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Vertebrate Assemblages of the Skelley Limestone (Conemaugh Group : Carboniferous, Gzhelian) in Noble and Muskingum Counties, Ohio

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VERTEBRATE ASSEMBLAGES OF THE SKELLEY LIMESTONE (CONEMAUGH GROUP: CARBONIFEROUS, GZHELIAN) IN NOBLE AND MUSKINGUM COUNTIES, OHIO

A thesis submitted in partial fulfillment of the
requirements for the degree of
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By

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Daniel Austin Cline ENTITLED Vertebrate Assemblages of the Skelley Limestone (Conemaugh Group: Carboniferous, Gzhelian) in Noble and Muskingum Counties, Ohio BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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ABSTRACT

Cline, Daniel Austin. M.S. Department of Earth and Environmental Sciences, Wright State University, 2022. Vertebrate Assemblages of the Skelley Limestone (Conemaugh Group: Carboniferous, Gzhelian) in Noble and Muskingum Counties, Ohio.

Three outcrops of the Gzhelian-aged Skelley Limestone (Casselman Formation, Conemaugh Group) were explored for vertebrate macrofossils and vertebrate microremains. The purpose of this exploration was to construct a better ecological history of the marine communities in the Late Pennsylvanian of eastern Ohio. Bulk limestone samples were collected, washed with acid, sieved and the resulting residues produced 21 distinct taxa of near-shore marine vertebrates. Osteichthyans were represented by an unknown palaeonisciform, an unknown platysomid, and an unknown palaeoniscoid. Holocephalians were represented by symmoriforms, helodontiforms, cochliodontiforms, and petalodontiforms. Elasmobranch groups included ctenacanthiforms and euselachians which contained representatives of hybodontiforms, protacrodontiforms, and neoselachians. All osteichthyan taxa are reported from the Skelley Limestone for the first time. Furthermore, three chondrichthyan genera, *Ossianodus*, *Diablodontus*, and *Adamantina*, represent significant extensions to the temporal or geographic distributions of these genera. While the few previous studies on the fauna of the Conemaugh Group have indicated that the marine units within were fairly biodiverse overall, these studies focused primarily on invertebrates or only specific groups of vertebrates. Significantly less work has been done towards overall analyses of the vertebrate fauna of the constituent cyclothems of the Conemaugh Group. This examination of the Skelley Limestone shows that marine vertebrate biodiversity at the end of the Conemaugh Group, and by extension the Pennsylvanian, remained high. Further analysis of the Skelley

Limestone, along with similar explorations of other stratigraphic units with the Conemaugh Group, may generate further revelations in the paleobiogeography, biostratigraphy, and evolutionary history of a number of Paleozoic marine vertebrates.

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DEDICATION

To my family for their love and support: my parents, Brent and Deborah, my brother, Matthew, and my sister-in-law, Alexis.

1. INTRODUCTION

The North American sequence stratigraphy of the Carboniferous Period is divided into two subperiods: the Mississippian and the Pennsylvanian (Moore, 1933). The reason for this distinction is that rocks of the lower Carboniferous (Mississippian) of North America primarily consist of marine limestones (Menning et al., 2006) whereas rocks of the upper Carboniferous (Pennsylvanian) of North America consist of a more diverse assemblage of sedimentary rocks such as the coals, shales, and sandstones of the Conemaugh Group (Menning et al., 2006). The appearance of this diverse assemblage of rocks on the North American craton was driven by variations in depositional forces during the Pennsylvanian Period (Sturgeon et al., 1958). Among these forces, the climate-driven rise and fall of sea levels (called cyclothems) led to the deposition of alternating marine and terrestrial sediments into the Appalachian foreland basin during the Kasimovian and Gzhelian Faunal Stages (307.0 +/- 0.1 to 298.9 +/- 0.15 million years ago), which are now referred to as the Conemaugh Group (Moore et al., 1944; Gradstein et al., 2004).

The Late Carboniferous featured the tectonic assembly of the supercontinent Pangaea, which, in North America, was primarily expressed as the Appalachian Orogeny (Feldman and Hackathorn, 1996). While previous orogenic events had already begun to shape the Appalachian foreland basin as far back as the Early Ordovician, these were primarily the result of subduction between tectonic plates while the Appalachian Orogeny was the result of collision (Ettensohn, 2008). This orogeny led to the meeting of the North American, Eurasian, and African cratons and also caused local foreland basins to form on either side of this orogenic belt, of which the Appalachian foreland basin is an example (Feldman and Hackathorn, 1996).

Much of Pangaea, especially the land around the Appalachian foreland basin, appeared tropical and featured vast assemblages of lycopsid-dominated rainforests (Moore, 1933). These assemblages later fossilized as coal, from which the Carboniferous Period is named, and the coal-producing rocks of the Appalachian foreland basin led to the naming of this broad period of time as the Pennsylvanian, after coal deposits in the U.S. state of Pennsylvania (Moore, 1933). As the late Carboniferous progressed, a Late Paleozoic Ice Age began and persisted in the southern parts of Pangaea (Godderis et al., 2017). The climatic fluctuations related to this change had an impact on local and global sea level, and the Conemaugh Group preserves a portion of this record of sea level change in the Appalachian foreland basin (Sturgeon et al., 1958).

Remains of vertebrates living in or near the Appalachian foreland basin were deposited into the sediments of the Conemaugh Group (Feldman and Hackathorn, 1996). As changing climate and sea level led to changes in the depositional character of the Conemaugh Group, the assemblages of vertebrate fossils also changed: freshwater fishes can be found in riverine deposits, tetrapods from floodplain deposits, and marine vertebrates from marine deposits (Feldman and Hackathorn, 1996). Despite the fact that a number of charismatic Paleozoic vertebrates are known from the Conemaugh Group – the shark *Petalodus ohioensis* was originally recovered from these rocks (see Safford, 1853;

Itano and Carpenter, 2020) – many of the high-stand sequences of the Conemaugh may require further exploration by vertebrate paleontologists.

Certain units of the Conemaugh Group, such as the Brush Creek Limestone, Cambridge Limestone, and Ames Limestone have produced significant amounts of vertebrate remains (see Hansen, 1986). Other layers, such as the Skelley Limestone: a thin set of two limestones that includes an intervening shale unit that was deposited during a Gzhelian transgression into the Appalachian foreland basin., as well as the Noble and Portersville layers, have received little attention and only a handful of specimens have been recovered (Hansen, 1986; Huffer, 2007). The goal of this study was to conduct a closer examination of the Skelley Limestone, thoroughly describe any vertebrate fossils present, and compare assemblages across multiple sites to assess the geographic range (see Table 1) and diversity of the fauna in the Skelley Limestone.

Table 1. Details of the localities included in this investigation.

Locality Description	**Coordinates**
Roadcut along Interstate-77 near Mile Marker 33	N 39.85389 W 81.54449 (+/- 65 meters).
Roadcut along Rockville Rd, near Blue Rock, Ohio	N 39.78398, W 81.85240 (+/- 50 meters).
Roadcut along Wilsonwood Rd, near Blue Rock, Ohio	N 39.79467, W 81.82552 (+/- 50 meters).

2. HYPOTHESIS

Despite a poor record of study, vertebrate material has been reported from the Conemaugh Group, and the Skelley Limestone specifically, before, though the biodiversity of vertebrates within the unit is not well known (Neff, 1965; Baker, 1967; Hansen, 1986). The results of this study could reveal that vertebrate biodiversity in the Skelley is higher than previously reported, is lower than previously reported, or is as poorly understood as previously reported. High vertebrate biodiversity in the Skelley Limestone would imply high primary productivity in this ecosystem during the Carboniferous and may reveal paleobiogeographic information relating to the evolution and migration of vertebrate taxa during this interval. Conversely, low (or unknown) vertebrate biodiversity in the Skelley could demonstrate that depositional forces during the formation of the unit were not conducive to the preservation of vertebrate fossils. It could also imply that ecological conditions in the aquatic ecosystems during this time did not allow for the colonization of the area by vertebrates, or that the methodology employed in this investigation (and the methodologies of Neff, 1965 and Baker, 1967) is an inadequate tool in understanding the vertebrate paleoecology of the Skelley Limestone.

Because the Skelley Limestone is thin vertically and partially dominated by siliciclastic sediment, it is possible that it was deposited in shallow marine water. This, in turn, implies that the depositional environment of the Skelley may grade into other shallow water environments, which sometimes are geographically diverse even over a small area. Therefore, there exists the possibility that assemblages at each site will be similar or dissimilar to one another. Similar faunas at each locality will imply that the Skelley Limestone represented an ecosystem (and depositional environment) that was geographically broad. Dissimilarity between the faunas, on the other hand, could imply methodological problems or subtle variations in the ecology or depositional character of the Skelley.

3. PROCEDURE

Over the course of this study, outcrops exposing the Skelley Limestone were identified and explored (see Table 1). Because the sites explored are all exposures on large roadways, a Right-of-Way Permit was obtained from the Ohio Department of Transportation (Permit No. 10-13836) to ensure the safe exploration and recovery of samples from these localities.

At each outcrop, GPS coordinates were taken digitally (see Table 1). The stratigraphy of the Skelley, as well as the beds immediately above and below it, were characterized, measured, and recorded to aid in the construction of stratigraphic columns (see below). These columns are used to report the location of recovered fossils within the vertical expanse of the Skelley, while coordinates report their location in map view (see Table 1). These columns also form the basis of stratigraphic correlation between the sites and provide context relating to any variances in the vertebrate fauna recovered during the study. Because much of the field work done in this study occurred over the global COVID-19 (SARS-CoV-2) pandemic, additional measures as recommended by the United States Center for Disease Control and Transmission were taken to ensure a safe environment.

Specimens were primarily recovered from Skelley samples through micropaleontological techniques similar to those of Armstrong and Brasier (2005). Bulk samples of the Skelley Limestone were gathered from each site, and these samples were soaked in a 10% solution of formic acid. The volume of each bulk sample was approximately 0.015 cubic meters. Once sufficient dissolution of the sample occurred, the resulting residue was rinsed with water to remove excess acid, sifted in a 250-μm sieve (U.S #80), and then dried in the air. Vertebrate fossils visible to the naked eye and under stereomicroscopy (AmScope and Omano stereomicroscopes, 10x – 40x magnification) were removed, imaged, and curated into the Wright State University Paleontological Collections (Institutional abbreviation: WSU). Vertebrate fossils are systematically described and the language describing their anatomical features primarily followed the work of Stahl (1999) and Ginter et al. (2010).

Imaging of specimens was done using a process of digital image stacking. A Nikon D7100 DSLR camera was combined with two lenses, one a 4x infinity-corrected Nikon microscope objective lens, the other a macro extension tube lens, before being mounted to a StackShot macro rail. To obtain the images, the camera system moved closer to the specimen along the rail at incremental (<1 millimeter) steps with one image being taken at each step along a fixed focal plane. These photos were then saved as .jpg files to be processed by the Helicon Focus 7 program. The exact set of images would be selected manually and combined by the program to create the final stacked image. Within such composite images, the specimens would be isolated through the use of the Adobe suite of image-editing software and saved as either .tiff or .jpg files. The final results of this process were images of the selected specimens that show greater depth and identifiable features than through traditional microscopy.

4. HISTORY OF STUDY ON THE CONEMAUGH GROUP

While fossils have been recovered by humans in the Ohio River Valley during the later Pleistocene and Pre-Columbian era of North American history, the first fossils to enter the historical record from this region were recovered in 1739 (Bellin, 1755; Jillian, 1936; Mayor, 2005). As part of the end of the Age of Enlightenment, the rest of the eighteenth century featured the publication of somewhat conflicting reports as to the nature of these and other fossils as the field of paleontology was conceptualized (see Franklin, 1767).

The nineteenth century featured the rise of geology as a scientific discipline, that began with the work of Hutton in the late eighteenth century (1795), though it culminated with the publication of Lyell's *Principles of Geology* (1830-1833). The propagation of the Industrial Revolution in North America over the 1750-1850 interval led to an interest in the geological exploration of coal as a source of fuel. Wide-ranging outcrops of coal in Europe and North America were thought of as having been deposited during a "coal-rich," or "Carboniferous," interval of time (Conybeare and Phillips, 1822). These factors led to the work of Bowen (1848) reporting on the occurrence and geology of coal beds in the Conemaugh region of Pennsylvania, which were also thought to have been deposited during the Carboniferous Period of time. These coal beds were immediately interpreted by Bowen (1848) and Lyell (in Bowen 1848) as relating to fossilized forested, paludal environments. Similar coal seams had previously been reported from Ohio, and fossils of both plants and animals in the coals of eastern Ohio were first reported by Hildreth (1836), who correlated the rocks of Ohio to Pennsylvania and interpreted both marine and non-marine sequences based on the presence of plant fossils in some horizons and marine animals in others.

Geologic literature in eastern Ohio from 1850-1869 was primarily concerned with the exploration of coal. However, a chondrichthyan, *Petalodus ohioensis*, was described from limestones in what would become the Conemaugh Group by Safford (1853) during this interval of history. This description reaffirms the marine character of portions of the coal-bearing rocks in eastern Ohio and establishes the possibility that marine vertebrates such as *Petalodus* were able to colonize many of these marine depositional environments.

The study of the coal-bearing portions of Carboniferous rocks in the Conemaugh region of Pennsylvania and the correlatable rocks in eastern Ohio remained an important facet of local scientific literature during the 1870s and 1880s (Macfarlane, 1877; Lesley, 1886). Considering the importance of coal to the economy of the twentieth and twenty-first centuries, the study of the geology of coal in this and other North American regions continues to the present day. Because coal consists of the densely packed remains of fossil plants, many reports on fossils made during the late 1800s tend to focus exclusively on the plant life of the Carboniferous of this region (see Lesley, 1886).

While vertebrate fossils were not totally ignored from these rocks during this interval of time (see Safford, 1853), investigations into vertebrates did not begin in earnest until the exploration work of Cope (1885). However, work in fossil vertebrates from this time was mostly centered on tetrapods (see Feldman and Hackathorn, 1996), and the rocks of the region were all generally referred to as “coal-measures” with little emphasis on stratigraphic boundaries (Newberry, 1870).

The latest 1800s also featured a shift in stratigraphic nomenclature evidenced by Selby’s (1887) division of the coal measures of the Pennsylvania-Ohio region into Upper and Lower Measures. The rocks that would become the Conemaugh Group were roughly correlatable to what Selby (1887) referred to as “Lower Barren Measures” (see Wanless, 1939). It was not until the early years of the twentieth century that Condit (1912) began to characterize these rocks as “the Conemaugh Formation,” and it was around this time that the Skelley Limestone was first recognized as a distinct lithographic unit.

