Fossil Marine Vertebrates from the Codell Sandstone Member of the Upper Cretaceous Carlile Shale in Jewell County, Kansas

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Recommended Citation
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Fossil Marine Vertebrates from the Codell Sandstone Member of the
Upper Cretaceous Carlile Shale in Jewell County, Kansas

A Thesis Presented in
Partial Fulfillment of
the Requirements for the Degree of
Master of Science

August 2015

By
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ACKNOWLEDGEMENTS

Foremost, I owe a debt of gratitude to Ramo Decker and his family (Pam, Kerstin, Kelsey, and Ray) who collected and donated the fossil specimens to FHSM for the purpose of my study. Without their hard work and generous contribution, this work would not have been possible. I would like to thank Dr. Laura Wilson (FHSM) for curating the specimens. I would also like to thank William Simpson, Dr. Lance Grande, Dr. Peter Makovicky, and Dr. Olivier Rieppel (Field Museum of Natural History, Chicago, Illinois) for their assistance with identifying specimens. I would also like to thank Michael Everhart (FHSM) for his assistance with identifying specimens and reviewing the taxonomic list of vertebrate taxa from Kansas, Nebraska, and Colorado. I would also like to thank Dr. Jalene LaMontagne for her assisting me with project design and statistical tests. Special thanks to my committee members, Dr. Windsor Aguirre, and Dr. Jason Bystriansky, for their friendly guidance, suggestions, and time, and the entire Department of Biological Sciences at DePaul University for their support, feedback, and friendship. Finally, I would like to express my deep appreciation and gratitude to Dr. Kenshu Shimada for his encouragement and guidance, from when I was considering applying to the Master’s program in the Department of Biological Sciences at DePaul, through to completion of this degree. I am fortunate to have had such a supportive and patient mentor and advisor.
ABSTRACT

Reported here is the first collective description of a marine vertebrate assemblage from the Codell Sandstone Member (middle Turonian) of the Upper Cretaceous Carlile Shale in Jewell County, Kansas. The Codell Sandstone was deposited during a regression of the Western Interior Seaway, and the fossil locality is described as a relatively shallow, near-shore environment. The collection contains larger, surface collected materials and microfossils washed from sediments represented by isolated teeth, vertebrae, and other skeletal elements as well as coprolites. The fauna consists of 38 taxa, including at least 22 chondrichthyans, 13 osteichthyan fishes, and tetrapod remains belonging to mosasauridae, plesiosauria, and testudines. The fauna is dominated by active, pelagic carnivores, such as *Meristodonoides*, *Anomotodon*, *Scapanorhynchus*, *Odontaspis*, *Cretalamna*, *Archaeolamna*, *Cretothyrsina*, *Cretodus*, *Dallasiella*, *Pseudocorax*, *Paranomotodon*, *Belonostomus*, *Apateodus*, *Aulopiformes* indet., *Mosasauridae* indet., and *Plesiosauria* indet. The fauna also includes benthic, durophagic fish taxa (e.g., *Ptychodus*, *Rhinobatos*, *Psychoptychus*, *Ischirhiza*, *Sclerorhynchus*, *Micropycnodon*, and *Anomoeodus*), a possible planktivore (*Cretomanta*), and probable scavengers (*Squalicorax*). Notable occurrences include the oldest example of *Ptychodus mortoni* from North America, the geologically youngest record of *Squalicorax*. *cf. S. pawpawensis*, and the first reported *Anomotodon* and the second reported *Paranomotodon* from Kansas.

The examination of the Codell fauna here is significant, because it also allowed the examination of any pattern of change in vertebrate communities as sea-levels and marine habitats changed in the central portion (Colorado, Kansas, and Nebraska) of the Western Interior Seaway. The faunas from different stratigraphic units were grouped based on lithology, designated as near-shore (siliciclastic-based) or off-shore (carbonate-based) ‘community assemblages,’ and reported vertebrate taxa at the genus level were classified based on presumed body size, preferred habitat, and diet. Based on previously published contentions and known ecological patterns of extant marine organisms, I tested the hypotheses that 1) generic richness would be greatest in the near-shore community assemblages, and 2) that near-shore assemblages would generally resemble one another and would differ significantly in ecological composition from the off-shore assemblages. My statistical analyses did not support these hypotheses. Generic diversity was greater in off-shore community assemblages and there were no significant differences in the proportions of vertebrates based on presumed size, habitat, or diet between the near-shore and off-shore assemblages. An inverse relationship between the proportions of lamniform sharks and carnivorous reptilian taxa was found, which may have been due to their similar ecological roles. These findings indicate that, whereas taxonomic compositions of paleocommunities did change or fluctuate as their depositional environment changed, the overall paleoecological dynamics of vertebrate paleocommunities in the central Western Interior Seaway was relatively stable for at least at the generic level regardless of different lithological environments over the 18 million year span investigated here.
INTRODUCTION

