geometry.

Photography was completed 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 mounted on tripods, a camera tripod with a swivel mount and extension arm, and a portable Wi-Fi LAN router for control of the camera with a tablet computer. This was in addition to the standard caving gear of helmet, three additional light sources (head lamps, flashlights, etc.), pack, knee and elbow pads, lunch, and water for the day. Images were captured with a Nikon D810 fitted with a Nikor 24-mm f/1.4 AF lens. The lights used to illuminate the fossils have variable temperature and brightness settings. These were used in lieu of flash units that might be brighter, but tend to have an outwardly dimming circumference of light. The LEDs provide a more uniform if slightly dimmer illumination. The camera was mounted on the tripod with a counterbalanced extension arm; this permitted inverting the camera to follow the pattern of photogrammetric photography as suggested by Mallison and Wings (2018) 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, often with the use of nails or tacky putty or both, with placement determined solely by where they could remain in place. The control sticks provide scaling: the distance between targets is known to 0.1 mm or better, with errors of ±0.03 mm or better. Imagery was recorded 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.

Like the 3D-printed voucher specimens, all collected specimens, approximately 700 in total, are housed in the Mammoth Cave National Park Museum collections. A database on the collected specimens, as well as those left in place, including their distribution, are on file in the park archives. Larger collected specimens are housed in foam-lined trays and smaller specimens are placed in small foam-lined acrylic containers, then in trays. Tiny fossils are placed in empty gel caps that are placed in the small foam-lined acrylic containers. For documenting these tiny fossils, some specimens were imaged by scanning electron microscopy at Western Kentucky University's biology imaging lab or photographed via microscope with a mounted camera connected to a computer.

CHONDRICHTHYAN ASSEMBLAGES OF MAMMOTH CAVE

During the Mississippian Subperiod, cartilaginous fishes of the class Chondrichthyes reached a high degree of diversification, with many species filling ecological niches now occupied by bony fishes (class Osteichthyes) (Long 1996). Two major subclasses of chondrichthyans are recognized, Elasmobranchii, which includes extant sharks and rays; and Euchondrocephali, which includes extant holocephalans (ratfish and kin) (Stahl 1999; Ginter et al. 2010). Chondrichthyan skeletons are composed primarily of calcified cartilage that only preserves under special environmental conditions (Long 1996; Stahl 1999; Ginter et al. 2010). Most of what we know of ancient chondrichthyans is largely from isolated teeth and dermal elements (denticles, spines, and facial plates) (Stahl 1999; Ginter et al. 2010). Isolated skeletal cartilage to complete skeletons with soft tissues usually will preserve best when they are quickly buried in fine-grained sediments under anoxic conditions (Long 1996; Stahl 1999; Ginter et al. 2010).

From the PRI, we have identified more than 25 localities within four geologic horizons spanning the Middle to Late Mississippian Subperiod (Figure 2). The two Middle Mississippian horizons have recently been briefly presented (Hodnett et al. 2021, 2022). During the Middle Mississippian Subperiod, central Kentucky was part of the southern Illinois Marine Basin, which also extended through what is now Illinois, Indiana, Tennessee, and Missouri (Saber and Dever 1990) (Figure 3A). At this time, Laurentia (an ancient continental landmass representing the core of North America) was slowly beginning to collide with Gondwana (an ancient continent that included Africa, Madagascar, South America, Antarctica, India, and Australia) to form the supercontinent of Pangea. As the two ancient continents were moving towards one another, the Rheic Ocean, which connected marine waters extending to what is now Europe and southern North America, was beginning to close. This slow closure of marine waters affected the environments these ancient fishes thrived in (Figure 3B).

The oldest rocks at MACA are from the St. Louis Formation, found in the lowest cave passages within the park. Many of these St. Louis Formation passages still have flowing underground rivers that continue to cut new passages within the main Mammoth Cave system. The St. Louis Formation contains a fairly diverse assemblage of 24 taxa of chondrichthyans, identified from isolated teeth and dorsal fin spines (Table 1). Most of these fossils are large macroscopic elements of 1 cm or more in diameter, and the St. Louis Formation is the only geologic horizon at MACA where large dorsal fin spines have been collected (Figure 4E). Sharks from the St. Louis Formation include large macro-predatory forms such as *Saivodus striatus* and a new *Cladodus*-like taxon (Figure 4C). Unique to the St. Louis Formation is the presence of the petalodont *Polyrhizodus concavus* (a distant ratfish relative), which had broad-bladed teeth and a tooth base with multiple finger-like projections (Figure 4F). *Polyrhizodus* has not yet been found in the younger shark-bearing geologic horizons at MACA and may be a useful index taxon to determine more specific ages during the Mississippian Period.