By the 1930s, Conemaugh rocks were generally referred to in terms broader than that of a formation, such as the “Conemaugh Series” (Moore, 1933) and the “Conemaugh Strata” (Wanless, 1939). Moore, et al. (1944), however, continued to refer to these rocks as the Conemaugh Formation, and it was not until the work of Flint (1965) that the Conemaugh rocks were raised to the level of a group and the Skelley Limestone was considered to be part of the Casselman Formation (see Figure 1).

Newberry, 1870	Selby, 1887	Condit, 1912	Moore, 1933	Wanless, 1939	Moore et al, 1944	Flint, 1965		
"Coal Measures"								
	"Lower Barren Measures"	"Conemaugh Formation"	Conemaugh Series	Conemaugh Strata	Conemaugh Formation	Conemaugh Group	Casselman Formation	Skelley Limestone
							Glenshaw Formation	
		Skelley Limestone		Skelley Limestone				

Figure 1. This diagram details the historical transition in understanding of the stratigraphy of the Pennsylvania/Ohio “Coal Measures” into what is today called the Conemaugh Group. The position of the Skelley Limestone within each named section is also reported where available. The work of Newberry (1870), Selby (1887), Condit (1912), Moore (1933), Wanless (1939), Moore et al. (1944), and Flint (1965) was compiled in the creation of this diagram.

Paleontologically, the early and mid-twentieth century featured continued focus on the tetrapods from this region, to the exclusion of other vertebrate groups (Romer, 1930; Carrol and Baird, 1968). However, the marine beds of the Conemaugh Series had been known to researchers since at least the beginning of the nineteenth century (see Hildreth, 1836) and reports of marine vertebrates in these rocks began in the 1960s (see Sturgeon and Hoare, 1968).

Biostratigraphic investigations on vertebrates in the late Paleozoic of this region began in the 1970s (Lund, 1976) and continue well into the twenty-first Century (Lucas, 2013). These investigations, however, generally focus more on terrestrial taxa from the latest Pennsylvanian and Permian Periods (Lucas, 2013). While marine vertebrates have been known from the Pennsylvanian limestones of this area since the work of Safford (1853), the community composition of marine vertebrates from limestones within the Conemaugh Series (such as the Skelley Limestone) does not appear in the literature except for the work of Hansen (1986). Hansen (1986) reported numerous chondrichthyan remains across several marine beds within the Conemaugh Group. However, many of the vertebrate microremains he reported were taxonomically indistinct, and major changes in Paleozoic vertebrate taxonomy have occurred since Hansen's unpublished Ph.D. dissertation (1986), which have potential to lend context to many of the trends he observed.

5. RESULTS

The outcrops reported in Table 1 of the Skelley Limestone were surveyed regularly from 2019 to 2021. Measurements taken at these localities allow for an improved understanding of the geology in and around these Skelley Limestone outcrops. Fossils recovered during these field investigations are systematically described below and their biostratigraphic position in the Conemaugh Group is also discussed.

5.1 GEOLOGY

All sites investigated are located in southeastern Ohio (see Figures 2, 3, and 4), on what could be regarded as the eastern limb of the Cincinnati Arch or the western limb of the synclinorium which contains the Permian-aged Dunkard and Pennsylvanian-aged Appalachian foreland basins. The deformation leading to the formation of the Cincinnati Arch and the Appalachian foreland basin appeared to occur contemporaneously to the deposition of the Conemaugh Group. In the vicinity of these localities, other subunits of the Conemaugh Group can be observed (the Ames Limestone, for example, appears in outcrop at the Rockville Rd exposure). Other upper Carboniferous units, such as the Allegheny and Pottsville Groups, can be observed to the north and west of the area, while the Monongahela Group is present at higher elevations to the east and south (see Figure 3). Rare outcrops of the Dunkard Group, as shown in the southwest corner of Figure 4, are also present above these Carboniferous exposures (Sulcher et al., 2006).

The outcrop at the I-77 Skelley Limestone locality was characterized by a series of rock units composed primarily of mudstones, siltstones, and sandstones (see Figures 5, 6, and 7). The initial base of the exposure had stratigraphic layers no larger than 24.0 cm, followed by mudstone, siltstone, and shale layers ranging between 50.0 to 100.0 cm (Figures 6 and 7). The Skelley Limestone was situated just above the last of the large (> 50.0 cm) units and was distinguished by its fossiliferous, nodular facies (see Baker, 1967; Fahrer, 1996) (Figure 5). Above the Skelley Limestone were several smaller rock units, the largest measuring 31.0 cm in height. Unidentified plant fossils were noted in a bioturbated layer 54.0 cm above the uppermost exposure of the Skelley Limestone.

In contrast to the I-77 site, the exposure of the fossiliferous Skelley Limestone at the Rockville Rd site was composed of fewer stratigraphic units, but with the exception of the Skelley Limestone and its intervening mudstone layer, each unit was 40.0 cm or greater in height (see Figures 8 and 9). The largest of the stratigraphic units at this site was the mudstone immediately overtop the Skelley Limestone, which measured 250.0 cm in height. Another notable difference between the I-77 and the Rockville Rd sites was the height of the Skelley Limestone. At the I-77 site, the maximum height of the Skelley Limestone was 10.0 cm while at the Rockville Rd site, the maximum height was 30.0 cm.

The outcrop at the Wilsonwood Rd site produced slabs of the Skelley Limestone similar in height and dimension to those found at the Rockville Rd site, although these slabs were significantly more glauconitic and fragmentary vertebrate material was visible on the surface without the aid of magnification. Measurements of the stratigraphic units at the Wilsonwood Rd site were not obtained due to dense vegetation that covered most of the site, which precluded accurate measurements.

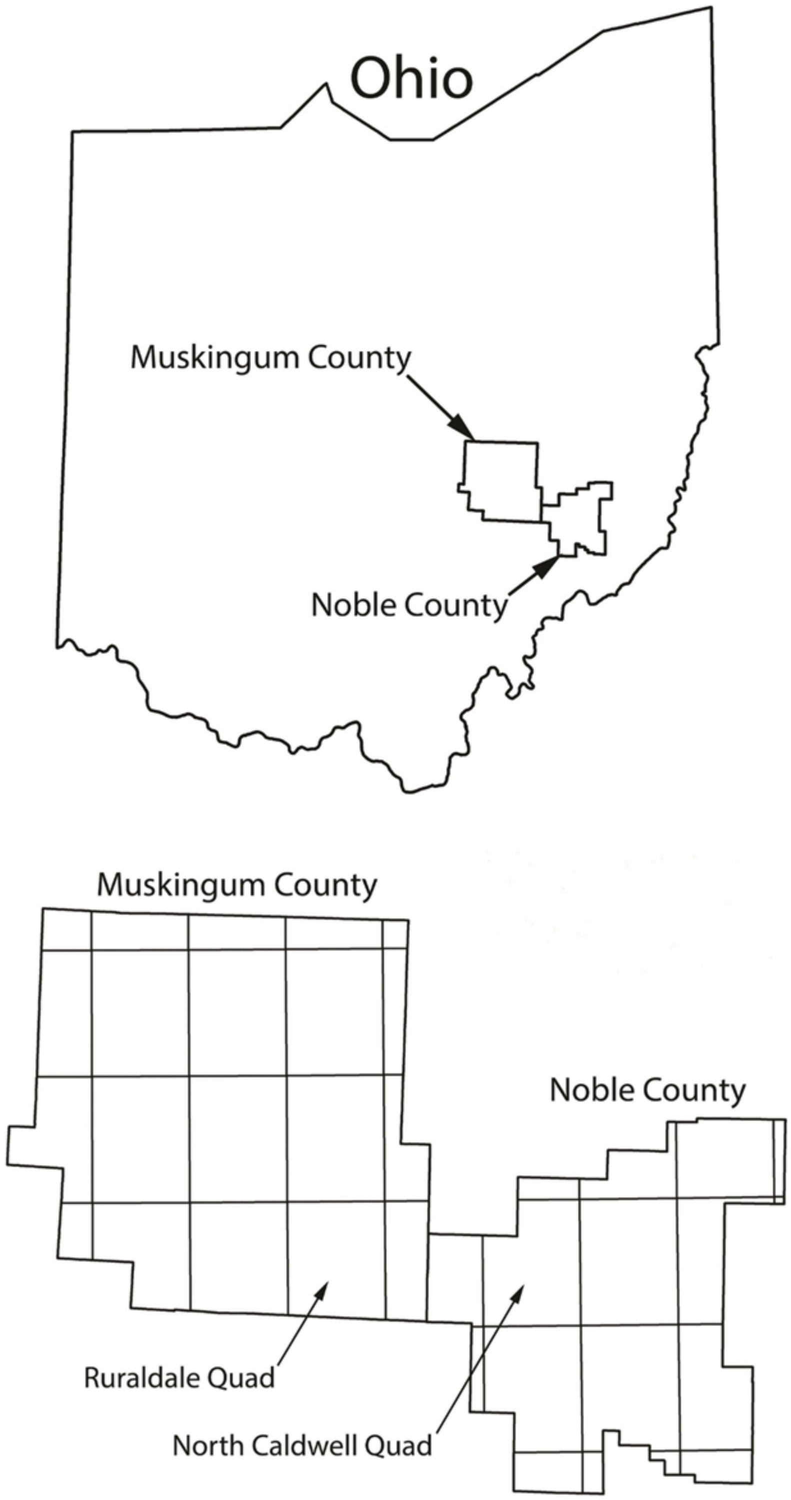


Figure 2 – Map of the state of Ohio with Muskingum and Noble Counties highlighted, along with the location of the Ruraldale Quad within Muskingum County and the North Caldwell Quad within Noble County.

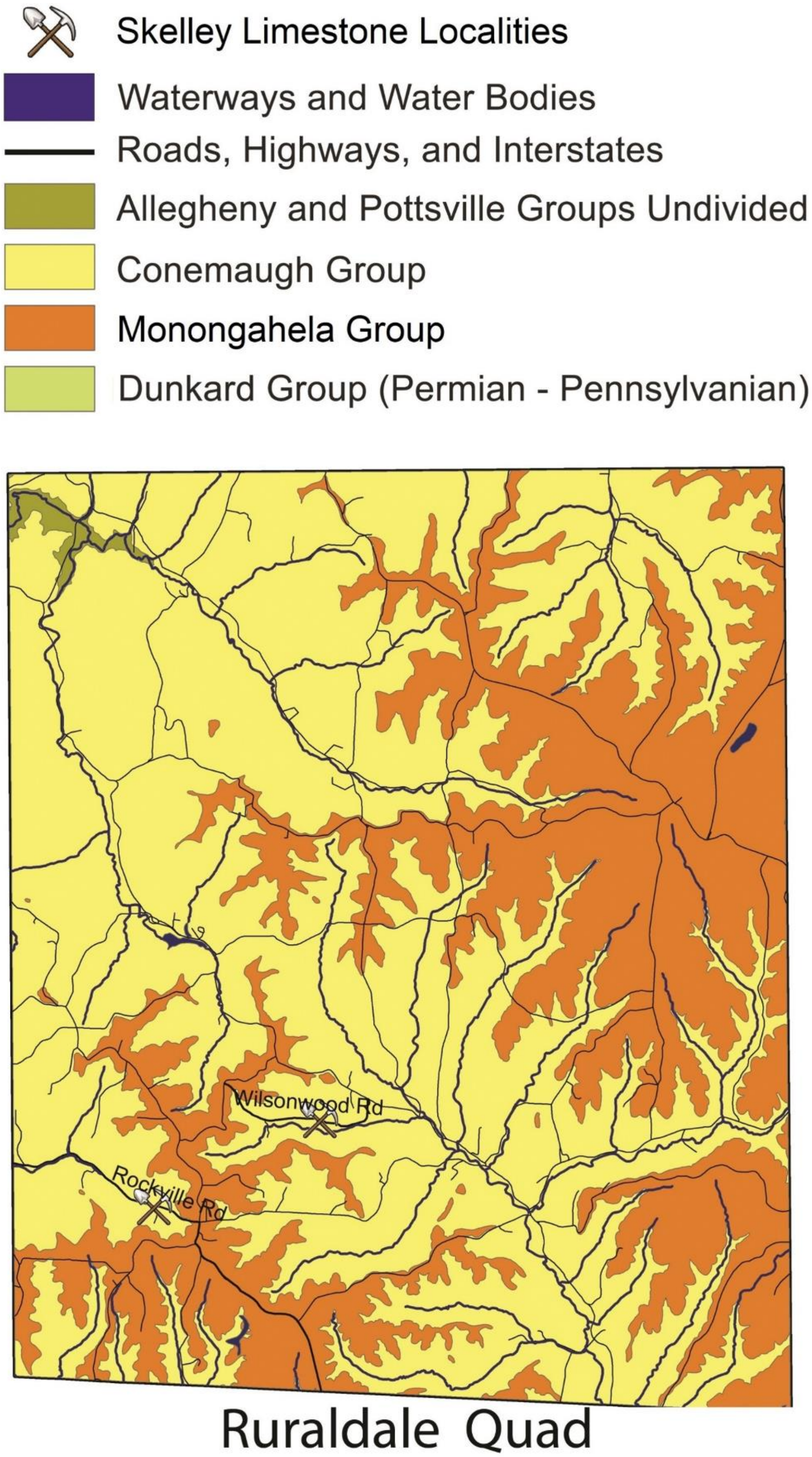


Figure 3 – The Ruraldale Quad showing the location of the two Skelley Limestone sites from Muskingum County at Rockville Rd and Wilsonwood Rd.