The Cretaceous Period extended from about 140 million years ago to about 65.5 million years ago (Obradovich, 1993). Globally, surface temperatures then were more than 10°C warmer than today with no evidence of significant, permanent ice cover over the north and south poles (Glancy et al., 1993; Gradstein et al., 2012). During the last half of the Cretaceous, sea levels were 300 m or more above present levels, and an epicontinental sea flooded the North American continent (Glancy et al., 1993). This sea, called the Western Interior Seaway, extended from the Arctic to the Gulf of Mexico (Kauffman and Caldwell, 1993). The Western Interior Seaway was home to a wide variety of marine vertebrates, including sharks, bony fishes, and marine reptiles (Russell, 1988; Everhart, 2005). The history of the Western Interior Seaway is marked by periods of rising and falling sea levels as a result of repeated transgressions and regressions of ocean water (Kauffman and Caldwell, 1993). These transgressive and regressive episodes continued until the seaway dried up near the end of the Cretaceous.

The Carlile Shale Formation was deposited in the Western Interior Seaway during the Turonian stage of the Late Cretaceous, extending from North Dakota in the north to New Mexico in the south (Hattin, 1962). The Turonian Stage of the Late Cretaceous spans the time between 90 and 94 million years ago (Gradstein et al., 2012), and approximately 17% of the North American continent was covered by the Western Interior Seaway (Glancy et al., 1993). During the Middle Turonian, while the Carlile Shale formed, the sea level of the Western Interior Seaway started to fall (Kauffman and Caldwell, 1993). In Kansas, the Carlile Shale extends generally from the northeast to the southwest through 21 counties and reaches a maximum width of 160 km (Hattin, 1962). The Carlile Shale is divided into three stratigraphic members: in ascending order, the Fairport Chalk Member, the Blue Hill Shale Member, and the Codell Sandstone Member (Fig. 1A). The Fairport Chalk was deposited far from shore in calm, less turbulent waters, whereas the Blue Hill Shale and Codell Sandstone were deposited in a more turbid, near-shore environment (Hattin, 1962).

The Codell Sandstone is a marine deposit formed between 90.5 and 90.4 million years ago (Kauffman et al., 1993). In Kansas, the Codell Sandstone was deposited in a turbid, near-shore environment as the eastern coastline moved west across the state (Hattin, 1962; Kauffman and Caldwell, 1993). Codell sediments consist mostly of fine quartzose sand and coarse quartzose silt (Hattin et al., 1987). In Kansas, the thickness of the Codell sandstone ranges from less that 0.5 m to 9.5 m (Hattin et al., 1987). The stratigraphic unit gradationally overlies the Blue Hill Shale, and the Fort Hays Limestone Member of the Niobrara Chalk Formation disconformably overlies the Codell Sandstone (Hattin, 1962). Sedimentation during the deposition of the Codell Sandstone was slow and, as the eastern shoreline retreated, it was followed by a long period of non-deposition until the Niobrara cycle of sedimentation (Hattin et al., 1987). In Kansas, Codell Sandstone fossils are from the zone of the ammonite Prionocyclus wyomingensis (Hattin et al., 1987). Reports of macrofossils from the Codell Sandstone are rare, but some vertebrate and invertebrate remains have been reported. Hattin (1962) lists several invertebrate fossils and trace fossils reported from the Codell Sandstone, including annelid worm burrows, inoceramid bivalves (Inoceramus cf. I. dimidus, Inoceramus cf. I. flaccidus, and Inoceramus sp.), and ammonites (Baculites? sp., Prionocyclus
wyomingensis, and Scaphites sp.). Fossil vertebrates include chondrichthyan such as Meristodonoides sp., Ptychodus whipplei, Cretalamna appendiculata, and Rhinobatos incertus (Hattin, 1962; Russell, 1988; Everhart, 2007, 2011), teleosts (Miller, 1958; Hattin, 1962; Russell, 1988), and russellosaurine mosasaurs (Polcyn et al., 2008). The most common microfossils are fecal pellets, spores, and foraminifers (Hattin, 1962). Overall, the vertebrates present in Kansas during the deposition of the Codell Sandstone are not well known due to a scarcity of reported fossils.

