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VERTEBRATES OF THE BLUE RIDGE ESKER (MISSISSIPPIAN, MARSHALL SANDSTONE) OF MICHIGAN

BY

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Abstract — The state of Michigan is known for abundant invertebrate and vertebrate fossils from Devonian carbonates. Vertebrate fossils from overlying Carboniferous horizons are far less abundant and poorly known. Recent teaching and avocational trips exploring the Carboniferous clastic facies of the Blue Ridge Esker near Jackson, Michigan have revealed a previously undescribed vertebrate fauna—a diverse assemblage of chondrichthyans, along with the first actinopterygian and sarcopterygian remains known from the Early-to-Middle Mississippian Marshall Sandstone of Michigan. Here, we contextualize the Marshall Sandstone within Michigan's Paleozoic stratigraphy and provide anatomical descriptions and identifications of 11 new vertebrate fossils from this poorly represented time period in Michigan's past. We analyze these fossils to begin a discussion of the importance of avocational and student paleontologists in new discoveries, as well as to reveal a more detailed depiction of Michigan's Carboniferous seas, highlighting potential new directions in vertebrate paleontological research.

INTRODUCTION

Paleozoic seas covered what is now the state of Michigan, leaving behind a rich fossil record atop Precambrian igneous and metamorphic basement (Dorr and Eschman, 1977). Today, these Paleozoic rock units are in most places buried beneath sediments from the most recent Pleistocene glaciation. Precambrian igneous and metamorphic rocks crop out in the far northern part of the state, with the Keweenaw Peninsula and Lake Superior islands preserving flood basalts that are remnants of Precambrian volcanism, and other areas of the Upper Peninsula representing the edge of the Precambrian Canadian Shield metamorphic complex. Along the shores of the Great Lakes, some Paleozoic marine sedimentary rocks are exposed, offering evidence of shallow seas that covered the state. Inland, where rivers have cut through Pleistocene and Holocene sediments, sequences of Paleozoic marine sediments are exposed, suggesting that the shallow Paleozoic seas were present across nearly the entire region. The most recent glaciation heavily altered the rocks of Michigan—carving out the Great Lakes, heavily eroding sediments deposited between the Pennsylvanian and the Pleistocene, and leaving a glacial landscape of moraines, eskers, drumlins, and kettle lakes across the state (Dorr and Eschman, 1977; Krist and Lusch, 2004).

Post-Pennsylvanian rocks in Michigan are of uncertain temporal origin (Catacosinos et al., 2001), because depositional episodes during the Permian and Mesozoic were likely limited to geographically isolated terrestrial fluvial deposits; otherwise, the region experienced nondeposition and surface erosion, leading Dorr and Eschman (1977) to label the span of time from the Pennsylvanian through most of the Cenozoic as the "Lost Interval." To supplement the few and sparse outcrops with exposed stratigraphy, exploration of the sub-

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surface by drilling and quarrying has provided a more comprehensive view of Michigan's geologic past, allowing us to construct a fuller history of the state across its geography.

Subsidence prior to the Paleozoic allowed for the accumulation of marine sediments in the Michigan Basin beginning in the early Paleozoic. Rocks deposited during this interval form a pattern of concentric rings of increasingly younger age towards the center of the Lower Peninsula of the state. This bowl resulted from an apparent shallowing of seas and loss of accommodation space in the late Paleozoic, concurrent with the uplift of the Appalachians to the east. The first evidence of a continuous depositional sequence begins with Cambrian clastic and carbonate formations of the Upper Peninsula, followed by Ordovician and Silurian rock that round out the southeastern portion of the Upper Peninsula (Dorr and Eschman, 1977). Devonian carbonate reef formations predominate an outer ring around the Lower Peninsula of Michigan, followed by a ring of younger Devonian and early Carboniferous shales (Dorr and Eschman, 1977). The Paleozoic shallow seas also left numerous deposits of evaporites, especially associated with shale and gypsum deposits in areas near Detroit and Grand Rapids, where they are mined (Dockeray, 1983). Mississippian shales are bounded above by larger Pennsylvanian clastics, with the most central portion of the state bearing strata of putative Jurassic age (Shaffer, 1969). Several workers have called into question the Jurassic attribution of the central "red beds" (Catacosinos et al., 2001; Benison et al., 2011; Benison, 2018), instead suggesting a Pennsylvanian age for these rocks. More work is needed to resolve this and other questions of stratigraphy and absolute age of these rocks; here we focus on remains of past life in Michigan.

Michigan's geologic record has permitted extensive exploration of fossils from two intervals of Earth's history: the Devonian, known for its placoderms and reef-dwelling invertebrates that occupied shallow seas during this interval (see Ehlers and Kesling, 1970 for in-depth locality data and associated faunas); and the mammal fauna present after the ice sheet receded at the end of the most recent glacial episode. The focus of fossil studies has largely been on the Devonian reef faunas (especially marine invertebrates) and human-associated Pleistocene proboscideans (Shipman et al., 1984; Fisher, 1987). Reflecting these focal study subjects, the Michigan state stone is the Devonian-age Petoskey stone (*Hexagonaria* rugose coral), and the state fossil is the American mastodon (*Mammut americanum*).

The various vertebrate faunas from the Carboniferous of Michigan have been studied by paleontologists to a lesser extent than their Devonian counterparts (Dorr and Moser, 1963; Stack and Sallan, 2018). Taxa deriving from Devonian reef deposits are attributable to numerous placoderm families (Stack and Sallan, 2018), and a depauperate chondrichthyan fauna has been documented from the Carboniferous of Michigan (Dorr and Moser, 1963; Dorr and Eschman, 1977). Carboniferous deposits and their fossils are less accessible than most Devonian strata, which are common along the coastlines of northeastern Lake Michigan and southern Lake Huron and frequently exposed in limestone quarries (Ehlers and Kesling, 1970). In contrast, Carboniferous deposits crop out in only a handful of locations (Dorr and Eschman, 1977) and are visible mostly at quarried localities. Prior work on Michigan's Carboniferous deposits has focused on short descriptions of mostly invertebrate faunas (Kelly, 1930), water quality and oil studies (Cerone, 1984; Catacosinos et al., 1990), and geomorphology and historical geology (Ells, 1979). Here, we describe a much richer vertebrate fauna than previously known from the Carboniferous of Michigan, before discussing the importance of this fauna in the context of Michigan paleontology and future research directions for Carboniferous localities.