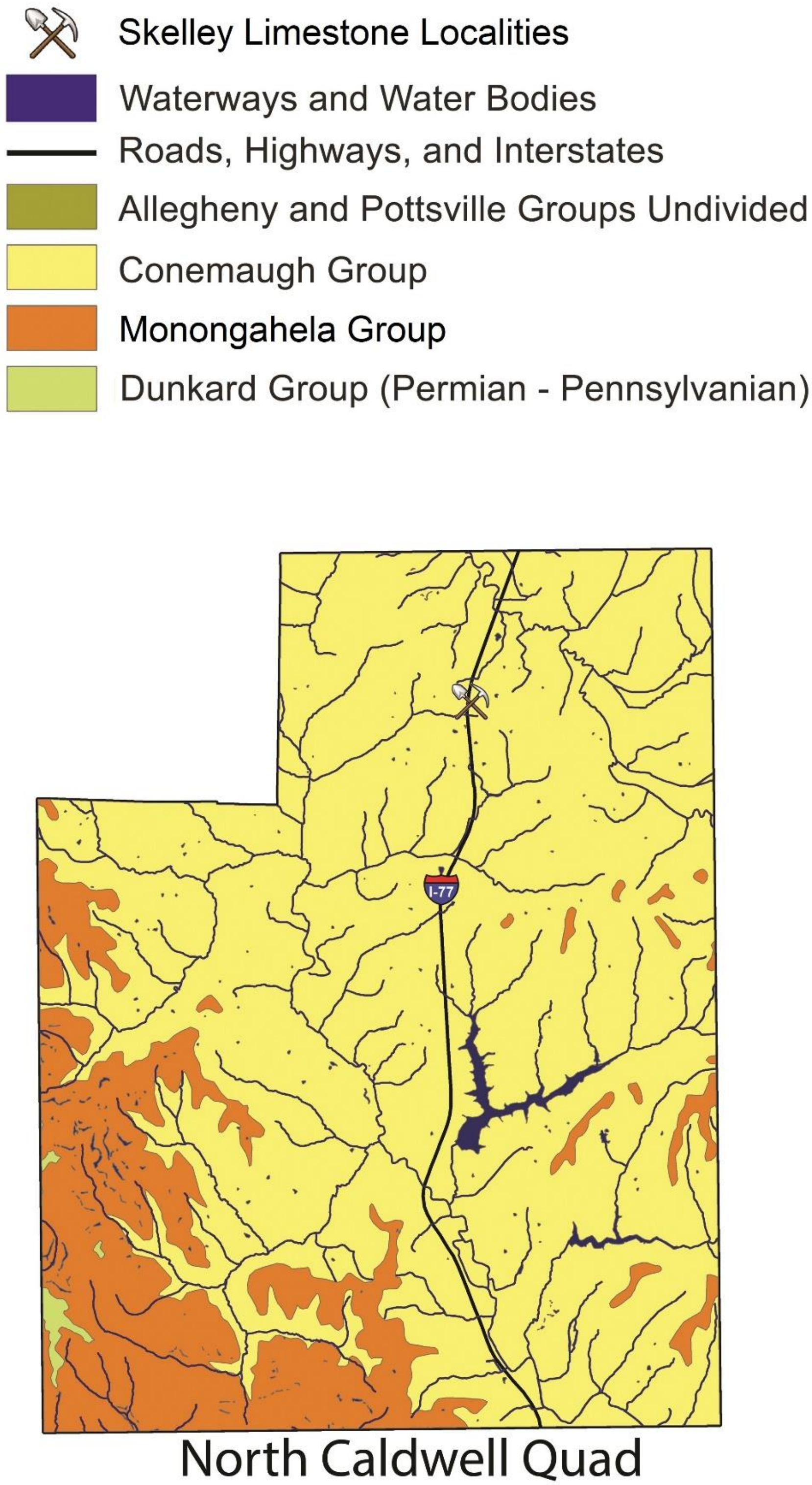


Figure 4 – The North Caldwell Quad in Noble County showing the location of the I-77 Skelley site at Mile Marker 33.5.

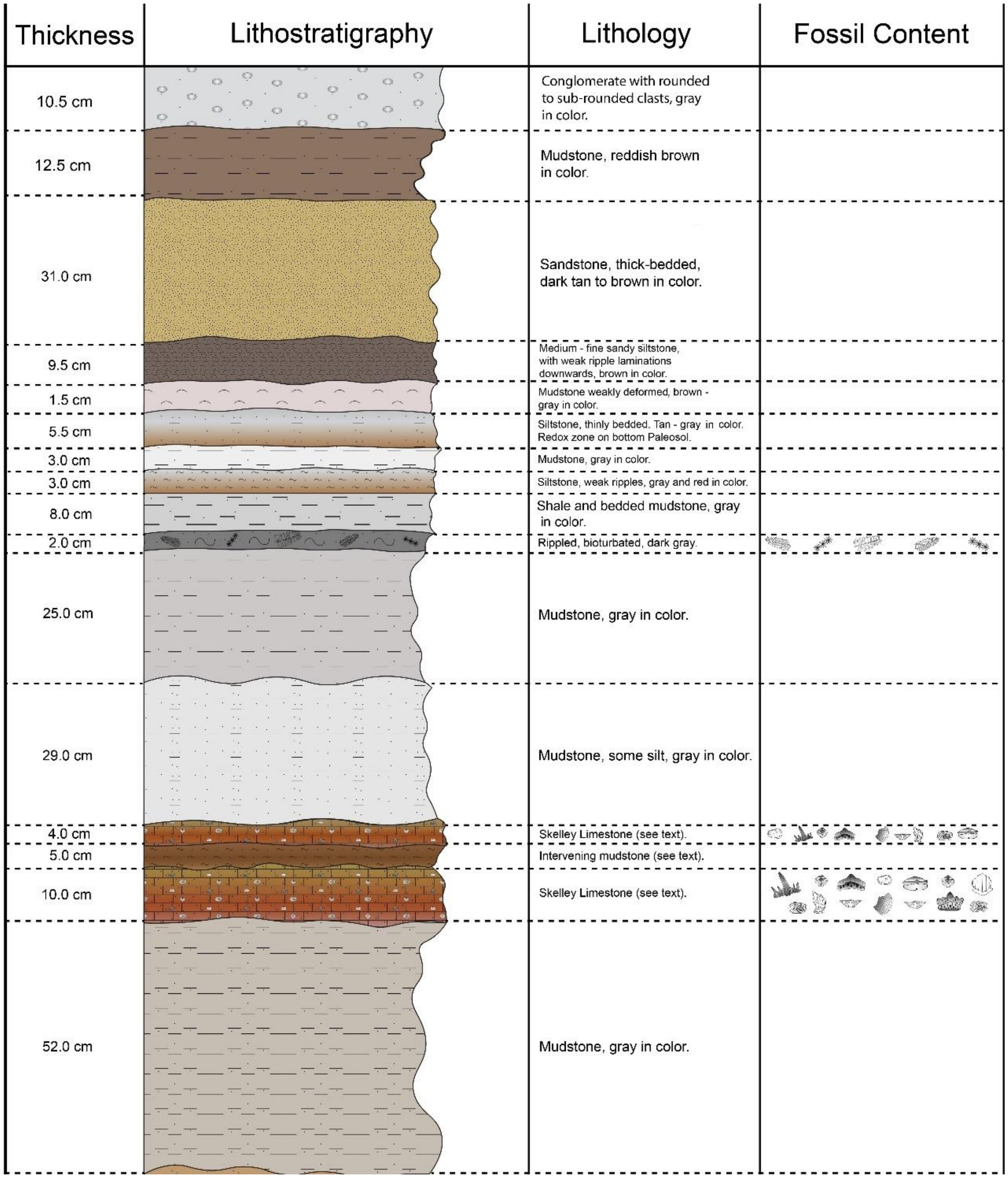


Figure 5 – Uppermost section of the stratigraphic column from observations of the I-77 Skelley Limestone site.

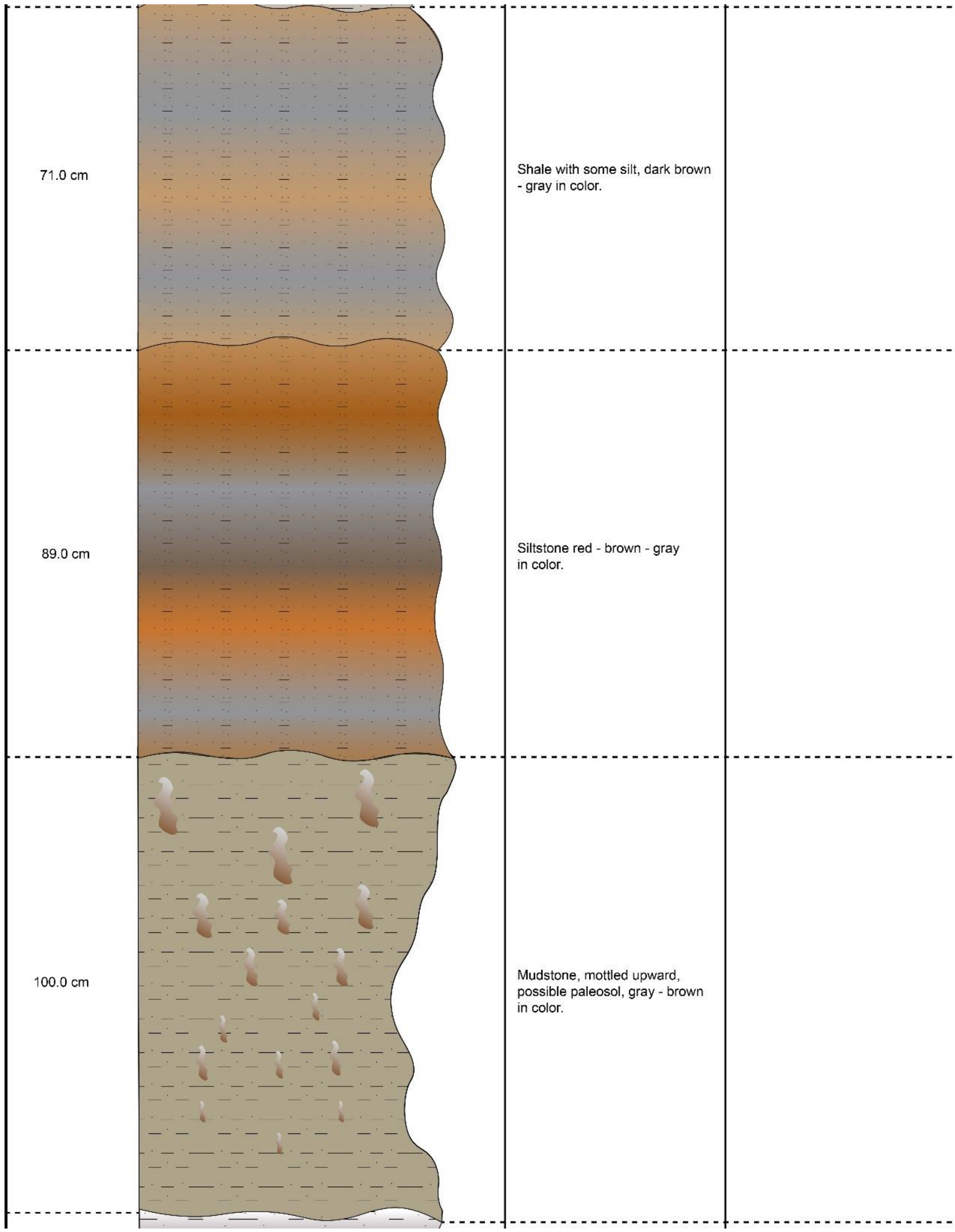


Figure 6 – Middle section of the stratigraphic column from observations of the I-77 Skelley Limestone site.

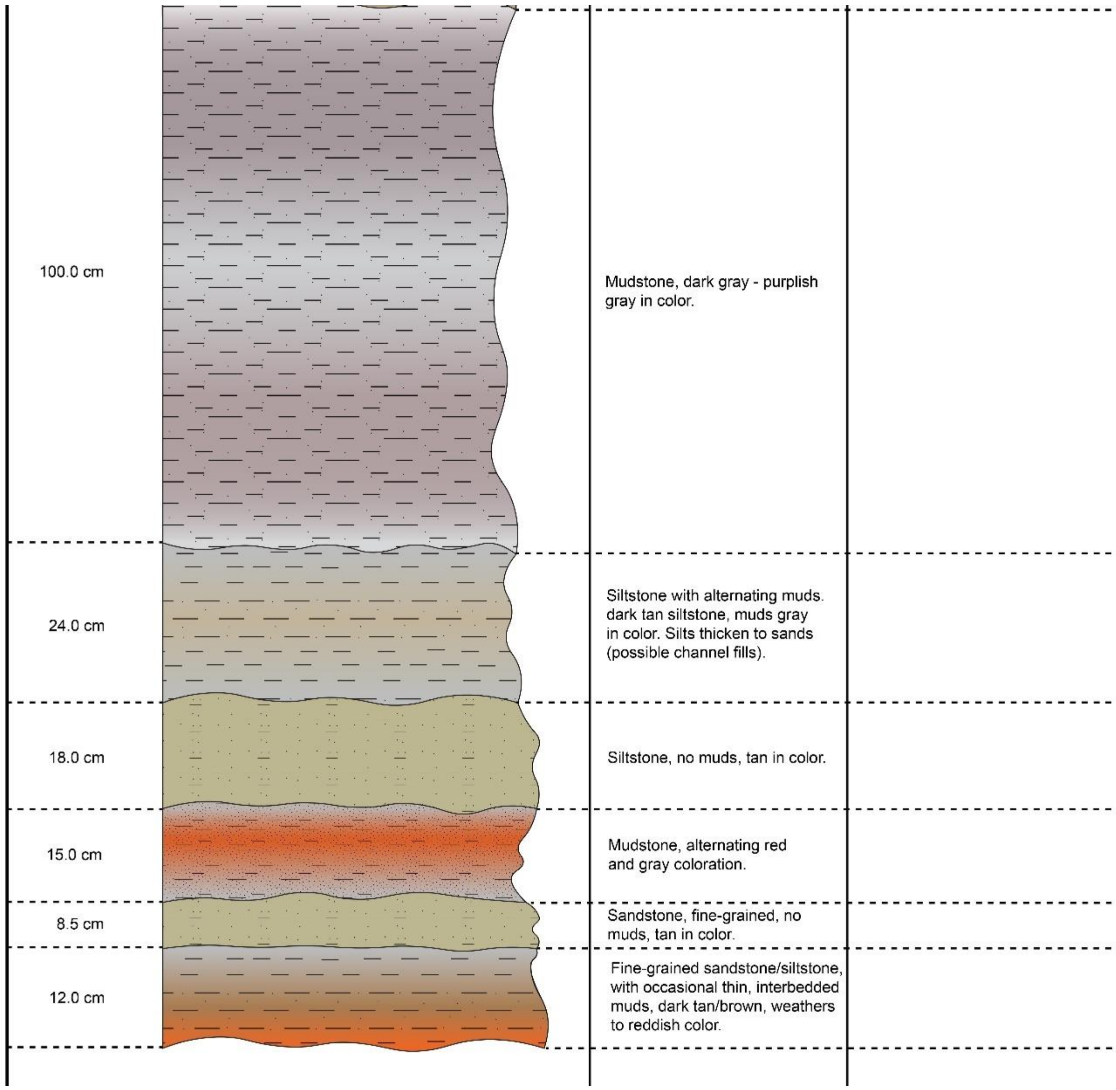


Figure 7 – Lowermost of the stratigraphic column from observations of the I-77 Skelley Limestone site.