The focus of this thesis is on an assemblage of vertebrate fossils collected from a Codell Sandstone locality in Jewell County, Kansas (Figs. 1B and 2). The collection consists of a large quantity of teeth and skeletal elements from chondrichthyan (sharks and rays), osteichthyan (bony fishes), and marine reptile such as turtles, plesiosaurs, and mosasaurs. The assemblage also includes coprolites (fossilized feces). The aims of this thesis are two-fold. The first aim is to describe the vertebrate taxa from the Codell Sandstone locality because vertebrate remains from the Codell Sandstone in Kansas are not well documented. This research will be the first, most comprehensive report of fossil marine vertebrates from the Codell Sandstone in Kansas, and will provide a more complete picture of vertebrate life through the history and evolution of the Western Interior Seaway. The second aim is to compare the composition of the vertebrate fauna in the collection to that of other vertebrate fossil assemblages from other Late Cretaceous localities in the Western Interior. With previous reports on vertebrate faunas from underlying and overlying Late Cretaceous formations, the fossil assemblage from the Codell Sandstone can be used to examine how vertebrate communities changed as the coastline moved back and forth across the North American continent. This analysis will include marine vertebrate collections from older and younger rock formations to observe more long-term patterns of change, with the expectation that the near-shore faunal assemblages would be composed of different types of organisms than the off-shore assemblages.
Figure 1. Stratigraphy and Locality. A, Generalized stratigraphy of Upper Cretaceous marine deposits in Kansas. Codell Sandstone indicated by “X”. (modified from Shimada and Bell, 2006, fig. 3; stratigraphic information based largely on Hattin et al., 1987, and Kauffman et al., 1993). Members included in each community assemblage noted on right (see Materials and Methods for detail). B, Map of Jewell County, Kansas, showing Codell Sandstone fossil locality (indicated by “X”).
Figure 2. Exposure of Codell Sandstone (CS) in Jewell County Kansas where fossils reported here were collected. Note beige-colored, rocky remnants of Fort Hays Limestone (FHS) in background on top of Codell Sandstone and dark-colored Blue Hill Shale (BHS) in foreground. Photograph taken by K. Shimada September, 2012.
MATERIALS AND METHODS

The fossil locality is represented by an abandoned rock quarry where the Codell Sandstone became widely exposed due to the quarrying of the overlying Fort Hays Limestone (Fig. 2). All fossil specimens described here represent isolated dental or skeletal elements. They were collected by Ramo Decker and his family through two methods: surface collecting at the locality as well as through picking under dissecting microscopes indoors. Surface collecting involves collecting fossil specimens by walking or crawling over fossil bearing sediments and collecting the fossils in sight. This method is effective for fossils >1cm and can lead to a collecting bias where only relatively large elements are collected (Welton and Farish, 1993). Picking under dissecting microscopes, or micro-sorting, involves sorting through collected sediment to find smaller fossils that require a microscope to find. This method can mitigate collecting biases and provides a more accurate representation the species that would have been present (Welton and Farish, 1993).

The fossil specimens were identified primarily by comparing their morphology to descriptions and illustrations in published literature. After the specimens were identified and organized by taxon, the collection was divided in half, with half of the specimens per taxon being returned to the Decker Family. The other half of the specimens, that is the basis of my present study, was then donated to the Vertebrate Paleontology collection of Fort Hays State University’s Sternberg Museum of Natural History (FHSM) in Hays, Kansas, with catalogue numbers ranging from FHSM VP-18526 through FHSM VP-18651. Individual teeth and skeletal elements were given a catalogue number, organized taxonomically. Several taxa reported here have many specimens present in the collection. For taxa with a large number of specimens, not every fossil received its own unique catalogue number. Specimens that were characteristic examples of a specific taxon or were pathological, and therefore noteworthy, were given their own unique specimen numbers, whereas the rest of the specimens were given a batch catalogue number. The fossils given unique catalogue numbers (not batch numbers) were then photographed on a 1-mm-grid using a Canon PowerShot SX210 IS digital camera. Microscopic specimens were photographed through the ocular of a dissecting microscope. Images were edited using Free GNU Image Manipulation Program GIMP Version 2.8.3 (http://www.gimp.org), primarily to remove the background from the images and to add the scale bars.