Above the St. Louis Formation lies the Ste. Genevieve Formation, which until the discoveries at MACA had no records of marine vertebrates anywhere. The Ste. Genevieve Formation has a rich invertebrate fossil assemblage that is well-known to both scientist and cavers alike (Palmer 1981; O'Connor Olson 2017). Surprisingly, the Ste. Genevieve Formation now has the most prolific record of marine vertebrates within the park, which previously was not known for marine vertebrate fossils. At present, 72 species of fishes have been identified from various passages within this geologic horizon (Table 1). Most of the records are based on isolated teeth, dermal spines, scales, and isolated bones of both chondrichthyans and osteichthyans (bony fishes). Small marine vertebrate taxa make up the bulk of the rich record of fish in the Ste. Genevieve Formation, including a number of bizarre forms that evolved elaborate dentitions (Figures 4I, J, and L). However, at some of these passages, isolated to nearly articulated skeletal cartilages of chondrichthyans have been found well-preserved within cave surfaces.

FIGURE 2. Stratigraphy and distribution of major chondrichthyan groups at Mammoth Cave National Park, Kentucky. Yellow: Phoebodontiformes; Orange: Ctenacanthiformes; Red: Euselachii; Lime green: Symmoriiformes; Green: Paraselachii; Light blue: Eugenodontiformes and Orodontiformes; Blue: Petalodontiformes; Purple: Holocephali.