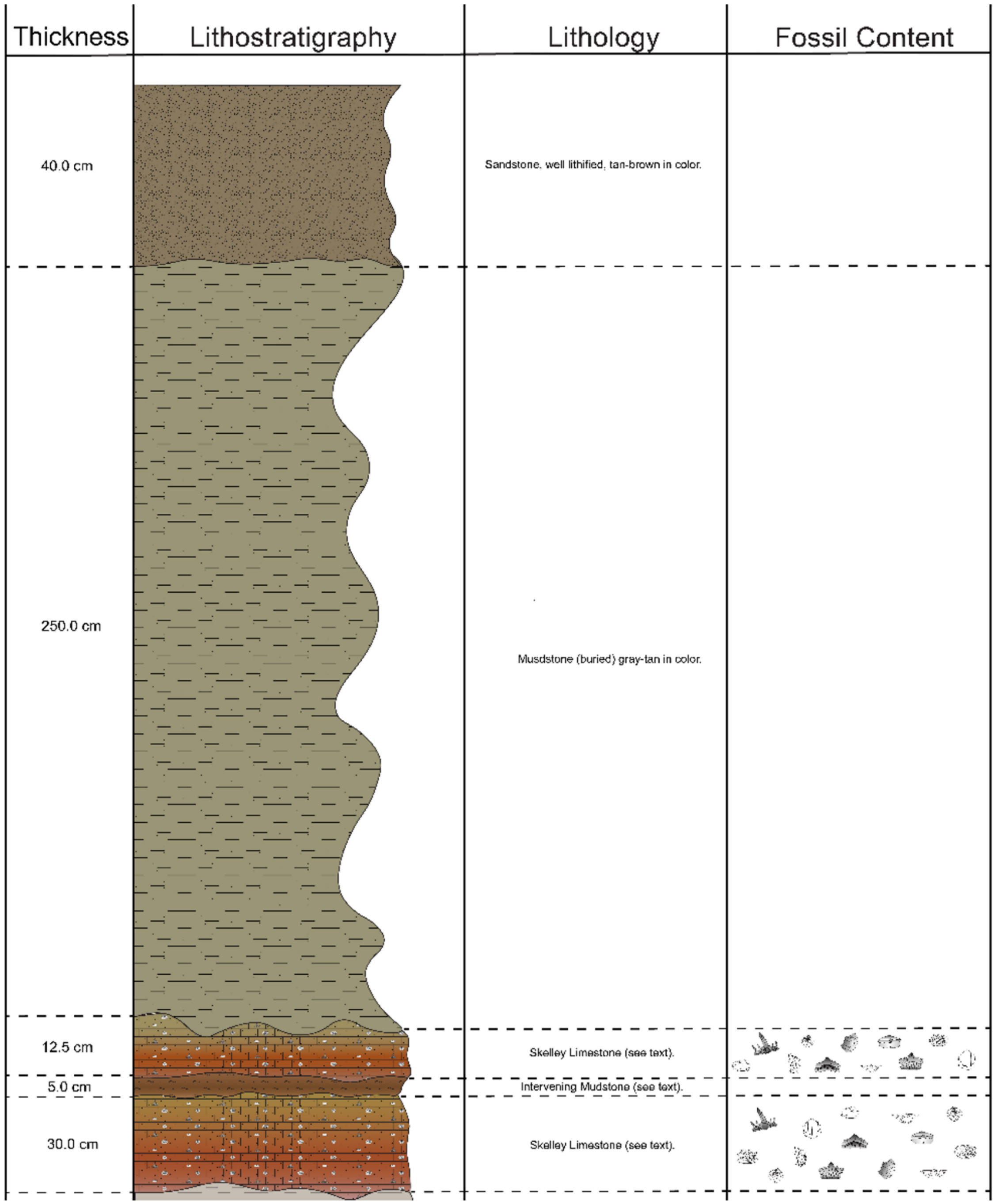


Figure 8 – Top half of the stratigraphic column from observations of the Rockville Rd Skelley Limestone site.

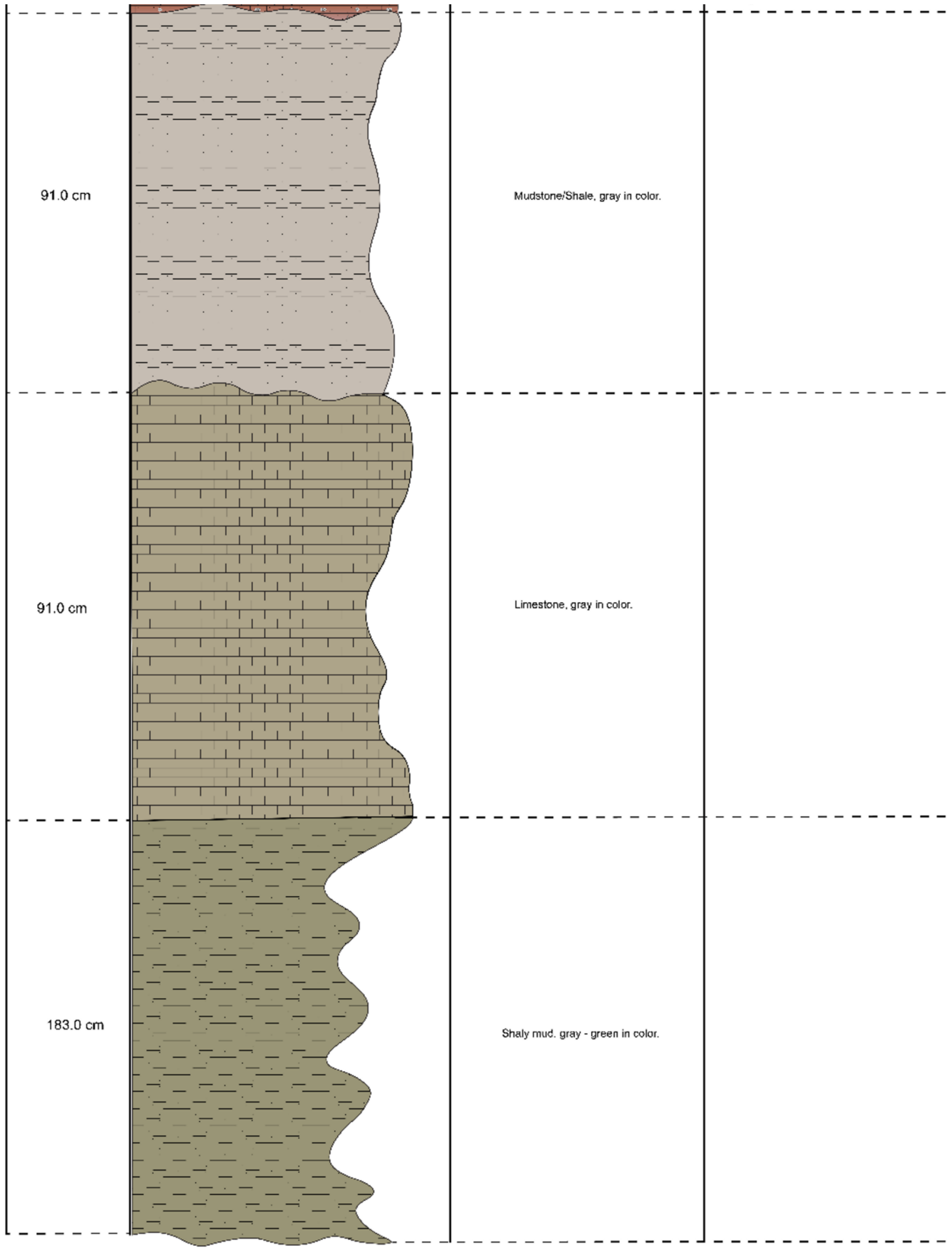


Figure 9 – Bottom half of the stratigraphic column from observations of the Rockville Rd Skelley Limestone site.

5.2 SYSTEMATIC PALEONTOLOGY

Kingdom Animalia Linnaeus, 1758

Phylum Chordata Haeckel, 1874

Subphylum Vertebrata Lamarck, 1801

Class Chondrichthyes Huxley, 1880

Subclass Holocephali Bonaparte, 1832

Order Symmoriiformes Zangerl, 1981

Family Symmoriidae Dean, 1909

Genus *Stethacanthus* Newberry, 1889

Stethacanthus sp.

Material Studied: WSU 1529 (A & B), WSU 1550 (A, B, & C), WSU 1565

Locality: I-77 (WSU 1529 A & B), Rockville Rd (WSU 1550 A, B, & C), Wilsonwood Rd. (WSU 1565)

Description: All specimens recovered from this investigation measure 1-2 mm in mesiodistal length and 1-4 mm in base to crown height. The central cusp of these specimens is flattened along the labial side and D-shaped in cross-section. In addition, the central cusp is primarily convex near the root-crown junction, though the overall shape is weakly sigmoidal. The central cusp and lateral cusplets are ornamented both labially and lingually by numerous weak, parallel striations/cristae that appear to run the entire length of each cusp/cusplet. Of lateral cusplets, there are two pairs, which appear curved in a similar fashion to that of the main cusp, and the outermost lateral cusplet is the largest of these pairs, though their maximum height is less than one-fifth the height of the central cusp. There is a minor basolabial depression, which appears to articulate each tooth to a well-developed oral-lingual button on the oral surface of what would have been the next tooth in the tooth file. On some specimens, there may be rare additional cusplets between the central cusp and the innermost lateral cusplet, though their size and asymmetric occurrence implies a lack of functionality. On many specimens, such as WSU 1529 A, the labial striations on the central cusp are worn away near the top of the crown, and the point of the central cusp is rounded. This is presumed to indicate *syn vivo* wear as opposed to weathering during taphonomic processes.

Remarks: The taxonomy of species within the genus *Stethacanthus* is complex and poorly understood, therefore an assignment of this material to any one *Stethacanthus* species cannot be easily verified at this time.

The recurve and slight sigmoidal shape of the large central cusp in WSU 1529 A is consistent with *Stethacanthus*, as are the number of lateral cusplets (see Ginter et al., 2010). The lack of a basolabial projection (as well as overall tooth size) separates teeth of this genus from other symmoriiform chondrichthyans, such as *Denaea*. Furthermore, the shape and size of the striations preserved on WSU 1529 A appear similar to known *Stethacanthus* examples, such as NMS 1911.62.521, which is housed at the National Museums of Scotland and figured by Ginter et al., 2010.

Figure 10 – Labial and lateral views of specimen WSU 1529 A (*Stethacanthus* sp.) from the I-77 site in Noble Co., Ohio. Scale bar 1 mm.

Family Falcatidae Zangerl, 1990

Genus *Denaea* Pruvost, 1922

Denaea saltsmani Ginter and Hansen, 2010

Material Studied: WSU 1551, WSU 1548 (A, B, & C), WSU 1552 (A &B)

Locality: I-77 (WSU 1551), Rockville Rd (WSU 1548 A, B, & C), and Wilsonwood Rd (WSU 1552 A & B)

Description: Dimensions of all teeth recovered from these localities measured approximately 500 μm to 1 mm in mesiodistal length. Base to crown height was up to 1 mm, and the central cusps represented 75% of that measurement or more. Most examples from these localities have three pairs of lateral cusplets, of which the second-most lateral is longest. All cusps/cusplets are conical or weakly D-shaped in occlusal view (with the flattest side of the cusp on the labial portion of the tooth), however the central cusp is somewhat sigmoidal while the surfaces of the lateral cusplets are either straight or convex in the labial direction. The bases of these teeth are relatively thin, trapezoidal in occlusal view, and each possesses a single basolabial projection. The shape of this projection is flattened or reduced (see remarks) compared to other examples of *Denaea*.

Remarks: The thin, trapezoidal tooth base observed in specimen WSU 1548 A as well as its size is consistent with known reports of *Denaea* (see Ginter et al., 2010). Additionally, the basolabial projection on these and other teeth helped to differentiate them from similar symmoriids such as *Stethacanthus* (Ginter et al., 2010). The shape and number of lateral cusplets, together with the reduced, flattened basolabial projection, suggests an affinity of these teeth with those of *Denaea saltsmani*, especially those of the holotype, OSU 51973, which is housed at Ohio State University and figured by Ginter and Hansen (2010).

Chondrichthyans of this genus are found in a wide range of depositional environments, including limestones, sandstones, and black shales. *D. saltsmani* had been found in marine transgressive sequences elsewhere in the Conemaugh Group, though only a single specimen was previously reported from the limestones of the Skelley cyclothem (see Hansen, 1986).


Figure 11 – Labial, lingual, and lateral views of *Denaea saltsmani* specimen, WSU 1548 A, from the Rockville Rd locality. Scale bar 1 mm.

Order Helodontiformes Patterson, 1965

Family Helodontidae Patterson, 1965

Genus *Helodus* Agassiz, 1838

Helodus sp.

Material Studied: WSU 1540

Locality: Rockville Rd

Description: The specimen recovered (WSU 1540) is approximately 1 mm high and just over 1 mm in width. The specimen consists of a mostly complete crown that is composed of tubular dentine, though taphonomic abrasion seems to have removed much of the base and damaged the surface of the crown. Despite this damage, it is clear that the median crown is low and that the overall specimen is somewhat labiolingually expanded. Only one distal margin is present, however, it forms a rounded point.

Remarks: The histology and overall shape of the crown of *Helodus* indicates a durophagous diet and while this specimen is the first known occurrence of this genus in the Skelley Limestone, its appearance in this ecosystem is not surprising given the presence of teeth from other chondrichthyans with crushing dentitions (*Deltodus*, see below). The overall shape and many of the anatomical features in this specimen are consistent with other known *Helodus* specimens, such as GRCA 121976, which was recovered from Grand Canyon National Park and is described and figured by Hodnett et al., 2021.