For the faunal analysis portion of this thesis, marine vertebrate fossils from the Codell Sandstone and underlying and overlying Upper Cretaceous deposits in Kansas, Nebraska, and Colorado were compared to observe any potential changes in paleocommunity structure as sea-levels changed in the Western Interior Seaway. Paleocommunities in the Western Interior Seaway have been observed to differ in faunal diversity and abundance due to differences in latitude (Nicholls and Russell, 1990; Cumbaa et al., 2013). Constraining the analysis to the three adjacent states (Kansas, Colorado, and Nebraska) minimizes latitudinal differences in paleocommunities. To compare the composition of marine paleocommunities through time in the Western Interior Seaway, previous published data on marine vertebrates were used. First, Upper Cretaceous rock formations were grouped based on their distance from shore using the lithologic types as proxy. Formations that are composed of carbonate rocks were
deposited far from the shoreline and are considered off-shore formations (Prothero, 1990). Formations composed of siliciclastic rocks were deposited closer to the shoreline and are considered near-shore. Then, fossils reported from near-shore and off-shore formations (Fig. 1A) were grouped together into community assemblages for comparison. These community assemblages, based on distance from shore, were the units of comparison for the faunal analysis. Assemblage 1 includes vertebrate fauna from the following Cenomanian-aged, siliciclastic formations: the Dakota Sandstone (Everhart et al., 2004), Graneros Shale (Liggett et al., 2005; Schumacher and Everhart, 2005; Meglei et al., 2013), and Graneros Sandstone (Jansen et al., 2013). Assemblage 2 is compiled from faunas reported from the following Cenomanian through Middle Turonian carbonate formations: the Lincoln Limestone (Shimada and Schumacher, 2003; Shimada et al., 2006b; Shimada and Martin, 2008), Hartland Shale (Shimada and Nagrods, 2010; Nagrods et al., 2012), Jetmore Chalk/Pfiefer Shale (Dickerson et al., 2012; Bice et al., 2013; Nelms et al., 2014) and the Fairport Chalk (Bardack, 1965; Martin and Stewart, 1977; Stewart, 1978a; Schultze et al., 1982; Hattin et al., 1987; Russell, 1988; Everhart and Darnell, 2004; Shimada and Ystesund, 2007; Polcyn et al., 2008; McIntosh et al., 2013). Assemblage 2 also includes fauna reported from formations identified as only Greenhorn Limestone (Welles, 1962; Bardack, 1965; Meyer, 1974; Teller-Marshall and Bardack, 1978; Schultze et al., 1982; Schultze et al., 1985; Russell, 1988; Everhart and Pearson, 2014) and from the contact between the Greenhorn Limestone and Fairport Chalk (Schumacher and Everhart, 2005; Polcyn et al., 2008). Assemblage 3 consists of the Codell Sandstone fauna reported here in this thesis and from other Turonian-aged siliciclastic rocks, such as the Blue Hill Shale (Everhart et al., 2003; Shimada, 2006) and the Codell Sandstone at other localities (Edwards, 1976; Polcyn et al., 2008). Assemblage 4 contains fauna reported from the Niobrara Chalk, a Coniacian through Lower Campanian carbonate formation. Faunas were reported from both the Fort Hays Limestone (Welles, 1962; Russell, 1988; Shimada, 1996; Shimada and Everhart, 2003; Polcyn et al., 2008) and the Smoky Hill Chalk members (Everhart, 2005, 2006; Shimada and Fieltz, 2006; Cicimurri et al., 2008; Polcyn and Everhart, 2008; Fieltz and Shimada, 2009; Shimada and Everhart, 2009) as well as from rocks identified as only Niobrara Chalk (Shimada, 2008). Assemblage 5 includes fauna reported from the Campanian-aged, siliciclastic Pierre Shale (Cook et al., 2011) and the Sharon Springs member of the Pierre Shale (Carpenter, 1990, 2003). From the Dakota Formation, dated at around 95 million years old (Kauffman et al., 1993), to the Sharon Spring Shale, dated around 77 million years old, (Carpenter, 2003), the scope of this analysis thus covers around 18 million years of the history of the Western Interior Seaway.