The Paleozoic Vertebrate Record of Michigan

In 1963, Jack Dorr and Frank Moser remarked that "pre-Pleistocene fossil vertebrates are sufficiently rare in Michigan that new discoveries, even of fragmentary remains, still are of local interest" (p. 105). This statement still rings true today: the Mississippian ctenacanth sharks that were the subject of Dorr and Moser (1963) remain some of the only Carboniferous vertebrate material collected within Michigan housed at the University of Michigan Museum of Paleontology (UMMP). Several factors contribute to this tendency: there are few localities that preserve identifiable material; remains are so fragmentary, they are easily confused for non-vertebrate remains; fossil hunters in Michigan are largely avocational and collecting marine invertebrates for personal collections; and Devonian carbonate reefs are more accessible areas for fossil collection than other types of fossiliferous rocks or rocks from other geologic periods.

Prior to the Devonian, vertebrates are virtually undocumented in Michigan. A putative ostracoderm scale is the earliest evidence of vertebrate life in Michigan, collected from the Middle Ordovician Black River Formation, approximately 3 miles south of Bony Falls along the Escanaba River in Delta County, Michigan (Hussey, 1947; Dorr and Eschman, 1977). This locality and the associated fossil are enigmatic and should be an active area of collection in the future. Whereas marine sequences from the Cambrian are well documented in Michigan's Upper Peninsula, there are no known vertebrate fossils found in those strata. Likewise, there are no Silurian vertebrates known from Michigan.

The Devonian vertebrate record of Michigan was recently reviewed by Stack and Sallan (2018). Primarily, it comprises abundant arthrodire remains and far fewer antiarchs, usually preserved as isolated plates and jaw elements, with a sizable chondrichthyan fauna of acanthodians and holocephalans represented by isolated fin spines and teeth. A well-preserved skull of a Middle Devonian lungfish from Presque Isle County, *Chirodipterus onawayensis* (UMMP 118356), represents the only described sarcopterygian body fossil from Michigan (Schultze, 1982). No definitive actinopterygian material is known from the Devonian of Michigan.

Geological and fossil context of the Mississippian of Michigan

Sea level fell at the end of the Late Devonian, with shelf reefs giving way to shallower Carboniferous seas (Gutschick and Sandberg, 1999a). This regression is thought to correlate with global glaciation and occurs on a similar timescale as the Hangenberg extinction event (Sandberg et al., 1988; Isaacson et al., 1999). The Devonian–Carboniferous transition of Michigan possibly exists in a series of laterally equivalent shale units that together span that boundary but lack adequate index fauna for proper placement of the contact layer (Harrell et al., 1991). Alternatively, the boundary could be represented along an unconformity at the top of the Antrim, Bedford, Ellsworth Shales, or Berea Sandstone (Gutschick and Sandberg, 1991b; Over, 2021), with Mississippian units unconformably overlying these units. The first Mississippian units in the Michigan Basin vary depending on location: the Berea Sandstone occasionally overlies the Bedford Shale; the Kinderhookian–Osagean Coldwater Shale overlies the Antrim, Ellsworth, and the Devonian–Carboniferous Sunbury Shales (Shaver, 1985); or, as the Coldwater, Sunbury Shales, or Red Rock Formation that overlie the Berea Sandstone and the Bedford and Ellsworth Shales (Gutschick and Sandberg, 1991a). The Mississippian lithofacies recorded in the Michigan Basin predominantly grade into coarser clastics than Devonian-or-older facies and coincide with the Waverly Sandstones in Ohio and elsewhere in the midwestern U.S.A. (Ells, 1979; Pepper et al., 1954). The Mississippian of Michigan consists of four major named lithofacies, all found in the Lower Peninsula: the Sunbury or Coldwater Shales (depending upon location), the Marshall Sandstone, the Michigan Formation, and the Bayport Limestone (Monnett, 1948; Harrell et al., 1991). These vary not only in their lithology, but also in their fossil composition. The Coldwater Shale vertebrate fauna is limited, with a sparse chondrichthyan record comprising cf. *Cladodus*, cf. *Ctenacanthus*, and cf. *Orodus* (Monnett, 1948; Dorr and Eschman, 1977).

The Marshall Sandstone is divided between two formations deposited in the Early-to-Middle Mississippian—the younger, fossiliferous Lower Marshall Member and the non-fossiliferous Napoleon Formation (Harrell et al., 1991; Adducci and Barnes, 2018). Both are predominantly sandstone in lithology, with the Napoleon Formation being characterized by coarser grains than the Lower Marshall Member. Each unit is reddish in color and easily distinguished from the dark shales and limestones from the earlier Paleozoic formations that underlie the Marshall Sandstone and from the lighter-colored shale and gypsum Michigan Formation and Bayport Limestone that overlie it. Finer-scale details in the lithologies of the formation are evident in well cores, including gradations between shales, mudstones, sandstones, dolomitic wackestone, and anhydrites (Adducci and Barnes, 2018).

The middle Mississippian Michigan Formation, exposed primarily as a gypsum alabaster mine in the vicinity of Grand Rapids, preserves a wide array of fishes, ranging from chondrichthyan teeth, such as cf. *Psephodus* (UMMP 23742), cf. *Cochliodus* (UMMP 23743), and cf. *Ctenacanthus* (UMMP 45738), fin spines (Dorr and Moser, 1963), and chondrichthyan coprolites and cololites, along with actinopterygian teeth and scales (Regenmorter et al., 2008). Kenaga and Sellepack (1995) mention the presence of a rhipidistian lower jaw from the formation, but this appears to be an actinopterygian dentary instead (M. Friedman, pers. comm.). Along with these remains, there are undescribed putative fragments of calcified cartilage, suggesting that additional chondrichthyan skeletal elements could be present.

The Bayport Limestone rounds out the Mississippian-age units of the Michigan Basin and includes chondrichthyan fin spine remains, identified as cf. *Gyracanthus* (UMMP 13663), *sensu* Agassiz (1834), along with cf. *Cladodus* and cf. *Ctenacanthus* (UMMP 45738) (Dorr and Moser, 1963), and cf. *Pleuracanthus* (UMMP 33463). Fossilized chondrichthyan teeth are also present in the Bayport Limestone, represented by the durophagous holocephalans cf. *Helodus* and cf. *Psephodus* (Dorr and Moser, 1963).