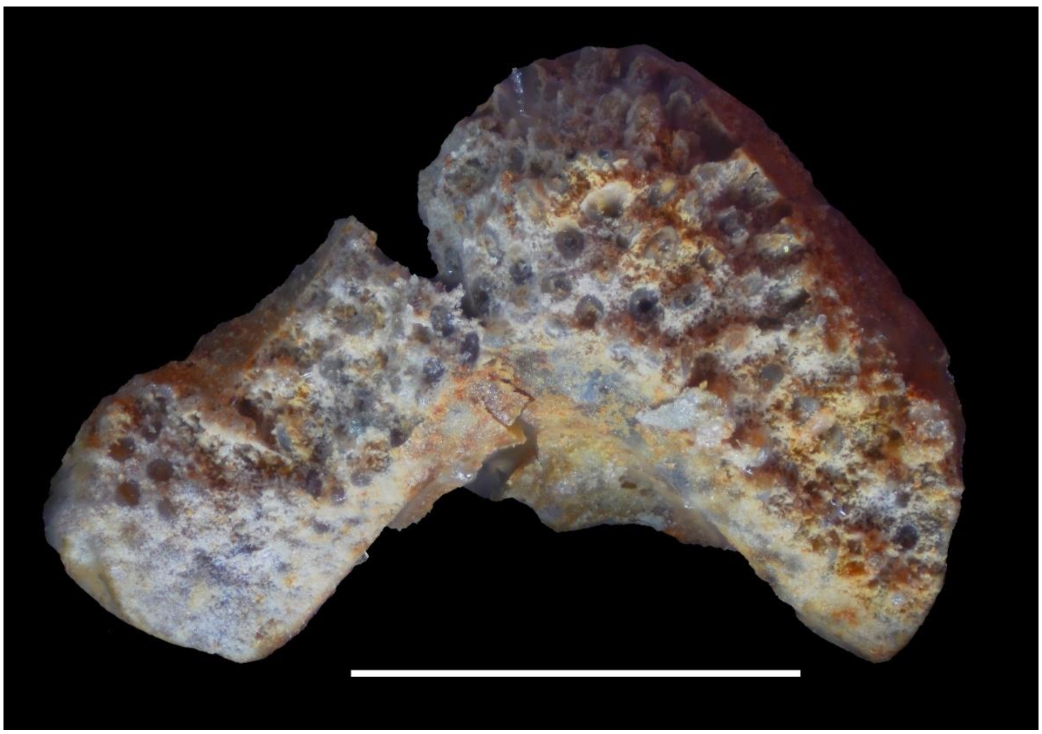


Figure 12 – *Helodus* sp. specimen WSU 1540 from the Rockville Rd locality. Scale bar 1 mm.

Order Cochliodontiformes Obruchev, 1953

Family Cochliodontidae Owen, 1867

Genus *Deltodus* Morris and Roberts, 1862

Deltodus sp.

Material Studied: WSU 1528 (A & B), WSU 1553 (A & B)

Locality: I-77 (WSU 1528 A & B), Wilsonwood Rd (WSU 1553 A & B)

Description: Both specimens of WSU 1528 (A & B) measure less than a centimeter in greatest dimension. The oral surfaces appear heavily worn, though it is unclear whether this wearing was functional wear or related to taphonomic processes. The exposed dentine tubules are similar to descriptions of *syn vivo* wear and to postmortem decalcification reported by Casier (1942) and Stahl (1999), though the latter explanation appears more likely, as both specimens are slightly fragmented on the margins.

The best-preserved tooth plate of this genus (WSU 1528 A) consists of a plate that is roughly triangular and convex orally. A basal lamella is present, as are a number of parallel/sub-parallel dentine tubules, though the presumed outermost layer of dentine has been removed though wear.

Remarks: Though not all mineralized tissues are present in these specimens, the presence of a basal lamella with tubule dentine above is consistent with the order Cochliodontiformes. The roughly triangular shape in oral view of WSU 1528 A is most consistent with the genus *Deltodus,* which derives its name from the Greek letter Δ.

The genus *Deltodus* was highly diverse during the Carboniferous Period. Because such a large number of species are known, with a wide variety of body sizes (see Stahl, 1999), it is unclear whether the specimens recovered during this investigation represent extremely anterior tooth plates of large bodied *Deltodus* species or whether they represent medial or posterior tooth plates of an extremely small individual.

Figure 13 – Specimen WSU 1528 A, *Deltodus* sp. Scale bar 1 mm.

Order Petalodontiformes Zangerl, 1981

Family Petalodontidae Newberry and Worthen, 1866

Genus *Petalodus* Owen, 1840

Petalodus ohioensis Safford, 1853

Material Studied: WSU 1541, WSU 1542

Locality: Rockville Rd (WSU 1541), Wilsonwood Rd (WSU 1542)

Description: The tooth, WSU 1541, recovered during this investigation is approximately 2 mm long. The crown is hemispherical in outline and may be weakly serrated. The labial side of the crown is partially obscured by what appears to be a large, asymmetrical root, while on the lingual side, approximately 5 weak imbricated ridges are present. These ridges form a somewhat U-shaped depression medially. Overall, the tooth appears somewhat worn, though given its small size compared to other specimens of this species, such as WSU 1542 (see Figure 15), some of this wear may instead be the weak expression of some structural characters. There is also a chip in the middle portion of the crown and breakages on both flanks.

Remarks: This tooth is compressed labio-lingually and the crown is convexo-concave with a depression on the baso-lingual portion of the crown. These traits are indicative of the Order Petalodontiformes (Zangerl, 1981; Ginter et al., 2010). Furthermore, the overall shape of this tooth and the weakly-developed imbricated ridges are consistent with lateral teeth of the genus *Petalodus* (Ginter et al., 2010). The relative narrowness of this band of imbricated ridges compared to other members of this family, as well as its biostratigraphic position, suggest an affinity of this specimen with *P. ohioensis* (Ginter et al., 2010). The overall outline of this tooth is consistent in shape with the extreme posterior teeth of *P. ohioensis* as reconstructed by Dalla Vecchia (1988) and Hansen (1986).

The type locality for *Petalodus ohioensis* is situated in the Conemaugh Group (the Ames Limestone). Its occurrence, therefore, in the Skelley Limestone is consistent with other reports and other predictions related to this chondrichthyan's biostratigraphy (Hansen, 1986).

Figure 14 – Specimen WSU 1541, a lateral/posterior tooth of *Petalodus ohioensis* in lingual view. Scale bar 1 mm.

Figure 15 – Specimen WSU 1542, the partial crown of an anterior tooth of *Petalodus ohioensis* from the Wilsonwood Rd locality. Scale bar 1 mm.

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Superfamily Protacrodontoidea Zangerl, 1981

Family Protacrodontidae Cappetta, Duffin, and Zidek, 1993

cf. Protacrodontidae indet.

Material Studied: Anterior tooth: WSU 1530 (A & B), WSU 1554

Locality: I-77 (WSU 1530 A & B), Wilsonwood Rd (WSU 1554)

Description: WSU 1530 A consists of a single anterior tooth that measures just over 1 mm in greatest dimension. The crown is triangular with a large central cusp and two lateral cusplets to one side while the cusplets are absent on the other side due to damage to the tooth. The base appears mostly complete, though parts of the root are worn due to erosion. While there are no obvious projections off the crown in the labial or lingual directions, it is ornamented with coarse sub-parallel cristae that extend from the root-crown junction up most of the crown height. It is possible that cutting surfaces are present, but erosion on the crown makes this uncertain.

Remarks: Similar to those of other primitive euselachian lineages, the bases of WSU 1530 A and B appear elongated, though erosion of the teeth obscure the degree of elongation in each tooth. The coarsely cristated crowns of these specimens are comparable to teeth of the genus *Protacrodus,* especially anterior teeth of *P. serra* and *P. sp.* (see Ginter et al., 2010) from the Devonian and Lower Carboniferous, respectively.

Figure 16 – Photograph of WSU 1530 A, cf. Protacrodontidae indet., in labial view. Scale bar 1 mm.

Order Ctenacanthiformes Glikman, 1964

Family Ctenacanthidae Dean, 1909

Genus *Glikmanius* Ginter, Ivanov & Lebedev 2005

Glikmanius myachkovensis Lebedev, 2001

Material Studied: WSU 1544 (A & B)

Locality: Rockville Rd (WSU 1544 A & B)

Description: WSU 1544 A is a small tooth, approximately 1.5 mm in mesiodistal length. The tooth has a central cusp with three to four pairs of lateral cusplets, though the central cusp and the outermost pair of lateral cusplets show signs of significant wear. Of the lateral cusplets, the outermost pair are the largest but are only one-quarter the height of the worn central cusp. What remains of the central cusp measures approximately 0.8 mm in height and is roughly triangular in shape. And while there are sub-parallel cristae on the central cusp, as well as the outermost pair of lateral cusplets, due to syn vivo wear, these are not as prominent as the cristae on other specimens, such as WSU 1544 B. The root of the tooth is shallow in height and there is a downward slope from the base of the central cusp to the lingual edge of the root. Present on the tooth base are two separate pairs of basal articulation devices, one pair of orolingual buttons and one pair of basolabial projections.

Remarks: The general appearance of WSU 1544 A is that of a cladodont tooth with the central cusp possessing a flattened labial side and a prominent basolabial depression, features that are consistent with Ctenacanthiformes (Ginter et al., 2010). The presence of the two separate pairs of basal articulation devices and the number of intermediate cusplets, as well as the downward slope on the lingual side of the tooth base, align with the features of *Glikmanius myachkovensis*, especially CM 44549a and CM 44549f as described and figured by Ginter et al. (2005).

Figure 17 – Labial, lingual, lateral, and occlusal views of WSU 1544 A, *Glikmanius myachkovensis*. Scale bar 1 mm.

Glikmanius sp.

Material Studied: WSU 1545

Locality: I-77 (WSU 1545)

Description: WSU 1545 is a fragmented specimen that measures approximately 3.0 mm in greatest dimension. Prior to further fragmentation of the tooth after the specimen was collected, the tooth possessed a central cusp with prominent sub-parallel cristae, though there is significant wear on the tip of this cusp. At least 25% of the tooth base is missing due to either taphonomic processes or damage incurred during recovery of the specimen from the limestone. As a result of this damage, only a single lateral cusplet remains, but given the intact portion of the tooth base, it is reasonable to suggest that the tooth possessed at least one pair of lateral cusplets. Similarly, there is one fully intact orolingual button while only a portion of the other button remains. The basolabial depression and the pair of basolabial projections are present, but shallow and worn, respectively.

Remarks: Despite the damages to the tooth, WSU 1545, like WSU 1544 A (*G. myachkovensis*), has features that place it within Ctenacanthiformes, as well as *Glikmanius* (see Ginter et al., 2010). Although the tooth is larger and more robust than that of WSU 1544 A, similar to the specimens of *Glikmanius occidentalis*, the shallower basolabial depression and worn basolabial projections preclude assigning WSU 1545 to *Glikmanius occidentalis*. And while the shallow basolabial depression is a notable feature of G. *myachkovensis* (see Ginter et al., 2005), there are not enough diagnostic features intact to confidently assign this specimen to anything beyond *Glikmanius* sp.

Figure 18 – Lingual and occlusal views of specimen WSU 1545, *Glikmanius* sp., after further fracturing and loss of the central cusp. Scale bar 1 mm.

Ctenacanthiformes incertae sedis

Genus *Heslerodus* Ginter, 2002

Heslerodus divergens Ginter, 2002

Material Studied: WSU 1543 (A, B, & C)

Locality: Wilsonwood Rd (WSU 1543 A, B, & C)

Description: WSU 1543 A is approximately 3 mm in greatest dimension with a wide and short tooth base extending in the lingual direction and five cusps. While all five of these cusps are broken to varying degrees, the size and shape of the remaining structures show that the central cusp is the largest, followed closely by the two lateral-most cusps. As opposed to the significant difference between the central cusp and lateral cusps observed in *Glikmanius*, what remains of the lateral cusps of WSU 1543 A show them to be almost as large as the central cusp. Between the central cusp and each of these large lateral cusps sits a much smaller lateral cusp. Atop the base are two orolingual buttons while below the cusps on the labial side are a pair of basolabial projections and a basolabial depression. There are cristae present on both sides of the cusp, though the cristae on the lingual side of the tooth appear more numerous and more parallel to each other than the fewer cristae on the labial side.

Remarks: The overall shape of WSU 1543 A is similar to that of phoebodont teeth, though the presence of a basolabial depression and the wide, short tooth base are indicative of Ctenacanthiformes. Due to this similarity to phoebodont teeth, prior to the work of Ginter (2002), *Heslerodus divergens* was sometimes assigned to the genus *Phoebodus* (Williams, 1985; Hansen, 1986). The appearance of WSU 1543 A is comparable to that of OSU 50490 and OSU 50491 as figured by Ginter (2002), as well as OSU 35439 as figured by Hansen (1986).

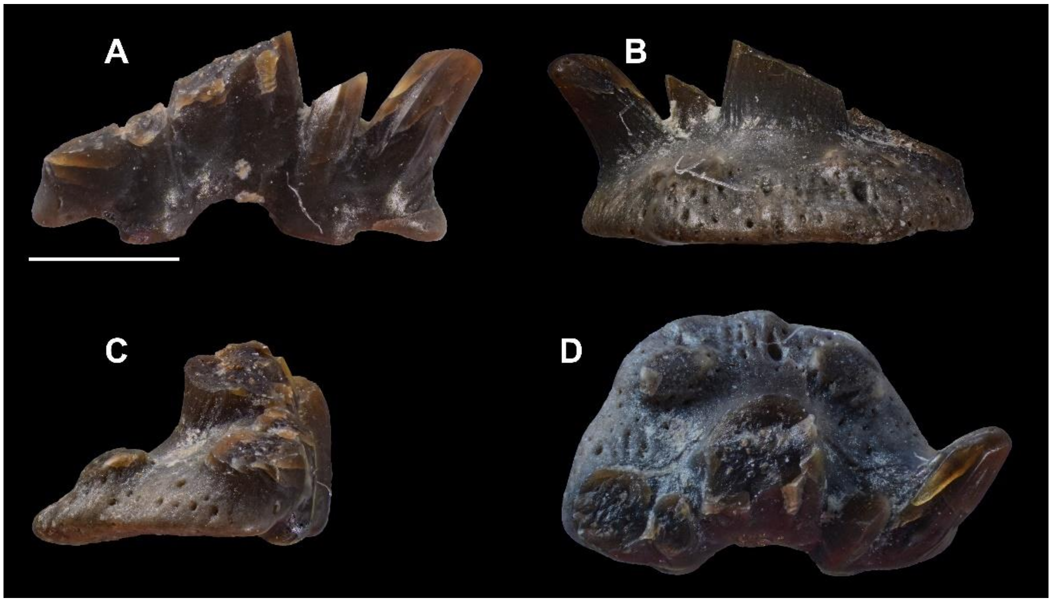


Figure 19 – Labial (A), lingual (B), lateral (C), and occlusal (D) views of *Heslerodus divergens* specimen WSU 1543 A. Scale bar 1 mm.