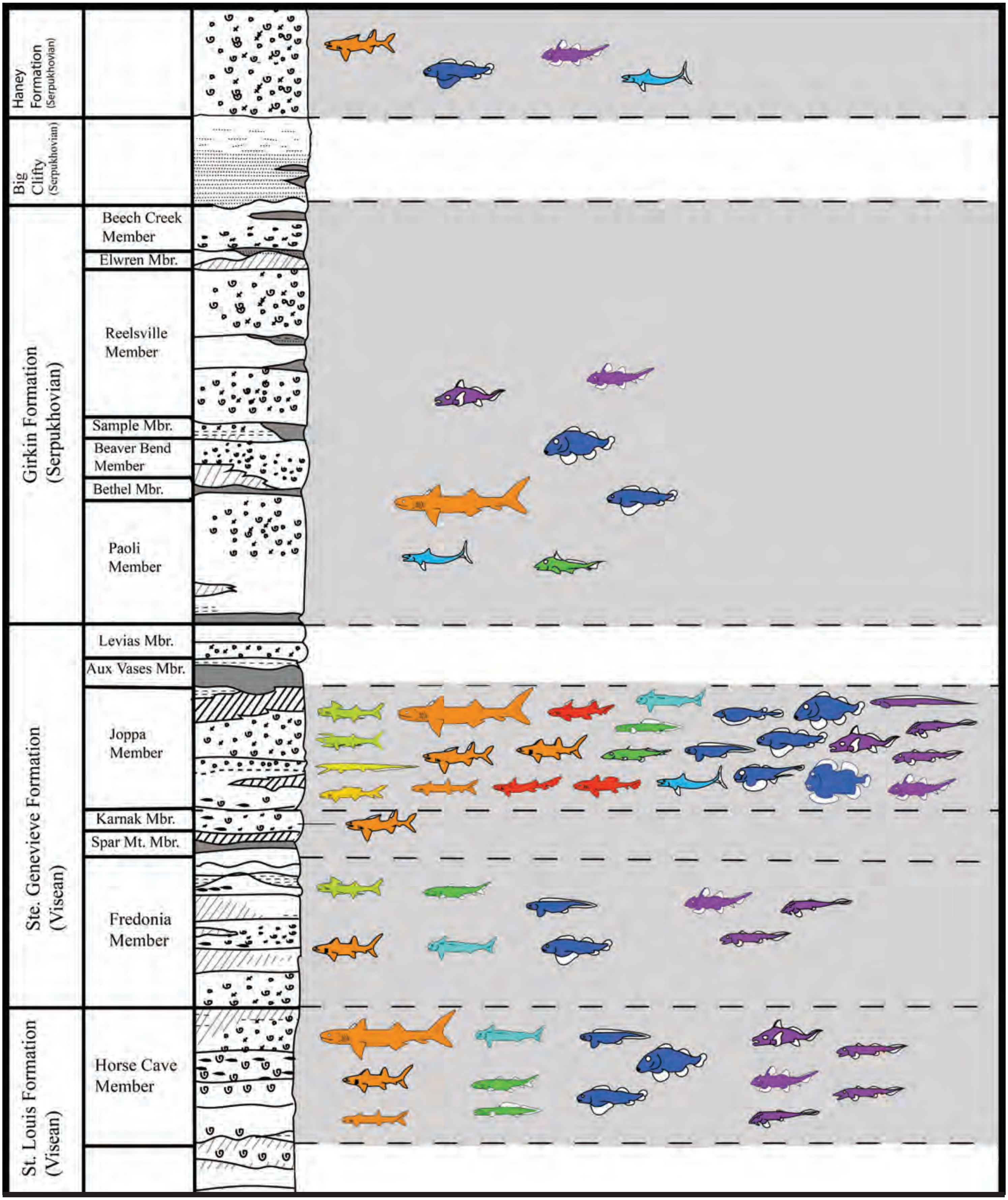


FIGURE 3. The paleogeographical and environmental reconstructions of the Middle Mississippian of the Mammoth Cave National Park region. (A) Paleogeographical map of the North American region of Laurentia sub-continent before the formation of Pangea. (B) Reconstruction of the shallow marine environment and its fauna of the Ste. Genevieve Formation at Mammoth Cave National Park, Kentucky. Art by Julius Csotonyi.