Vertebrate remains of unknown Mississippian age are also present from a quarry near Pigeon, Michigan (UMMP 56973) in the form of indeterminate palaeonisciform teeth and scales, but little else is known about this specimen and its geologic context.

Finally, the earliest known evidence of lungfish aestivation is located in the Middle Pennsylvanian Saginaw Formation of Grand Ledge, MI (Carroll, 1965). After the Carboniferous, there are no fossiliferous strata in Michigan until the Pleistocene.

The Mississippian Marshall Sandstone of Michigan

Pleistocene glacial episodes in Michigan eroded much of the surface sedimentary strata, depositing till and flour debris from previously deposited geologic formations. As a result, outcrops of *in situ* stratigraphic sequences at the interior of the Lower Peninsula are constrained to small, fluvially eroded areas in the geodesic center of the state, like the exposed Pennsylvanian clastics at Grand Ledge. However, *ex situ* sediments may be exposed as eskers and moraines deposited via glacial processes, and these contain transported fossiliferous rocks without their original stratigraphic context. An example of this is the early Carboniferous (Mississippian) Marshall Sandstone, with a vertebrate assemblage reported to contain cf. *Ctenacanthus* (UMMP 23845; UMMP 45739) and cf. *Cladodus* (UMMP 13613) (Dorr and Moser, 1963). Fossils of the Marshall Sandstone Formation are easily collected along the Blue Ridge (or Ackerson) Esker of Jackson County, Michigan (Fig. 1), where there is an active surface-level gravel quarry operated by the Jackson County Department of Transportation, approximately 10 kilometers southeast of the city of Jackson. Gravel mining of the Blue Ridge Esker has occurred across an area of approximately 47,000 m^2 (Google Maps), along the edges of which scree piles of the fossiliferous Marshall Sandstone can be accessed (Fig. 1). A secondary point of access is the Liberty Landfill waste disposal site, approximately 1.6 km to the southwest of the gravel quarry, where

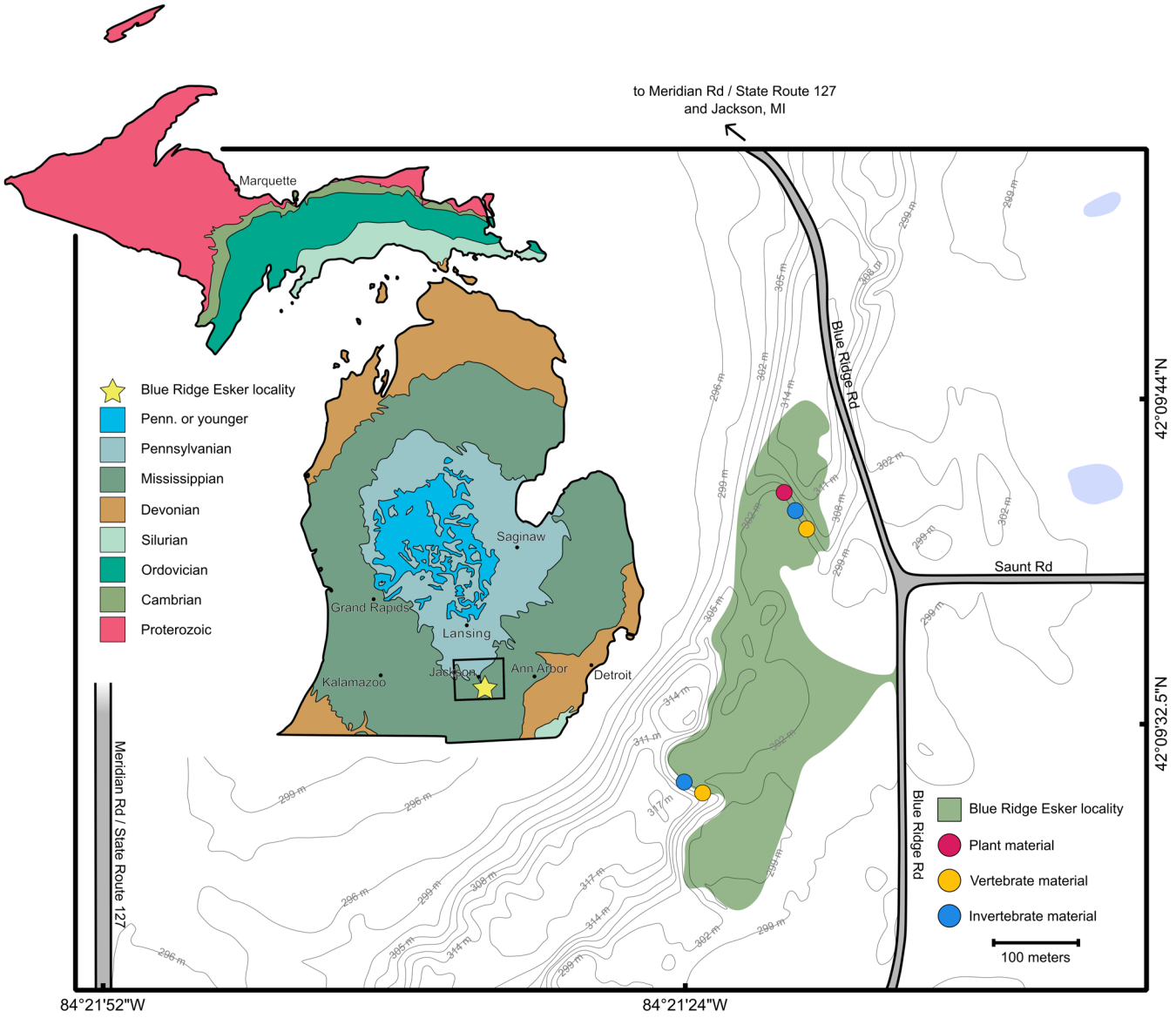


FIGURE 1 — Geologic context of Blue Ridge Esker locality. Inset showing the geology of the state of Michigan modified from Horton et al. (2017), with Jackson County within a black box and the Blue Ridge Esker locality marked by a yellow star. Outset of the Blue Ridge Esker and surrounding area, with the Jackson County DoT gravel mining area highlighted in Early Mississippian green. Invertebrate fossils are copious in the southwestern portion of the locality, with occasional vertebrate material. Invertebrate, vertebrate, and plant fossils are all present in relatively low quantities in the northeastern portion of the locality. Generated with data from Google Maps (google.com/maps) and Jackson County GIS (gis.mijackson.org).

cf. *Stethacanthus depressus* (UMMP 118281) was collected.