Primitive Elasmobranchii incertae sedis

Genus *Adamantina* Bendix-Almgreen, 1993

Adamantina sp.

Material Studied: WSU 1556, WSU 1555, WSU 1547

Locality: I-77 (WSU 1556), Rockville Rd (WSU 1555), Wilsonwood Rd (WSU 1547)

Description: The overall shape of WSU 1547 is that of an extremely compressed cladodont tooth with a size no greater than 0.7 mm in mesiodistal length. The crown and base of the tooth are almost equal in proportion to each other. Along the labial side of the tooth base is a pair of basolabial projections while on the lingual side of the tooth, a small lingual torus is present. The crown is defined by three short cusps of equal size that are covered in triangular cristae.

Remarks: Most of the teeth of *Adamantina* sp. recovered from the Skelley Limestone in this investigation are comparable to type IV and V of the "*Z. williamsi*" tooth morphologies hypothesized by Hansen (1986). The specimen WSU 1547 is most comparable to morphology type IV (see Figure 20), as are most of the other teeth, though a substantial number of type V teeth have also been recovered. Hansen (1986) assigned "*Z. williamsi*" to Ctenacanthoidea due to similarities observed between the teeth of "*Z. williamsi*" and the teeth of *Heslerodus divergens* (referred to as *Phoebodus heslerorum*). However, the presence of prominent cristae on the crown and the basolabial projections are the most significant similarities between these two genera. "*Z. williamsi*" lacks the orolingual buttons, large base, and the large cusps found on other Ctenacanthiformes, such as *Glikmanius* and *Heslerodus* (see Ginter, 2010). The work of Ivanov (1999) presents teeth similar to that of "*Z. williamsi*" from the Early Mississippian to the Early Permian of Russia. These teeth, referred to as *Adamantina foliacea*, bear strong resemblance to the teeth of "*Z. williamsi*" recovered by Hansen (1986) and the specimens recovered in this investigation. Present in *A. foliacea* are the same triangular cristae, basolabial projections, and compact, tricuspid crown observed in "*Z. williamsi*" (Ivanov, 1999). Due to the similarities of the teeth of "*Z williamsi*" to those of the genus *Adamantina*, especially *A. foliacea*, it is suggested that specimens of “*Zangerlodus williamsi*” from the Conemaugh Group be reassigned to *Adamantina* sp.

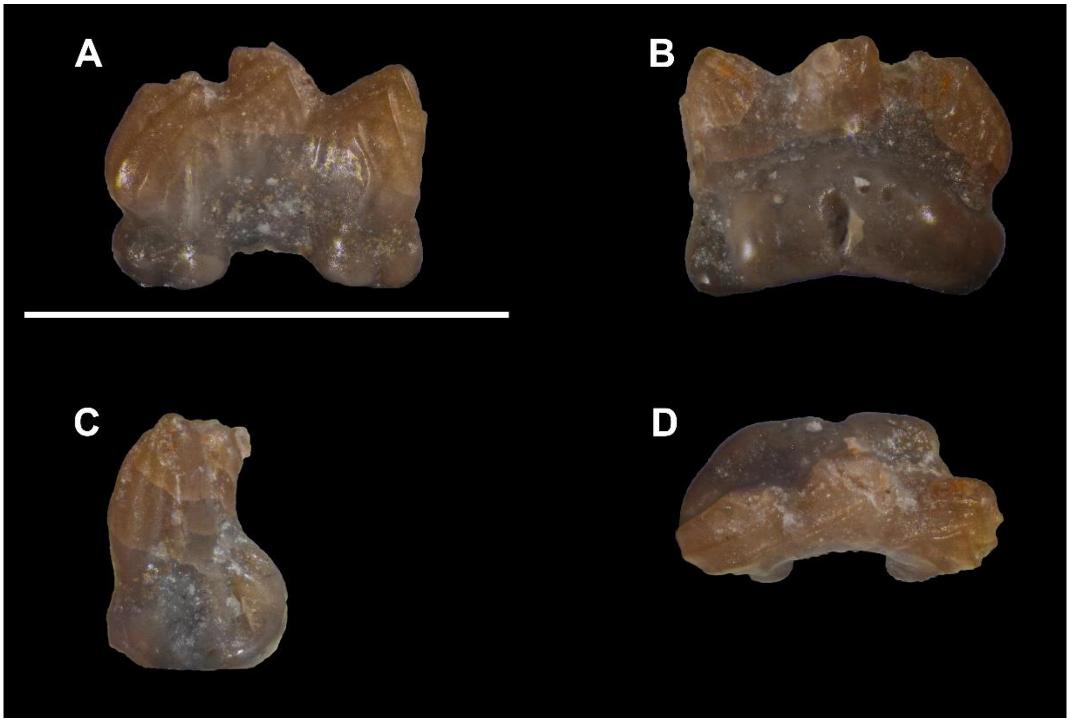


Figure 20 – Labial (A), lingual (B), lateral (C), and occlusal (D) views of WSU 1547, a specimen of *Adamantina* sp. from the Wilsonwood Rd. locality. Scale bar 1 mm.

Order Hybodontiformes Maisey, 1975

Superfamily Hybodontoidea Owen, 1846

Family Hybodontidae Owen, 1846

Genus *Ossianodus* Ginter, 2016

Ossianodus nebraskensis Ginter, 2016

Material Studied: WSU 1535, WSU 1557 (A, B, & C), WSU 1558

Locality: I-77(WSU 1535), Rockville Road (WSU 1557 A, B, & C), and Wilsonwood Rd (WSU 1558)

Description: WSU 1557 A appears cladodont in overall form, with a single central cusp and three to four pairs of lateral cusplets, all one-quarter the height of the main cusp or less. The outermost pair of lateral cusplets is the smallest of the cusplets. The base is arcuate and the vascularization pattern appears anaulacorhize. A number of vertical cristae ornament the labial side of the tooth, running the total length of the lateral cusplets, and at least half the length of the main cusp.

Remarks: The arcuate base of this specimen, as well as its anaulacorhize vascularization pattern, are consistent with the Hybodontiformes (Ginter et al., 2010). Even with a large fracture in the specimen (see Figure 21), the shape of the tooth, its central cusp, and the number and shape of lateral cusplets compare well to CM 44547b, the holotype of *Ossianodus nebraskensis* described and figured by Ginter (2016). WSU 1557 A was recovered in rocks of the same age that produced the *Ossianodus nebraskensis* holotype, though the 1,000+ kilometers separating the localities of these two fossils suggest a wide-ranging shark species. As described by Ginter (2016), the shape of the crown, the number and relative sizes of the lateral cusps, as well as the ornamentation on all cusps, suggests this tooth to be representative of a hybodontiform with a dentition suited for catching and holding onto prey. These features are still clear in heavily worn teeth of this species, such as WSU 1535 (see Figure 22). Such dentition is similar to that of earlier cladodont sharks and phoebodont sharks, as well as modern frilled sharks (Ginter and Ivanov, 1992; Williams, 2001). This could suggest that *Ossianodus nebraskensis*, as well as other hybodontiform sharks with similar dentition, also had similar diets as the modern frilled shark and primarily preyed upon cephalopods and smaller fishes (Kubota et al., 1991).

Figure 21 – Lingual view of a specimen of *Ossianodus nebraskensis* (WSU 1557 A) from Rockville Rd. Scale bar 1 mm.

Figure 22 – Labial and lingual views of WSU 1535, a specimen of *Ossianodus nebraskensis* from the I-77 Skelley Site. Scale bar 1 mm.

Family *Incertae sedis*

Genus *Diablodontus* Hodnett et al., 2013

Diablodontus sp.

Material Studied: WSU 1546

Locality: Rockville Rd

Description: The specimen, WSU 1546, recovered from this investigation measures 2 mm in greatest dimension and is roughly cladodont in overall shape, with two pairs of lateral cusps that decrease in size away from the main cusp by about fifty percent from their preceding neighbor. The main cusp is approximately twice the size of the highest lateral cusp. Minor damage to the base of the root on the labial side and additional sediment on the lingual side obscure some anatomical features. The tooth base is anaulacorhize in its vascularization and the root is rectangular and roughly concave. The overall crown is trident-shaped and the cusps are ornamented by vertical cristae (see Figure 23).

Remarks: The vascularization of the root, as well as its overall shape, are consistent with anterior and mediolateral examples of *Diablodontus michaeledmundi*, as is the concave base of the root. Similar to the teeth of *Ossianodus nebraskensis*, given the crown shape, as well as the distribution, size, and ornamentation of the main cusp and lateral cusplets, this tooth could represent another hybodontiform shark with dentition designed to catch and hold prey. In shape, WSU 1546 appears most similar to teeth from *D. michaeledmundi*, such as the mediolateral tooth MNA V10475, which was described and figured by Hodnett et al. (2013). The slightly flatter arch of the tooth base, the parallel orientation of lateral cusplets, as well as the disparity in size between WSU 1546 and examples of *D. michaeledmundi* (which is 2 to 3 times the mesiodistal length of WSU 1546), suggest an affinity to an unknown species within this genus.

WSU 1546 represents the first Carboniferous occurrence of this genus, which was previously only known from the Roadian Stage of the Permian Period (Hodnett et al., 2013). Furthermore, it appears approximately 2,500 kilometers further east on the North American craton than its original report in the Kaibab Formation of Arizona (Hodnett et al., 2013). Piscivory in hybodontiforms appears to have been most common during the Mesozoic Era. The first report of *Diablodontus* suggested a Paleozoic origin of this diet in hybodontiforms, and this occurrence indicates such piscivory in this order to have occurred at least 30.69 million years (from the earliest Roadian to the earliest Gzhelian) earlier in the Paleozoic than previously thought. However, the presence of another probable piscivorous hybodontiform shark, *Ossianodus nebraskensis*, from the Skelley Limestone suggests that the origin of piscivory in Hybodontidae is older still.

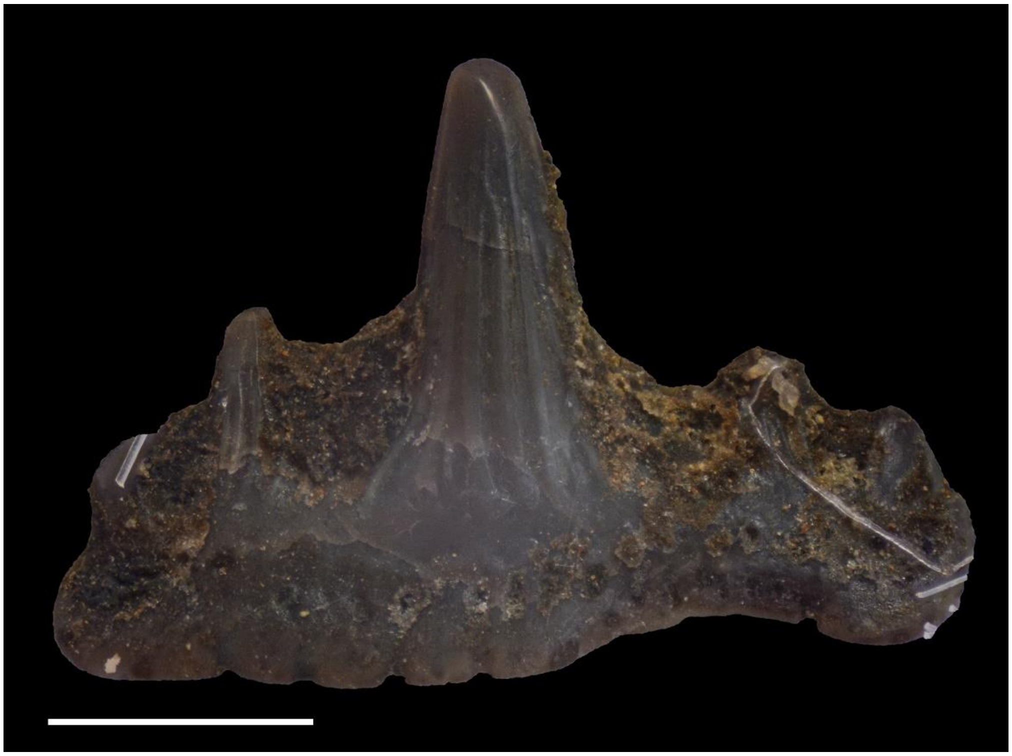


Figure 23 – Specimen of *Diablodontus* sp. (WSU 1546) from the Rockville Rd site. Scale bar 1 mm.

Genus “*Maiseyodus*” Hansen, 1986

“*Maiseyodus johnsoni*” Hansen, 1986

Material Studied: WSU 1559, WSU 1549

Locality: Rockville Rd (WSU 1559), Wilsonwood Rd (WSU 1549)

Description: WSU 1549 measures approximately 1.5 mm along its mesiodistal length. The labio-lingual and occlusal-aboral dimensions of the tooth are noticeably smaller. The appearance of this specimen is that of a long, narrow tooth base with a blunt multi-cuspid crown. Coarse cristae are present on both the labial and lingual surfaces of these joined cusps. The height of the crown represents the majority of the tooth height in this specimen, though other specimens recovered from this investigation show variation similar to that described by Hansen (1986). An almost parallel row of foramina is found on both the labial and lingual sides of the tooth base.

Remarks: The tooth base of WSU 1549, being arcuate and having the anaulacorhize vascularization pattern, match that of the Hybodontiformes (see Ginter et al., 2010). The durophagous, low-crowned nature of the teeth recovered from this investigation match the type III morphology of "*Maiseyodus johnsoni*" described and figured by Hansen (1986) (see Figure 24). Type II and type I morphologies may also have been recovered during this investigation but are fragmented and in need of further examination before they are assigned to this genus. In addition to the observations made by Hansen (1986), Hodnett et al. (2013) used "*Maiseyodus johnsoni*" as a reference for constructing dental morphologies for *Diablodontus michaeledmundi*. The type III teeth of "*Maiseyodus johnsoni*" also share similarities with that of the posterolateral teeth of *Ossianodus nebraskensis*, especially specimen CM 44547d, and *Sphenacanthus tenuis*, especially CM 44547h, as described and figured by Ginter (2016). Further comparison to similar teeth is recommended before assignment of these specimens to an established taxa or new genus. In addition, the genus *Maiseyodus* has since been assigned to teeth previously described as *Mcmurdodus whitei* through the work of Long et al. (2021).

Figure 24 – Specimen WSU 1549, "*Maiseyodus johnsoni*," from the Wilsonwood Rd site in labial, lingual, and occlusal views. Scale bar 1 mm.