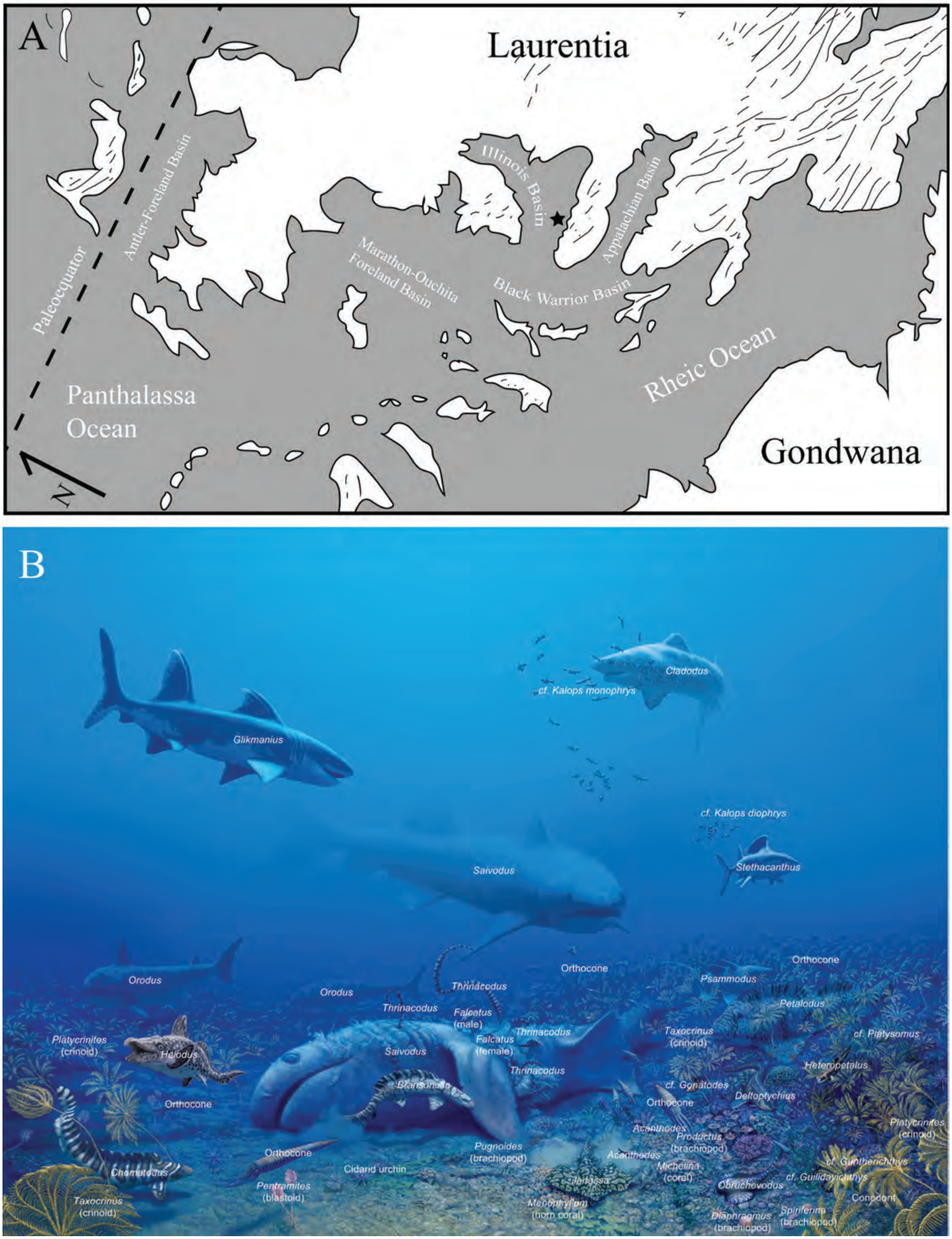


TABLE 1. Middle and Late Mississippian fishes found within the St. Louis, Ste. Genevieve, Girkin, and Haney Formations at Mammoth Cave National Park, Kentucky.

Taxon	Meramecian (Viséan)		Chesterian (Serpukhovian)	
	St. Louis Fm.	Ste. Genevieve Fm.	Girkin Fm.	Haney Fm.
Acanthodii				
Acanthodiformes				
Acanthodidae				
cf. *Acanthodes* sp.		*		
Chondrichthyes				
Cladodontomorphi				
Symmoriiformes				
Stethacanthidae				
Stethacanthus sp. 1 (5 cusped teeth)		*		
Stethacanthus sp. 2 (3 cusped teeth)		*		
Falcatidae				
"*Denaea*" sp. 1		*		
"*Denaea*" sp. 2		*		
Genus and species indeterminate		*		
Elasmobranchii				
Phoebodontiformes				
Thrinacodontidae				
Thrinacodus cf. *T. dziki*		*		
Family Indeterminate				
Genus and species indeterminate		*		
Xenacanthimorpha				
Bransonelliformes				
Bransonella nebraskensis		*		
Bransonella lingulata		*		
Ctenacanthiformes				
Ctenacanthidae				
Cladodus mirabilis	*	*		
Cladodus elegans	*			
?*Cladodus sp.* (Large form)		*		
"*Cladodus*" sp. nov.		*		
Genus and species indet 1	*	*		
"Tamiobatidae"				
Saivodus striatus	*	*	*	*
"Glikmanidae"				
Glikmanius sp. nov.	*	*		
?*Glikmanius* sp.				*
Glencartius costellatus	*	*		
Genus and species indeterminate		*		

TABLE 1 (cont'd). Middle and Late Mississippian fishes found within the St. Louis, Ste. Genevieve, Girkin, and Haney Formations at Mammoth Cave National Park, Kentucky.

	Euselachii						
	Protacrodontiformes						
		Family indeterminate					
			Genus and species indeterminate		*		
	Hybodontiformes						
		Family indeterminate					
			Genus and species indeterminate		*		
	Neoselachii						
		Anachronistidae					
			cf. *Cooleyella* sp.		*		
	Order indeterminate						
		Family indeterminate					
			Amelacanthus sp.		*		
			?*Eunemacanthus* sp.		*		
Euchondrocephali							
	Order indeterminate						
		Family indeterminate					
			Venustodus sp. 1		*		
			Venustodus sp. 2		*		
			Euglossodus sp.		*		
			Genus and species indeterminate 1		*		*
			Genus and species indeterminate 2		*		
	Paraselachii						
		Gregoriidae					
			Gregoriid indeterminate		*		
		Debeeridae					
			Heteropetalus sp.		*		
			Genus and species indeterminate		*	*	
		Family indeterminate					
			Paraselachid indet. 1	*			
			Paraselachid indet. 2	*			
	Orodontiformes						
		Orodontidae					
			Orodus sp. 1 (*O. ramosus* type)		*		
			Orodus sp. 2 (*O. elongatus* type)		*		
		Family Leiodontidae					
			Leiodus calcaratus	*			
			Leiodus sp.		*		
		Family indeterminate					
			Genus and species indet. 1	*	*		
	Eugenodontiformes						
		Family indeterminate					
			Genus and species indeterminate		*	*	