The Marshall Sandstone is known to preserve a variety of marine invertebrate fossils (Winchell, 1862; Winchell, 1869; Miller and Garner, 1953a, b, 1955; Driscoll, 1965; Squire, 1972) and flora that presumably washed in from the continent (Lane and Cooper, 1900; Monnett, 1948; Chaloner, 1954; Squire, 1972; Dorr and Eschman, 1977; See, 1980). Typical slabs show a diversity of bivalves, with frequent orthoconic cephalopods (cf. *Mooreoceras*), along with occasional crinoid columnals, brachiopods, and ammonoids (cf. *Merocanites*) (Fig. 2D, E). Whereas the invertebrate fauna from the Marshall Sandstone is well-known, there are only three vertebrate taxa described from the locality—all chondrichthyans: *Stethacanthus depressus*, cf. *Cladodus*, and cf. *Ctenacanthus*. The vertebrate fauna from contemporaneous Carboniferous shallow seas were more diverse than this



FIGURE 2 — Photographs of the collection locality, exemplar specimens displaying common invertebrate material, and a sandstone with ripple marks from the Mississippian Marshall Sandstone. **A**, a sequence of strongly cross-bedded conglomerates, likely preserving original depositional bedding planes ex-situ. **B**, glacially redeposited pebble-to-boulder clasts in finer matrix, with clasts coming predominantly from the Marshall Sandstone (though clasts of metamorphosed igneous rocks from the Canadian Shield and some Devonian Traverse Group reef rock are also present). **C**, photograph of the Blue Ridge esker gravel quarry site in Jackson, Michigan from raised elevation on the northern side of the site, looking south. **D**, broken slab of invertebrate fauna, including crinoid columnals and bivalve impressions, and

(continued from previous page) **E**, a broken cobble surrounded by gravel matrix with impressions of bivalves. Both **D** and **E** are cataloged as UMMP 80806. **F**, ripple marks on sandstone, suggesting a shallow water marine lithofacies in parts of the Marshall Sandstone (UMMP 119501). Scale bars equal 10 cm.

(Ginter et al., 2015; Smith et al., 2017; Hodnett and Elliot, 2018; Hoenig, 2019; Ginter, 2022; Hodnett et al., 2024a, 2024b; Schnetz et al., 2024). The presence of occasional ripple mark specimens within the Marshall Sandstone (Fig. 2F), most notably at the southern portion of the Blue Ridge Esker Jackson County DoT locality, shows that shallow water lithofacies are present. Ripple marks, in conjunction with coarse sandstones, terrestrial plant debris, and lungfish remains suggest a nearshore, shallow water environment during much of fossil deposition.

Fieldwork, teaching, and incidental collection

We first visited the locality on September 27, 2020 with the Friends of the University of Michigan Museum of Paleontology. On March 25, 2022 and November 5, 2023, we visited the locality in the context of educational field trips for University of Michigan Earth and Environmental Sciences graduate students. We visited a fourth time on June 19, 2024 in the context of a conference field trip. On all four occasions, permission was given by the Jackson Department of Transportation to examine and collect for personal use. We collected from scree piles around the site and from excavated parts of the esker that form hills on the north and southwest sides of the site. There is sufficient mixing of lithologies (including examples of light gray Devonian corals) at the site that it is unlikely that any of these parts represent a particular unit of the Marshall Sandstone sequence. Upon reviewing collected materials, we recognized certain specimens that might be valuable for demonstration and teaching purposes. The specimens described herein were collected for personal use, but have now been donated to the University of Michigan Museum of Paleontology.

In this contribution, we briefly describe specimens that greatly expand the scope of the vertebrate fauna of the Mississippian Marshall Sandstone. We describe first the more numerous chondrichthyans, utilizing the descriptive terms for tooth morphology of Feichtinger et al. (2021), then move to the single sarcopterygian and actinopterygian fossils thus far discovered from the Marshall Sandstone. We close by offering a discussion of possible future research directions with yet uncollected material from Michigan's Carboniferous seas.

MATERIALS AND METHODS

Fossil Material

Over the course of the four half-day visits to the Marshall locality in Jackson, we recovered 10 new vertebrate specimens and several invertebrate specimens (Table 1). The invertebrate slabs were donated to the University of Michigan Museum of Paleontology teaching collection and are cataloged as UMMP 80806. The vertebrate specimens described here include our ten new specimens, plus one specimen collected in 2018, with associated catalog numbers and brief descriptions in Table 1. Most specimens are preserved as impressions in a clastic matrix, so preservation is often not usually sufficient for lower-level taxonomic identification. However, some specimens include fossil material. Institutional abbreviations are as follows: UMMP — University of Michigan Museum of Paleontology, Ann Arbor, U.S.A.

Imaging Methods and Data Availability

We used a Nikon D850 with a Nikon 80 mm macro lens to photograph each fossil, none of which have been removed from the matrix due to fragility. In several cases, we used a Nikon XT H 225 ST industrial Computed Tomography (CT) scanner at the University of Michigan Department of Earth and Environmental Sciences CTEES facility (Table 1, asterisks). Specimens were batch scanned using the following parameters: 180 kV and 145 μA, filtered with 1 mm of aluminum and 1 mm of copper to perform the CT scans, with 4 s exposures, 2 frames per projection and 2000 projections, ring artifact and flux correction on. These datasets were reconstructed in the Nikon XTECT software. CT data were processed in Mimics (Materialise, Belgium), and figures from photographs and CT data were created in Adobe Illustrator (Adobe, U.S.A.), Blender (blender.org), and Inkscape (inkscape.org).

Tomogram stacks were exported as TIFF files and uploaded to the Deep Blue Data digital repository where they received Digital Object Identifiers (DOIs). A digital collection was generated for all scanned specimens (https://doi.org/10.7302/k5vw-z082), housing the original batch scans (https://doi.org/10.7302/1gps-v958) and cropped individual specimens that preserved enough information to warrant figuring (https://doi.org/10.7302/pp2t-4t21). DOIs for these cropped individual specimens can be found in Table 1.