Hybodont Tooth "A" sensu Hansen, 1986

Material Studied: WSU 1537, WSU 1560 (A & B)

Locality: I-77 (WSU 1537), Rockville Rd (WSU 1560 A & B),

Description: In mesiodistal length, WSU 1537 measures just over 2 mm. The labio-lingual and occlusal-aboral dimensions of the tooth range from 0.5 mm to 0.7 mm. This specimen has long, narrow tooth base with a very blunt multi-cuspid crown where the height of the tooth is split evenly between the height of the tooth base and the height of the crown. A central cusp rises 0.1-0.2 mm above the rest of the crown and is covered in rough cristae, even distributed across the labial and lingual sides of the tooth. A single, subparallel row of foramina is found along the lingual torus while smaller, irregular foramina can be found on the labial side of the tooth base.

Remarks: Distinguishing characteristics of the Hybodontiformes include anaulacorhize vascularization in the tooth base, as well as the base having an arcuate shape (see Ginter et al., 2010). Both of these characteristics are observed in WSU 1537 (see Figure 25), as well as the other specimens of Hybodont Tooth "A" recovered from the Skelley Limestone in this investigation. These hybodont teeth were originally figured by the work of Tway & Zidek (1983) and further described by the work of Hansen (1986). As noted by Hansen (1986), due to the only material being a handful of complete specimens, as well as a number of incomplete specimens, assignment of these teeth to a particular genus was not recommended at the time of his work. However, given what material was available, it was suggested that these teeth did not belong to *Polyacrodus, Lissodus, Hybodus,* or *Acrodus* (Hansen, 1986). Given the complete and mostly complete teeth recovered during this investigation, there exists the possibility that a future review of the material from this study, as well as the specimens from the work of Hansen (1986), could finally assign this material to a new or existing taxon.

Figure 25 – Labial, lingual, and occlusal views of WSU 1537, Hybodont Tooth "A," from the I-77 locality. Scale bar 1 mm.

Family ?Acrodontidae Casier, 1959

Genus ?*Acrodus* Agassiz, 1838

?*Acrodus* cf. *olsoni*

Material Studied: WSU 1533 (A & B), WSU 1561

Locality: I-77 (WSU 1533 A & B), Rockville Rd (WSU 1561)

Description: Specimen WSU 1533 A is a single tooth that measures approximately 3.5 mm in greatest dimension. The oral surface of WSU 1533 A is rhomboid in outline, with ridges that appear to radiate out from the highest point on the crown, though *syn vivo* wear obscures much of this detail. The roots for both specimens are absent, likely due to erosion, though occlusal crests appear present, as well as small labial projections on the crown of both specimens.

Remarks: True examples of the genus *Acrodus* are exclusively Mesozoic in their temporal distribution. Following the work of Johnson (1981), we refer specimens to this genus tentatively based on its similarity to ?*A. olsoni* with its symmetrical crown shape, low central cusp, and crenulations on the crown (Figure 26). The overall shape of WSU 1533 A is comparable to ?*A. olsoni* specimens such as the paratype, SMP-SMU 64351, which is figured by Johnson (1981) and Ginter et al. (2010). While specimens of ?*A. olsoni* comparable to WSU 1533 A are generally recovered from the early Permian, upper Carboniferous examples are also reported by Johnson (1981).

Figure 26 – Labial, lingual, and occlusal views of WSU 1533A, ?*Acrodus cf. olsoni*. Scale bar 1 mm.

Family Lonchidiidae Herman, 1977

Genus *Lissodus* Brough, 1935

cf. *Lissodus* sp.

Material Studied: WSU 1531

Locality: I-77 (WSU 1531)

Description: The tooth, WSU 1531, is approximately 2mm in length and laterally elongated: the total base to crown height being 30% or less the width of the tooth. The crown is low and unornamented, but has a slightly raised portion in the central part of the crown. Weathering has damaged one side of the tooth. The labial projection is weak or absent, the base of the root is flat, and the crown-root junction follows the shape of the root base. The vascularization of the root appears anaulacorhize with visible vascular foramina on the root.

Remarks: The vascularization pattern mentioned above, as well as the extreme elongation of the tooth (see Figure 27), both help to place these specimens in the family Lonchidiidae (Ginter et al., 2010). *Lissodus* is the most diverse genus within this family and the lack of lateral cusplets and triangular occlusal outline differentiate the specimens recovered in this investigation from other Lonchidiid taxa, such as *Gansuselache* and *Dabasacanthus*, respectively. However, the genus *Lissodus* has been under heavy taxonomic scrutiny and revision (see Ginter et al., 2010), and any assignment of this material to the species level would be unlikely to represent any valid evolutionary patterns of these small-bodied sharks.

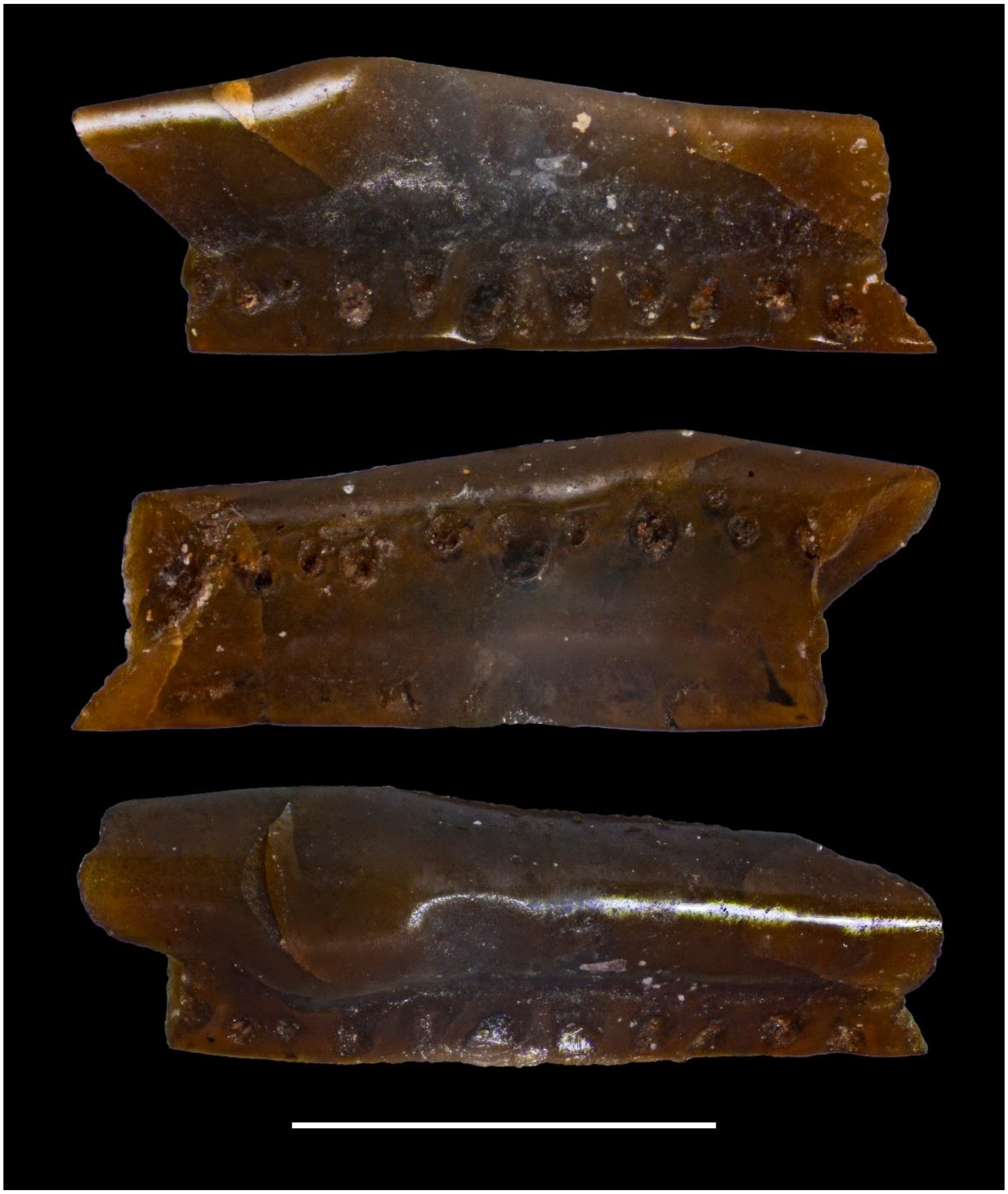


Figure 27 – Labial, lingual, and occlusal views of WSU 1531, *Lissodus* sp. Scale bar 1 mm.

Subcohort Neoselachii Compagno, 1977

Family Anachronistidae Duffin and Ward, 1983

Genus *Cooleyella* Gunnel, 1933

Cooleyella cf. *C. fordi*

Material Studied: WSU 1527

Locality: I-77 (WSU 1527)

Description: The tooth studied in this investigation is small and measures approximately 1 mm in greatest dimension. In general, the tooth appears unworn or only weakly worn. The crown of the tooth displays a notable central cusp that is conical and lingually inclined. The labial portion of the crown appears to show a visor, which obscures the crown-root junction. The overall shape of the root is consistent with *Cooleyella* and it appears vascularized by a single medio-external foramen which is visible on the root, as is typical of this genus (Ginter et al., 2010).

Remarks: The presence of the conical, lingually-inclined central cusp on the crown of WSU 1527, together with its labial visor (see Figure 28), are generally indicative of the genus *Cooleyella* (Gunnel, 1933; Ginter et al., 2010). The specimen WSU 1527 is comparable in size, ornamentation, and crown shape to the holotype of *C. fordi* (BMNH P.60670) and other specimens, such as BMNH P.60690, which were described and figured by Duffin and Ward (1983) and figured by Ginter et al. (2010). Furthermore, the basal surface of the labial root buttress of WSU 1527 is flat and has a weak crown-root junction, features represented in specimens BMNH P.60670 and BMNH P.60690 that distinguish *C. fordi* from other species within the genus *Cooleyella*.

Figure 28 – Labial, lingual, and occlusal views of WSU 1527, *Cooleyella* cf. *C. fordi*. Scale bar 1 mm.

Cooleyella sp.

Material Studied: WSU 1539, WSU 1562

Locality: Rockville Rd. (WSU 1539), Wilsonwood Rd. (WSU 1562)

Description: The specimen, WSU 1539, measures approximately 0.6 mm in greatest dimension and appears mostly unworn. The crown appears relatively flat and plate-like. While the labial portion of the crown does appear to also have a visor similar to that of WSU 1527, it is not as pronounced and the crown-root junction is not obscured by the feature. The features and shape of the root of this *Cooleyella* sp. specimen are consistent with that of the preceding specimen of cf. *C. fordi* (WSU 1527), as well as the genus at large (Ginter et al., 2010).

Remarks: As the specimen lacks the distinctive central cusp found on WSU 1527, as well as the other differences described previously, this particular specimen of *Cooleyella* cannot be assigned to *C. fordi* (see Duffin and Ward, 1983; Ginter et al., 2010). While the specimen bears some resemblance to the *Cooleyella* type species, *C. peculiaris*, the crown of WSU 1539 is flatter in appearance than the rounded crown common to *C. peculiaris*, so further comparison to multiple known specimens of different *Cooleyella* species is recommended before this specimen is assigned to a specific species within the genus *Cooleyella* (Gunnell, 1933; Ginter et al., 2010).

Figure 29 – Labial, lingual, and occlusal views of WSU 1539, *Cooleyella* sp. from the Rockville Rd locality. Scale bar 1 mm.

Superclass Osteichthyes Huxley, 1880

Class Actinopterygii Klein, 1885

Order Palaeonisciformes Hay, 1902

Palaeonisciformes indet.

Material Studied: WSU 1532 (A & B), WSU 1563, WSU 1564

Locality: I-77 (WSU 1532 A & B), Rockville Rd (WSU 1563), and Wilsonwood Rd (WSU 1564)

Description: Specimens recovered from this investigation appear conical with a circular occlusal cross-section. The distal-most quarter of the conical crown is less steep than the rest of the crown overall. This region is also composed exclusively of enamel/enameloid as opposed to the coating of enamel followed by dentine observed in the histology of the proximal portion of the crown. No root is present, which is typical in conical bony fish teeth in the fossil record. The majority of the length of the crown is ornamented by numerous fine parallel striations.

Remarks: These teeth are consistent with other specimens referred to this order as reported by Carpenter et al. (2011), Cione et al. (2010), and Štamberg et al. (2020). Furthermore, these specimens are consistent in appearance with other specimens referred to Palaeonisciformes such as WSU 1417, which is figured by Shell (2020). The conical shape of the tooth indicates a predatory, possibly piscivorous diet, though there is not enough morphological information to understand the taxonomic affinity of these teeth.

Figure 30 – Stacked image of WSU 1532 A, Palaeonisciformes indet. Scale bar 1 mm.

Family Platysomidae Young, 1866

Platysomidae indet.

Material Studied: WSU 1536 (A & B)

Locality: I-77 (WSU 1536 A & B)

Description: The tooth plates investigated represent a mandible which is broken on the posterior end, where it would have articulated to the cranium, and on the anterior end. The plate is trapezoidal or triangular in overall shape and measures approximately 5.0 mm in greatest dimension (ante-posterior), which creates an occlusal surface less than one square centimeter in overall area. The size of this tooth plate is comparable to those of the articulated specimen OUSM 00509, which suggests a small overall body size (less than 10 cm) (see Johnson and Zidek, 1981).

The teeth observed on the plate are circular in occlusal view and hemispherical in cross-section. They range in size from approximately 1 mm^2 to less than 1/10 mm^2. This range is bimodal, with teeth along the margin of the jaw being larger (and arranged in rows) and smaller teeth in the lingual region (arranged in a mosaic pattern). The surface of the plate is depressed ventrally on the medial line, meaning that the overall plate is somewhat U-shaped in anterior-posterior view.

Remarks: This phyllodont-style dentition (see Johnson and Zidek, 1981) is indicative of the family Platysomidae, which is generally thought to contain two upper Paleozoic genera: *Schaefferichthys* and *Platysomus.* The latter genus has been considered a form-genus in need of revision. Because the tooth plates of *Schaefferichthys* consist of teeth that are all the same size and arranged exclusively in a mosaic-pattern (see OUSM 00509, which is figured by Johnson and Zidek, 1981), it is likely that this fossil represents a member of the genus

Platysomus, though a lack of anatomical clarity in the cranial region of that genus suggests that an assignment of this material to *Platysomus* would be premature.