TABLE 1 (cont'd). Middle and Late Mississippian fishes found within the St. Louis, Ste. Genevieve, Girkin, and Haney Formations at Mammoth Cave National Park, Kentucky.

Petalodontimorpha				
Order indeterminate				
Family indeterminate				
Chomatodus sp. 1	*	*		
Chomatodus sp. 2		*		
Petalodontiformes				
Janassidae				
Janassa sp. nov.		*		
Petalodontidae				
Petalodus hastingsii		*		
Petalodus linguifer		*		
Petalodus sp. nov.		*		
Petalodus sp.				*
?*Petalodus* sp.		*		
Tanaodus pumilis	*			
Polyrhizodus concavus	*			
Antilodus sp.		*		
?*Lisgodus* sp.		*		
Harpacodus sp.		*		
Petalorhynchidae				
Petalorhynchus pseudosagittatus	*			
Petalorhynchus cf. *P. spatulatus*		*		
Petalorhynchus cf. *P. beargulchensis*			*	
Petalorhynchus sp.		*		
"Obruchevodidae"				
Fissodopsis sp.		*		
Genus and species indeterminate		*		
Belantseidae				
cf. *Belantsea* sp.		*		
Family indeterminate				
Genus and species indeterminate 1		*	*	
Genus and species indeterminate 2		*		
Holocephali				
Chondrenchelyiformes				
Chondrenchelyidae				
Genus and species indeterminate		*		
Helodontiformes				
Helodontidae				
Helodus sp.	*	*	*	
Cochliodontiformes				
Psephodontidae				
Psephodus sp.	*	*	*	
Cochliodontidae				

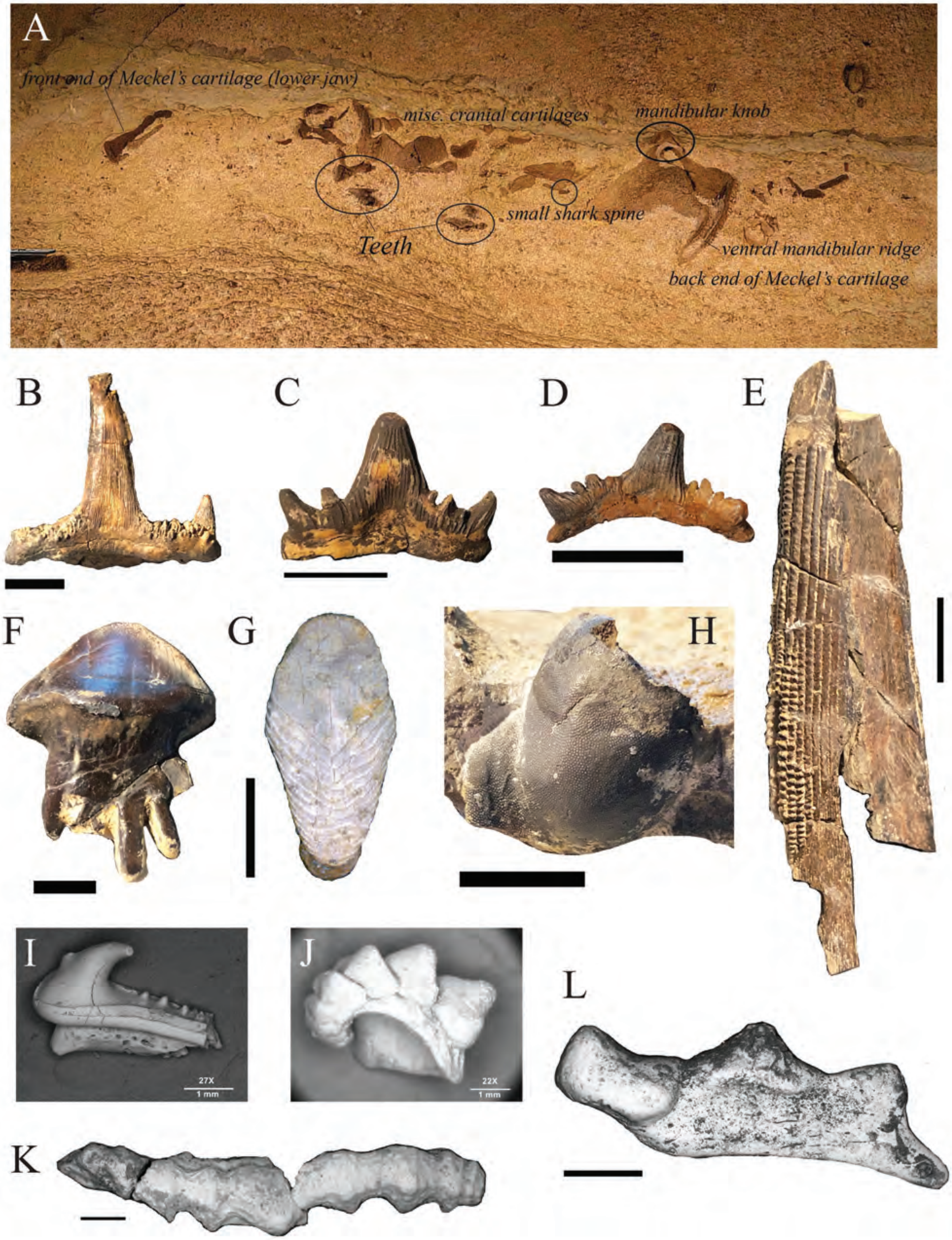
TABLE 1 (cont'd). Middle and Late Mississippian fishes found within the St. Louis, Ste. Genevieve, Girkin, and Haney Formations at Mammoth Cave National Park, Kentucky.