SYSTEMATIC PALEONTOLOGY

VERTEBRATA Lamarck, 1801
CHONDRICHTHYES Huxley, 1880
INDETERMINATE SPECIES

Referred specimens.—A single fin spine (UMMP 119350) roughly 4 cm in length is preserved as a mold showing the lateral profile of the spine (Fig. 3A). The lateral surface of the spine preserves a longitudinal ridge; no other ornament is evident, but it is not possible to confirm whether this absence is due to poor preservation. Both proximal and distal ends of this spine are missing, but the cross-section shows a highly

TABLE 1 — Newly accessioned specimens of vertebrates from the Marshall Sandstone, consisting of eight chondrichthyans, one sarcopterygian, and one actinopterygian. Field numbers are "MarshREJ" followed by the numbers in the table. MarshREJ005 and MarshREJ008 were originally collected as they appeared to be vertebrate remains, but further study revealed that they were not identifiable as such. As a result, these specimens are absent from the table below. Specimens that were subjected to μCT have an asterisk next to their accession number, and DOIs are provided for all specimens that had tomographic data figured.

Field #	Description	Accession #	DOI
Specimen previously collected by L. Lishman and A. Kaplan in 2018	*Stethacanthus depressus* fin spine; in sandstone concretion Chondrichthyes Symmoriiformes Stethacanthidae *Stethacanthus depressus*	UMMP 118281*	https://doi.org/10.7302/vq78-a005
001	Ctenacanthid tooth mold Chondrichthyes Ctenacanthiformes Ctenacanthidae	UMMP 119342*	
002	*Cochliodus contortus* tooth plate; 2 pieces Chondrichthyes Cochliodontiformes Cochliodontidae *Cochliodus contortus*	UMMP 119343*	https://doi.org/10.7302/6ym5-tp18
003	Lungfish ribs; partially preserved Dipnoi	UMMP 119344*	
004	cf. *Stethacanthus* sp. tooth mold; 2 pieces in part and counterpart Chondrichthyes Symmoriiformes Stethacanthidae cf. *Stethacanthus* sp.	UMMP 119345*	https://doi.org/10.7302/v9tn-9728
006	*Saivodus striatus* tooth mold Chondrichthyes Ctenacanthiformes incertae fam. *Saivodus striatus*	UMMP 119346*	https://doi.org/10.7302/ndhc-b042
007	Palaeonisciform cleithrum Actinopterygii "Palaeonisciformes"	UMMP 119347*	
009	*Saivodus striatus* tooth cusp; 2 pieces in part and counterpart Chondrichthyes Ctenacanthiformes incertae fam. *Saivodus striatus*	UMMP 119348	
010	cf. *Psephodus* sp. tooth plate; 2 pieces in part and counterpart Chondrichthyes Cochliodontiformes Psephodontidae cf. *Psephodus* sp.	UMMP 119349	
011	Chondrichthyan fin spine Chondrichthyes	UMMP 119350	
012	Chondrichthyan tooth mold Chondrichthyes	UMMP 119351	

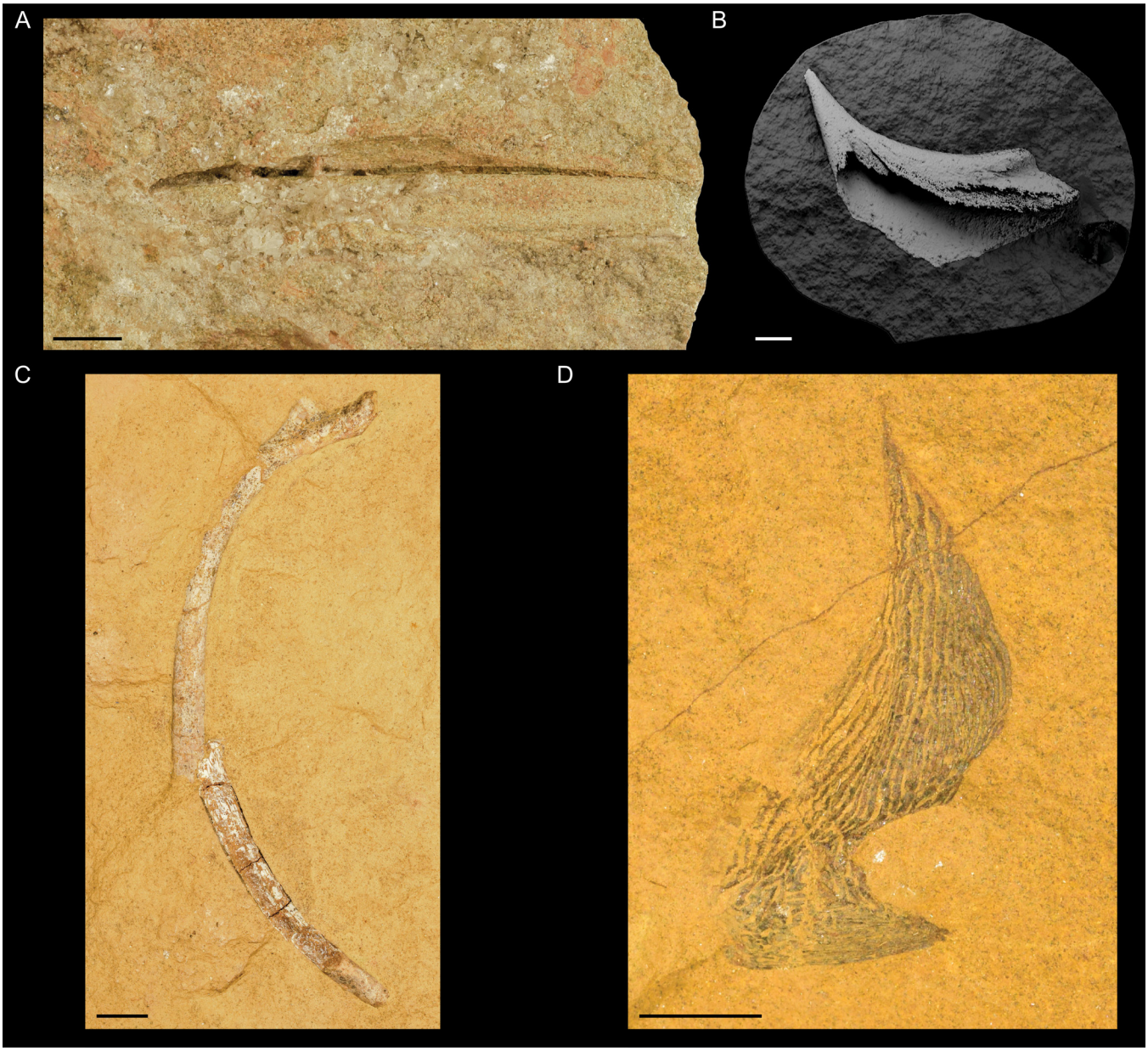


FIGURE 3 — Vertebrate postcranial elements from the Marshall Sandstone. **A**, Chondrichthyes indet. fin spine (UMMP 119350). **B**, *Stethacanthus depressus* dorsal fin spine base, rendered via void space (UMMP 118281). **C**, dipnoan pleural rib (UMMP 119344). **D**, "palaeonisciform" cleithrum (UMMP 119347). Scale bars equal 5 mm.

convex posterior surface. The lack of more diagnostic features hinders further interpretations of its affinities, and as such it can only be classified as an indeterminate chondrichthyan fin spine.