As platysomids are generally deep-bodied and laterally compressed, similar to the shape of the tooth plate from the Skelley Limestone, it is likely that this fossil represents part of a small, deep-bodied, laterally compressed, durophagous bony fish.

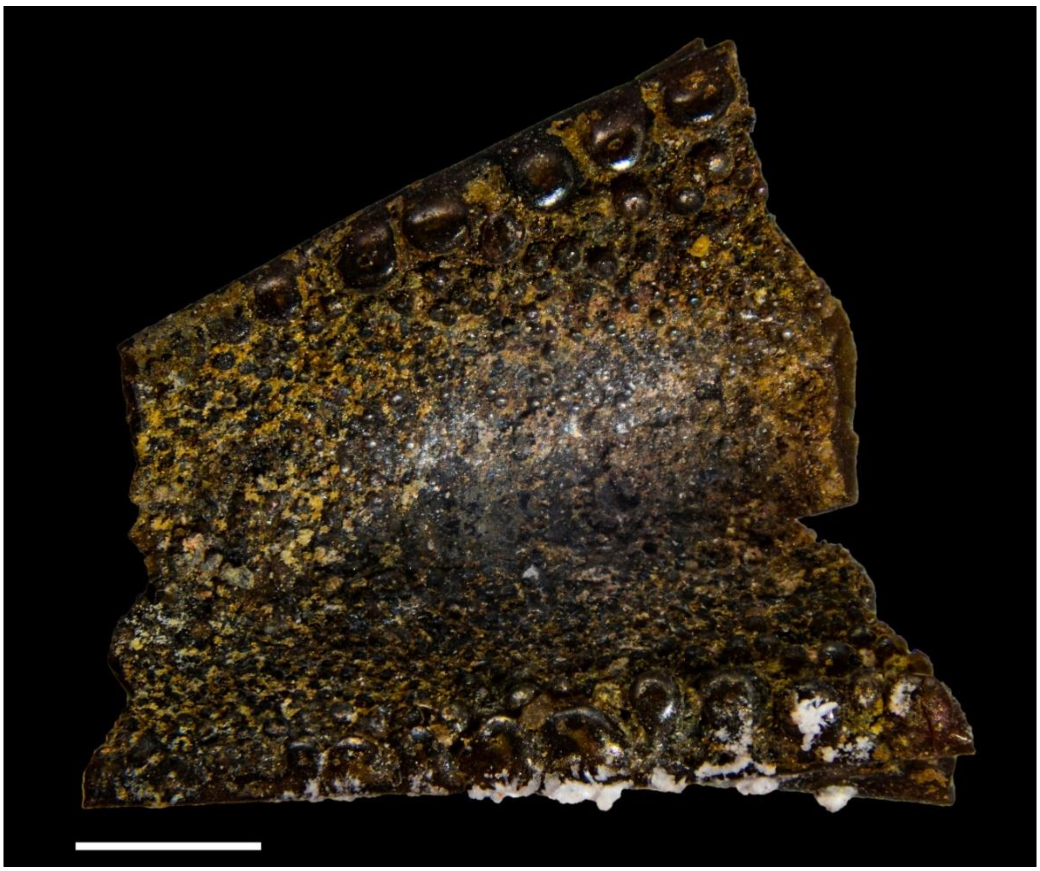


Figure 31 – Specimen WSU 1536A, Platysomidae indet. Scale bar 1 mm.

Family Palaeoniscoidae Rohon, 1890

Palaeoniscoidae indet.

Material Studied: WSU 1538

Locality: I-77 (WSU 1538)

Description: WSU 1538 appears to be a fragment of a mandible, just under 2.0 mm in maximum dimension. Similar to WSU 1536A, there are fractures on both the anterior and posterior ends of WSU 1538. On one side of the dentary fragment there is a platform structure that extends outward from just below the base of the teeth. This platform structure is similar to that of an uncatalogued actinopterygian fish jaw figured by Hodnett and Elliott (2021). And on the other side, a mosaic pattern of small, blunted hemispherical teeth are arranged. There are nine total teeth extending vertically from the occlusal surface of the mandible and all appear significantly worn.

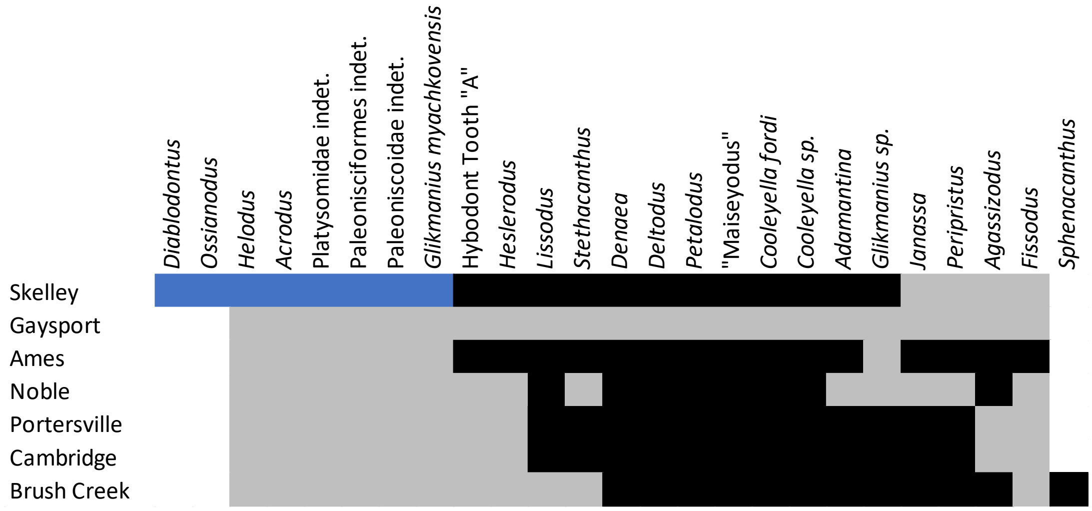
Remarks: As with the Palaeonisciformes indet. and Platysomidae indet. specimens recovered in this study, without additional, intact specimens, it would be premature to assign this specimen to anything more than Palaeoniscoidae indet. And due to the damage and wear observed on WSU 1538, assignment of this specimen to Palaeoniscoidae indet. is done so with caution.

Figure 32 – Specimen WSU 1538, Palaeoniscoidae indet. in occlusal and lateral views. Scale bar 1 mm.

5.3 BIOSTRATIGRAPHY

The table below (Table 2) reports the vertebrate occurrences from the Skelley Limestone in the context of other transgressions of marine conditions during the deposition of the Conemaugh Group below the Skelley Limestone. The upper row of this table lists each vertebrate taxon recovered in this investigation, as well as other vertebrates known from marine Conemaugh beds beneath the Skelley Limestone. The left-most column lists seven major marine intrusions into the region during Conemaugh deposition that are represented by limestones. Previously confirmed occurrences of a given vertebrate taxon are marked in black while occurrences that are possible (based on the chronostratigraphy of each group) are marked in gray. Confirmed occurrences of vertebrates that are new to this investigation are further colored blue. Eight of the vertebrate taxa reported in this investigation are reported in the Skelley Limestone for the first time. Data used in this table was obtained from Safford (1853), Seaman (1940), Neff (1965), Baker (1967), and Hansen (1986).

Table 2. Occurrences of Vertebrate Taxa in the Conemaugh Group.



Twenty-one taxa are reported from the Skelley Limestone from this investigation, 8 of which are reported for the first time. When each taxon's biostratigraphic range is examined, however, most of the marine vertebrates observed here do not represent extensions in biostratigraphic range. The main exception to this is *Diablodontus*, which is found to occur much earlier than its previous report from the Middle Permian (see Hodnett et al., 2013). This implies that the Skelley Limestone represents a fauna that is very characteristic of its time, significantly biodiverse, but not accounted for in broader biostratigraphic understandings. It would also appear that the vertebrate fauna of the Skelley Limestone is similar in biodiversity to that of the better-studied Ames Limestone (see Hansen, 1986).

While *Helodus* sp., *Acrodus* sp., Palaeonisciformes indet., Platysomidae indet., Palaeoniscoidae indet., and *Glikmanius myachkovensis* are reported for the first time from the Skelley Limestone in this study, it was predicted that these taxa occurred during the time of Skelley deposition. It is also likely that additional occurrences of *Diablodontus* may be found in strata with ages between the uppermost and lowermost occurrences for this genus. Similarly, occurrences of *Ossianodus* may be found in neighboring strata above and below the Skelley Limestone within the Conemaugh Group or other deposits of Gzhelian age. Given the new occurrence data presented here, it would appear that the Skelley cyclothem represented a period of faunal overturn within the marine vertebrates of the Conemaugh Group. However, the total amount of observed overturn from the Brush Creek cyclothem to the Skelley cyclothem accounts for approximately half of the animals investigated from the Brush Creek Limestone up to the Skelley Limestone (see Table 2). Furthermore, the vast majority of animals listed in Table 2 are predicted to occur across most of the upper Conemaugh's marine transgressions. This suggests that marine vertebrate communities in the Conemaugh Group were fairly resistant to the events that normally lead to faunal turnovers.

5.4 GEOGRAPHIC COMPARISONS

In the estuaries, shallow seaways, and among the archipelagoes which persisted on the North American craton during the Gzhelian Faunal Stage, feeding guild diversity among chondrichthyans and osteichthyans was surprisingly uniform. The differences in diversity between the I-77, Rockville Rd., and Wilsonwood Rd. localities seems to be representative of other Gzhelian aquatic vertebrate sites where one near-pelagic site is of notably higher biodiversity than neighboring, near-shore sites (see St. John, 1870; Hamm and Cicimurri, 2005). However, lower diversity observed at the I-77 locality could also be the result of preservation and/or sampling bias rather than a true indicator of low biodiversity.

Among the taxa reported from the Skelley Limestone in this study, several specimens extend the geographic range for that taxon beyond what was previously known. *Diablodontus* was previously only reported from Paleozoic rocks of northern Arizona (see Hodnett et al., 2013), which means that the *Diablodontus* sp. specimens recovered from the Skelley Limestone are the furthest north and east that this genus has been reported by approximately 2,600 kilometers (the majority of the North American continent's width). Similar comparisons can be made for *Ossianodus nebraskensis* and *Adamantina* sp., which were previously reported, in the United States, only from southeastern Nebraska and Oklahoma, respectively, over 1,000 kilometers west of the Skelley Limestone (see Ginter, 2016; Ginter et al., 2010).

Taxa recovered from all sites include the following animals: *Stethacanthus* sp., *Denaea* sp., *Adamantina* sp., *Ossianodus nebraskensis*, *Cooleyella*, and Palaeonisciformes indet. As most of these shared taxa were piscivorous, this suggests that there was an abundant nektonic food supply at all sites. Exclusive to the I-77 locality were several durophagous taxa: *Lissodus sp*., Platysomidae indet., and Palaeoniscoidae indet. This abundance and diversity of higher taxa with durophagous dental adaptations reflects the established high biodiversity of lower trophic level shelly fauna within the Skelley Limestone (see Baker, 1967). In contrast, while similar numbers of durophagous taxa were found at both the Rockville Rd. and Wilsonwood Rd. localities, the durophagous taxa were represented by *Helodus sp*. and *Petalodus ohioensis*. *Diablodontus sp*. was the only piscivorous taxa recovered from the Rockville Rd. locality not found at the I-77 or Wilsonwood Rd. localities. As the Rockville Rd. and Wilsonwood Rd. localities represents sites within this estuarine environment closer to the open sea, there may have been more niches available for free-swimming, piscivorous taxa at this locality than durophagous taxa which likely fed upon benthic invertebrates. However, the data may not be sufficiently robust for this pattern to truly indicate an ecological trend.

6. CONCLUSIONS

Among the Holocephalii, taxa reported as part of this investigation (the genera *Denaea*, *Stethacanthus*, and *Deltodus*) appear to have persisted in the Appalachian foreland basin for longer than previously thought. *Stethacanthus* also appears much further east, in what was probably farther into the embayment than its other occurrences (see Williams, 1985).

Euselachiian fauna are represented by an unknown protacrodontoid, plus the genera *?Acrodus*, *Lissodus*, and *Cooleyella*, are also found to occur farther east in North America than they are often reported. The occurrences of these chondrichthyans, alongside a report of the possible protacrodont "*Hybodus*" *alleghenensis* by Lund (1970) and Hansen's (1986) report of *Cooleyella* in the Upper Carboniferous of Ohio, indicate that a diverse assemblage of euselachiians migrated into and made use of the Appalachian foreland basin during the Gzhelian. The location of the Appalachian foreland basin relative to the Panthalassic Ocean further implies the inhabitation of the Panthalassic's near-shore seaways by a diverse assemblage of euselachiians.

The occurrence of bony fishes alongside this chondrichthyan assemblage is not surprising, given their reports in other aquatic Paleozoic vertebrate faunas (see Schultze and Bardack, 1987; Ivanov, et al., 2009). However, because conical palaeonisciform teeth cannot be easily identified to specific taxa, their paleobiogeographic significance in the

Skelley Limestone is not presently known. Platysomids, conversely, appear further east than other reports would indicate (see Olson, 1946; Lerner, et al., 2009) and their occurrence alongside durophagous euselachiians implies that there were diverse opportunities for durophagous vertebrates (regardless of taxonomic affinity) in the Appalachian foreland basin during this time.

Across the North American craton, Gzhelian assemblages of marine vertebrates are bimodal in terms of their reported species richness. Fossil localities with low species richness from Gzhelian seaways and estuaries are generally located near sites with high species richness, which implies the low biodiversity observed at some localities resulted from taphonomic biases and did not truly represent vertebrate ecology at the time. With this report of a diverse fauna from the Skelley Limestone, the ecology of the seaway and estuary in the Appalachian foreland basin appears similar in broad terms to vertebrate ecology elsewhere in the seaways that persisted on the North American craton during the Gzhelian.

7. SUGGESTIONS FOR FUTURE WORK

Given the high-species richness reported in the Skelley Limestone, as well as the nearby Ames Limestone, it would appear that marine transgressions during the Late Carboniferous into the Appalachian foreland basin resulted in multiple periods of colonization by marine vertebrates into newly formed habitats. Each Conemaugh-aged high-stand in the Appalachian foreland basin is therefore reasonably likely to produce vertebrate macrofossils and microremains. If a complex study on these high-stand sequences were able to find significant numbers of fossils, then the way these assemblages of vertebrates responded to climate and sea-level change in terms of habitat loss/appearance, niche-utilization, and evolution/extinction may be understood at a very high resolution, temporally speaking.

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