				Cochliodus sp.	*	*		
				?*Cochliodus* sp.			*	
				Deltodus cf. sublaevis		*		
				Deltodus sp.	*	*		
				?*Deltodus* sp.			*	
				Sandalodus sp.	*	*		
				Poecilodus sp.		*		
				?*Poecilodus* sp.	*			
		Psammodontiformes						
			Psammodontidae					
				Psammodus sp.	*	*		
		Copodontiformes						
			Copodontidae					
				Copodus cornutus	*			
		Menaspiformes						
			Deltoptychiidae					
				Deltoptychius sp.	*	*		
			Traquairiidae					
				cf. *Traquairius* sp.	*			
		Order indeterminate						
			Family indeterminate					
				Holocephalan indet.		*	*	
Osteichthyes								
	Actinopterygii							
		Palaeonisciformes						
			Family indeterminate					
				Genus and species indeterminate 1		*	*	
				Genus and species indeterminate 2		*		
				Genus and species indeterminate 3		*		
				Genus and species indeterminate 4		*		
				Genus and species indeterminate 5		*		
		?Eurynotiformes						
			Family indeterminate					
				Genus and species indeterminate 1		*		
				Genus and species indeterminate 2		*		

These include the first skeletal material for *Saivodus striatus*, a large apex predator that reached body dimensions similar to or exceeding those seen in the extant white shark with jaws reaching nearly 61 cm length (Figure 4A). The Ste. Genevieve Formation also showed evidence of several new species, including a distant relative to modern sharks (Figure 4D) and teeth of skate-like distant relatives of extant ratfish (4G).

By the beginning of the Late Mississippian Subperiod, the Rheic Ocean was nearly completely drained by tectonic uplifting, drastically changing the marine waters with new sedimentation draining into the southern Illinois Marine Basin. The Girkin Formation represents this dramatic environmental and depositional change at MACA. Invertebrate