An isolated right lateral tooth (UMMP 119351) bears a curved main cusp and a single pair of blunt, broad-based lateral cusps (Fig. 4A). The surface of the main cusp is ornamented with robust apico-basally oriented ridges that coalesce towards the apex. The tooth base is broad laterally but compressed labiolingually. The orolingual base is covered by strongly developed parallel grooves that are remnants of the vascular openings for the tooth. Although similar in overall geometry to the teeth of Paleozoic hybodontiforms such as *Mesodmodus* and *Sphenacanthus*, this specimen lacks the characteristic labial node near the proximal end of the central cusp of *Mesodmodus*, and it bears a straight tooth base unlike *Sphenacanthus* (Ginter et al. 2010, Hodnett and Elliott, 2018). The general features preserved in this isolated tooth are

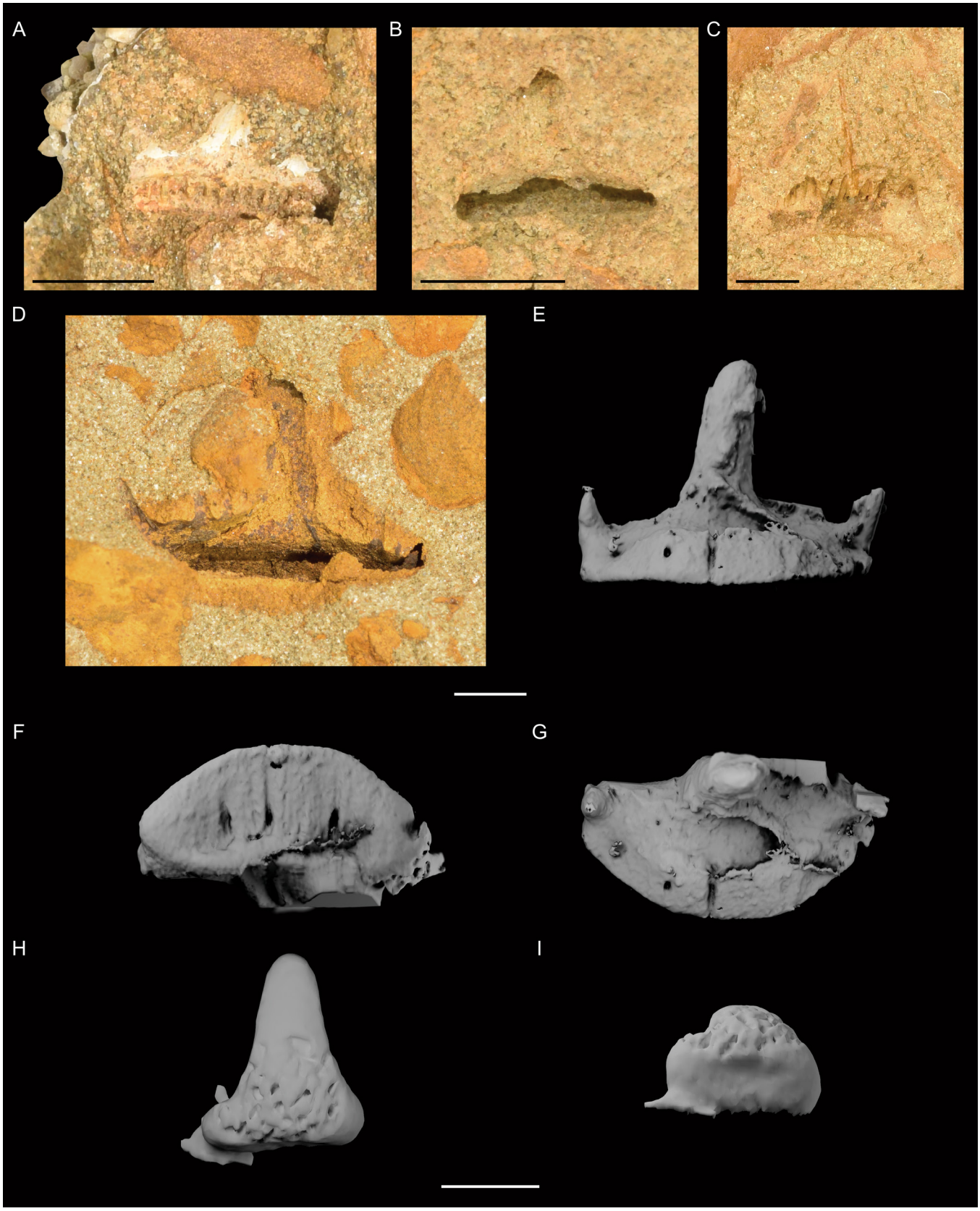

A
B
C
D
E
F
G
H
I

FIGURE 4 — Chondrichthyan dental elements from the Marshall Sandstone, represented by partial teeth and associated impressions. **A**, Chondrichthyes indet. (UMMP 119351). **B**, Chondrichthyes indet. (UMMP 119342). **C**, *Saivodus striatus* (UMMP 119348). **D–G**, *Saivodus striatus* (UMMP 119346), in labial (**D**), lingual (**E**), basal (**F**), and occlusal (**G**) views. **H–I**, *Stethacanthus* sp. (UMMP 119345) in labial (**H**) and basal (**I**) views. Scale bars equal 5 mm.

comparable to the genus *Synechodus*, which has been hypothesized to range from the Permian through the Cretaceous (see Ivanov 2005; Klug and Kriwet 2008; Ginter et al. 2010). Past research has cast doubt on whether this genus extends prior to the Jurassic (Klug and Kriwet, 2010; Rees et al., 2023), which would suggest that the similarities between UMMP 119351 and *Synechodus* represent convergent tooth geometry. The parallel grooves on the orolingual base are more strongly developed than seen in *Troglocladodus* (see Hodnett et al., 2024b), and the striations of the mesial cusp do not coalesce in *Troglocladodus*. Given that basal euchondrocephalans can show deep vascular grooves on the orolingual base and can have tooth cusps similar to elasmobranchs (see *Heteropelatus* in Ginter et al., 2010), only a coarse referral of chondrichthyan affinity is provided for this specimen.