FIGURE 4. Examples of chondrichthyan fossils from Mammoth Cave National Park, Kentucky. (A) Lower left jaw and cranial fragments of *Saivodus striatus* exposed in the cave wall. (B) Tooth of *Saivodus striatus* from the Ste. Genevieve Formation, scale 1 cm. (C and D) Tooth of a new ctenacanthiform taxon from the St. Louis and Ste. Genevieve Formations, scale 1 cm. (E) Spine fragment of cf. *Ctenacanthus venustus* from the St. Louis Formation, scale 1 cm. (F) Tooth of *Polyrhizodus concavus* from the St. Louis Formation, scale 1 cm. (G) A new janassid petalodont taxon from the Ste. Genevieve Formation, scale 5 mm. (H) Tooth plate of *Cochliodus* sp. from the Girkin Formation, scale 1 cm. (I) Tooth of *Venustodus* sp. type 1 from the Ste. Genevieve Formation, scale 1 mm. (J) Tooth whorl of *Helodus* sp. from the Ste. Genevieve Formation, scale 1 mm. (K) Tooth of an indeterminate eugenodontiform from the Girkin Formation, scale 1 mm. (L) Tooth whorl of an indeterminate euchondrocephalan, scale 2 mm.



fossils are still abundant in the Girkin Formation, representing a nearshore assemblage rich with gastropods and a few horn corals, crinoids, and cephalopods. The fish fossils from Mammoth Cave are the first to reported for the Girkin Formation as a whole. Presently, only nine fish taxa are known from the Girkin Formation at MACA (Table 1). Chondrichthyan fossils such as *Saivodus* teeth and a number of holocephalan (ratfish) tooth plates (Figure 4H) are known, but the diversity of chondrichthyans and the total number their fossils are greatly reduced. However, evidence of new forms, such as eugenodonts (whorl-toothed sharks), has been found in the Girkin Formation (Figure 4K). The eugenodonts would later become a very diverse group of macro-predatory chondrichthyans in the Pennsylvanian and Permian Periods (Ginter et al 2010).

After the Girkin Formation, the thick sandstone of the Big Clifty Formation caps the marine limestones, which helps with the stability of the Mammoth Cave system deep below (Palmer 1981). To date, no vertebrate fossils have been found in the Big Clifty Formation at Mammoth Cave, but chondrichthyan fossils are known in Big Clifty localities well north of Kentucky. Above the Big Clifty Formation is the Haney Formation, which is exposed in smaller cave drainages found in the park, which are not connected to the main Mammoth Cave system. Like the Girkin Formation, shark fossils are present but not as common in the Haney Formation, and at present we have identified only five distinct taxa from this geologic horizon (Table 1). As in Big Clifty, chondrichthyan fossils have been reported from the Haney Formation north of Kentucky, but most of these assemblages have not yet been described in their entirety.

DISCUSSION AND CONCLUSIONS

Our PRI of Mississippian Subperiod marine vertebrates found within the caves of MACA has already yielded a wealth of data pertaining the diversity and evolution of early cartilaginous and bony fishes, and the effects that environmental change from tectonic processes had on these organisms. Our work at MACA also demonstrates the importance caves have in preserving marine vertebrate fossils compared to fossils typically found exposed on the surface (Palmer 2017). The lack of external forces of nature (rain, ice, sunlight, wind, etc.) and stable internal environments of caves with their slower rate of erosion allow for greater detail to be preserved in samples of cartilaginous fishes. The marine vertebrate fossils of MACA are important because much of the original work on North American Mississippian-age chondrichthyans was published in the late 19th century (i.e., St. John and Worthen 1875, 1883) and little has been done to review or update these works, which are still cited as primary sources (Stahl 1999; Ginter et al 2010). For example, St. John and Worthen (1875, 1883) described many of their specimens from Illinois, Indiana, Kentucky, and Missouri as collected from the “St. Louis Limestone.” However, this is well before the stratigraphic work that divided the “St. Louis Limestone” into the St. Louis Formation, Ste. Genevieve Formation, Girkin Formation, and various members of these formations. By using the shark assemblages that we have identified at MACA, potentially we can refine the biostratigraphic distribution of chondrichthyans in the Mississippian Period for the classic localities that are still often cited. Additionally, we will be able to compare the MACA fossil sharks with other global assemblages to track how the formation of Pangea affected marine vertebrate assemblages.

In conclusion, the PRI of MACA affirms that this park is an important scientific benchmark in Mississippian marine vertebrate paleontology by providing new data on the distributions of early fish, revealing previously unknown species, and helping resolve conundrums of the historic fossil record by providing better biostratigraphic data, thanks to the special preservation aspects of caves. The above results also demonstrate how such inventories are important tools for managers of our national parks and monuments. They unveil previously unknown information which can be used for both science and as resource for public engagement and education that can be used for future generations.

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