CTENACANTHIFORMES Glikman, 1964
INCERTAE SEDIS
SAIVODUS Duffin and Ginter, 2006
SAVIODUS STRIATUS (Agassiz, 1843)

Referred specimens.— Two specimens are referred to *Saviodus striatus*, UMMP 119348 and UMMP 119346. A single tooth (UMMP 119348) is preserved in part and counterpart as a void and tooth base with at least four accessory cusps on each side (Fig. 4C). All cusps curve lingually, with the main cusp appearing significantly taller than the accessory cusps. The tooth base is linguolabially thin and imperfectly preserved. Based on these attributes, the tooth is most reminiscent of *Saivodus*.

An almost complete mold of an isolated tooth is preserved (UMMP 119346), bearing a single main cusp and two pairs of curved accessory cusps (Fig. 4D–G). The main cusp is missing its distal end but shows a biconvex aspect in cross-section and bears no evidence of surface ornamentation. The base of the tooth is reniform and shows a pair of delicate, elliptical basolabial projections flanking the median basolabial groove (Fig 4E). The tooth is deeply depressed basolabially, and shows three elongate foraminal openings (Fig. 4F). Given the overall shape of this tooth, the expanded central cusp, the presence of a large basal depression, a pair of thin, elliptical basolabial projections, and an approximately square orolingual ridge, we identify this tooth as *Saivodus striatus*. The void spaces of the two pairs of basolabial projections are exposed at the surface and cannot be rendered in Figure 4.

CTENACANTHIDAE Dean, 1909
INDETERMINATE SPECIES

Ctenacanthidae indet. (UMMP 119342).— A single tooth is preserved as a void exposed on the labial surface, with the main cusp plunging into the matrix lingually (Fig. 4B). The tooth possesses a large main cusp curving lingually and bounded on both sides by a single, minute lateral cusp. The main cusp is ornamented by delicate longitudinal ridges. The base of the tooth is broad, and no ornament is visible on the orolingual surface of the void. Given the preservation of this tooth, only a ctenacanthid affinity can be determined.

SYMMORIIFORMES Zangerl, 1981
STETHACANTHIDAE Lund, 1974
STETHACANTHUS Newbrey, 1889
INDETERMINATE SPECIES

cf. Stethacanthus sp. (UMMP 119345).— A single curved tooth cusp is preserved as a void (Fig. 4H, I). The cusp is exposed at its linguoproximal margin and is almost entirely bounded by matrix. The tooth base is approximately reniform, with the ventral margin possessing a single shallow pit. The lingual heel of the tooth is proportionately short relative to the remainder of the base. The labial surface of the main cusp is deeply convex, although the lingual surface is not especially concave. Presuming this is a median cusp, it is far forward of the tooth base. All of these characteristics suggest a symmoriid affinity, and we tentatively assign this taxon to cf. *Stethacanthus* sp. (see Ginter et al., 2010, fig. 58).

STETHACANTHUS DEPRESSUS St. John and Worthen, 1875

Stethacanthus depressus (UMMP 118281).— Stethacanthids are represented in the Marshall Sandstone by isolated dorsal fin spines (e.g., UMMP 118281) and were referred to *Stethacanthus depressus* by Eastman (1903). Although preservation compromises the description of these spines, UMMP 118281 resembles other stethacanthids in its broad and concave anterior margin and a shorter convex posterior margin (Fig. 3B). As noted by Eastman (1903) the surface of the spine bears delicate impressions of vasculature and no evidence of ornamentation, indicating the spine was deeply inserted in the body. Because this specimen does not show any evidence of the basal plate, it is unlikely that it was contiguous with the spine as in *Akmonistion* (Coates and Sequeira, 2001; Maisey, 2009).

COCHLIODONTIFORMES Obruchev, 1953
COCHLIODONTIDAE Owen, 1867
PSEPHODUS Morris and Roberts, 1862
INDETERMINATE SPECIES

cf. Psephodus sp. (UMMP 119349).— A toothplate part and counterpart were preserved as an impression on the coun-



FIGURE 5 — Cochliodonts from the Marshall Sandstone, represented by partial teeth and associated impressions. **A**, *Psephodus* sp. (UMMP 119349). **B**–**F**, *Cochliodus contortus* (UMMP 119343), photographed in cross-section (**B**) and µCT rendered in lateral aspect (**C**, labial view; **D**, lingual view with darkened portion representing rendered void), and µCT rendered in occlusal (**E**) and abocclusal aspects (**F**). Scale bars equal 5 mm.

terpart (Fig. 5A). The curvature of the occlusal surface of the toothplate is relatively minimal. The counterpart impression and edges of the part specimen preserve fine stippling along the occlusal surface, remnants of the tubular dentine that penetrated this cochliodont toothplate in life. Given these characteristics, an attribution to cf. *Psephodus* is given.

COCHLIODUS Agassiz, 1838
COCHLIODUS CONTORTUS Agassiz, 1838

Cochliodus contortus (UMMP 119343).— A partial right anterior mandibular toothplate was preserved in two parts and bisected along its long axis to create a labiolingual cross-sec-

tion (Fig. 5B–F). The distolingual edge gently curves basally, producing a U-shaped occlusal surface (Fig. 5C), whereas the mesiolabial edge loosely spirals into itself and forms an unfurled whorl (Fig. 5D). The dental battery was imbricated in life, evidenced by a pronounced shelf preserved at the labial margin—although this tooth plate was found in isolation (Fig. 5E). A stippling of tubular dentine is evident along the ventral margins of the fossil, further evidencing a cochliodontid affinity (Fig. 5F).

OSTEICHTHYES Huxley, 1880
SARCOPTERYGII Romer, 1955
DIPNOI Müller, 1845
INDETERMINATE SPECIES

No sarcopterygians have previously been identified from the Marshall Sandstone.

Referred Specimen.— Two partially preserved, overlapping pleural ribs were preserved (UMMP 119344; Fig. 3C). Given the size of these ribs and the shape of their bipartite proximal portion, we suggest a lungfish affinity. Unfortunately, lungfish ribs are not diagnostic enough to provide a better taxonomic assessment. Ceratodontiforms (represented by gnathorhizids in the Pennsylvanian) become prevalent after the Devonian, but a fleurantiid-phaneropleurid clade of freshwater and brackish Devonian lungfishes survived the Hangenberg Crisis and diversified in the Carboniferous (Challands et al., 2019). Given the inferred depositional setting of the Marshall Formation, we cannot rule out these taxa when attempting to identify lungfish remains. As such, only a broad dipnoan affinity may be attributed.

ACTINOPTERYGII sensu Goodrich, 1930
INDETERMINATE SPECIES

No actinopterygians have previously been described from the Marshall Sandstone.

Referred speciemen.— An isolated left cleithrum (UMMP 119347) of a small palaeonisciform-like ray-finned fish was preserved on the surface of a sandstone matrix (Fig. 3D). The external surface of this bone is ornamented with delicate, undulating ridges that form a fingerprint-like pattern at the base of the posterior margin. The anterior margin of the bone lacks the unornamented surface generally inferred to be the point of overlap for the opercular series. Instead, the anterior end of this bone, where it would articulate with the clavicle, is blunt and ornamented with closely spaced ridges. The posteroventral margin of the cleithrum is notched, representing the point of insertion for the pectoral fin. The cleithrum extends dorsally, and tapers towards its distal end. The shape and ornamentation of the bone suggests an actinopterygian affinity, similar to "palaeonisciforms." µCT of the specimen shows zero contrast between the fossil and the surrounding matrix, making description of the mesial margin of the bone impossible.

DISCUSSION

The new specimens from the Marshall Sandstone of Michigan modify our outlook of vertebrate research in the Paleozoic of Michigan. Instead of an early Carboniferous virtually devoid of vertebrate remains, we show Mississippian seas covering what is now Michigan were inhabited by several types of cartilaginous fishes, a dipnoan lobe-finned fish, and a "palaeonisciform" ray-finned fish. The presence of osteichthyans in the Marshall Sandstone, although previously undersampled in Michigan, is not unusual for this period elsewhere—ray-finned fishes are abundant by this interval (Henderson et al, 2022), encompass a breadth of body shapes by the late Mississippian (Lund et al., 2012), and may possess cryptic phenotypic variation as evident in later Paleozoic intervals (Argyriou et al., 2022; Figueroa and Andrews, 2022). Additionally, chondrichthyan specimens of the Marshall Sandstone frequently are preserved as molds and are virtually unrecognizable on initial examination of slabs. Recognition and identification of these remains has been made possible largely by the advent of CT use in paleontology (Rahman and Smith, 2014; Racicot, 2016), which allows both penetration of slabs to see void spaces not exposed on the surface, as well as the ability to generate three-dimensional models of anatomical elements that permit proper identification.

Given the poorly preserved nature of most of the specimens described here, it is not surprising that the Marshall Sandstone's vertebrate fauna has largely been overlooked since its earliest description in the 1800s (Winchell, 1862). However, the Marshall and other clastic sedimentary formations in Michigan do preserve many specimens well enough for taxonomic identification and comparison. The better preserved vertebrate fossils in our samples are in the otherwise largely non-fossiliferous parts of the formation. In more heavily fossiliferous slabs, there are voids and impressions in the shape of shark teeth, but few pieces of preserved bone. Invertebrate impressions are also common among the fossiliferous portions of the Marshall Sandstone, and three-dimensionally preserved bivalves are likewise visible via µCT.

This fish fauna from the Mississippian of southern Michigan also provides novel data on a poorly sampled interval of the late Paleozoic. Through the Late Devonian to the Mississippian there were important glaciation events that changed depositional settings mostly in the southern hemisphere, but reached up into North America (Isaacson et al., 2008). Due to this, fish faunas of Late Devonian and Mississippian age are relatively rare at higher paleolatitudes, such as South America and Africa, where only occasional isolated remains with few diagnostic features have been found (Janvier and Melo, 1987; Janvier and Maisey, 2010; Gess, 2016; Figueroa and Machado, 2018; Rezende et al., 2021). Moreover, within North America, similar-aged fish faunas are found mostly in limestone strata (Smith et al., 2017; Hoenig, 2019; Hodnett et al., 2024b), in contrast with the clastic shallow marine deposits of the Marshall Sandstone. Given the presence of this rather diverse fauna in Mississippian clastic deposits, it might

be feasible to expect that other similar deposits from North America and depauperate localities in South America might yield additional important fossil fish discoveries.

This work also serves to highlight the importance of avocational and educational paleontology trips in forwarding the field of paleontology and biology more generally. Although we do not have full collection details of previously collected materials, most, if not all, of the Marshall Sandstone vertebrate specimens in the UMMP collections were found not by professional paleontologists, but by quarry workers or avocational collectors (Dorr and Moser, 1963). As previously mentioned, the new specimens described herein were collected during a trip with the avocational group "Friends of the University of Michigan Museum of Paleontology" (FUMMP), and on two subsequent graduate student field trips. FUMMP have previously aided in other fossils discoveries (e.g., Kesling, 1982), and have elsewhere been recognized for their contributions in collecting and promoting paleontological science (Fisher et al., 2012; Clark, 2014). Without educational and avocational trips to less-visited fossil localities like the Blue Ridge Esker of the Marshall Sandstone, these important repositories of information about ecosystems in Earth's past would continue to be unexplored, in favor of other sites with better preservation and more easily identifiable and charismatic fossil taxa.

CONCLUSIONS

This work offers a direction for future research on the understudied Carboniferous of Michigan: detailed sampling of poorly known localities by a diverse set of collectors has the potential to yield important fossil discoveries. The Mississippian Marshall Sandstone of Michigan represents an important glimpse into shallow marine vertebrate and invertebrate faunas from the northern US and aids in our understanding of taxonomic diversity and distribution from a relatively depauperate portion of the vertebrate fossil record. Moreover, this work details the importance of μCT in visualizing difficult paleontological material—here due to poor visual contrast between fossil and matrix or due to fossils preserved as void spaces.

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AUTHOR CONTRIBUTIONS

All authors participated in fieldwork to discover fossils. JVA wrote and edited text, analyzed data, and created figures. EAS proposed the study, wrote and edited text, and CT-scanned specimens. RTF wrote and edited text, analyzed data, and photographed specimens.

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