For a measure of biodiversity and to compare the faunal data reported from the five lithology-based community assemblages, the genera reported (or the most specific taxonomic rank identified) were used. Due to the limitations of the fossil record to accurately measure species-level biodiversity, genus-, family-, and order-level measures of marine biodiversity are used to measure changes in biodiversity and have provided consistent pictures of past biodiversity (Raup and Sepkoski, 1982; Sepkoski, 1997). Using generic level data may also eliminate noise present in the data due to taxonomic uncertainty, particularly at the species-level for genera such as Squalicorax and Enchodus.
Biodiversity was measured by the number of different taxa present in each assemblage. The paleoecological roles of the taxa identified were then assigned to the reported fauna based on Bambach’s (1983) concept of “ecospace” that focused on bauplan (morphological features), space utilization, and food source. The reported fauna were categorized by their assumed space utilization in the water column (benthic or pelagic), their assumed food source based on dentition (durophagous or non-durophagous), and their estimated total body size (large or small). An organism was considered “large” if its estimated total body length was greater than 2 m. The proportions of taxa in particular paleoecological roles were compared between community assemblages using a contingency table analysis and chi-squared statistics with R statistical software (R Core Team, 2014).

RESULTS

SYSTEMATIC PALEONTOLOGY

Reported here are the vertebrate taxa identified in the examined Codell Sandstone collection, organized by their taxonomic classification. The taxonomic scheme of chondrichthians generally follow that presented by Capetta (2012) with the exception of Cretalamna appendiculata and Archaeolamna cf. A. kopingensis, which have been classified into previously defined families by Underwood and Cumbaa (2010).

Subphylum VERTEBRATA Lamarck, 1801
Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Order HYBODONTIFORMES Maisey, 1989
Family HYBODONTIDAE Owen, 1846
Subfamily HYBODONTINAE Owen, 1846
Genus MERISTODONOIDES Underwood and Cumbaa, 2010

MERISTODONOIDES sp.

Fig. 3A, B

Description—Teeth of the genus Meristodonoides are characterized by a median cusp and one pair of broadly spaced lateral cusplets. Both labial and lingual faces have prominent, widely spaced longitudinal ridges. A cutting edge runs medially along the tooth and is continuous between the cusplets and median cusp. FHSM VP-18526 (Fig. 3A) is the largest Meristodonoides sp. tooth in the collection. Only a median cusp remains and it measures 8 mm in total height.

Material—FHSM VP-18526, one tooth; VP-18527, one tooth; VP-18528, two teeth.

Discussion—Members of the genus Meristodonoides are North American hybodont sharks, previously assigned to the genus Hybodus Agassiz, 1837 (Underwood and Cumbaa, 2010). Species of Meristodonoides have been reported from various Cretaceous deposits throughout North America. Meristodonoides butleri has been reported from the Albian–Aptian of Texas (Thurmond, 1971) and the Cenomanian of Saskatchewan (Cumbaa et al., 2006; Cook et al., 2013). Meristodonoides montanensis
has been reported from the late Campanian of Montana, Wyoming, and Alberta (Case, 1978, 1987; Beavan and Russell, 1999). Teeth of *Meristodonoides rajkovichi* have been

Figure 3. Teeth of Hybodontidae (Hybodontiformes), Ptychodontidae (order incertae sedis), Mitsukurinidae (Lamniformes), and Odontaspididae (Lamniformes) from Codell Sandstone in Jewell County, Kansas. A, *Meristodonoides* sp. (tooth; FHSM VP-18526); B, *Meristodonoides* sp. (tooth; FHSM VP-18567); C, *Ptychodus mortoni* (tooth; FHSM VP-18529); D, *Ptychodus whipplei* (tooth; FHSM VP-18531); E, *Anomotodon* sp. (tooth; FHSM VP-18533); F, *Anomotodon* sp. (tooth; FHSM VP-18534); G, *Scapanorhynchus raphiodon* (tooth; FHSM VP-18535); H, *Scapanorhynchus raphiodon* (tooth; FHSM VP-18536); I, *Scapanorhynchus raphiodon* (tooth; FHSM VP-18537); J, *Odontaspis* cf. *O. watiniensis* (tooth; FHSM VP-18540). Orientations: A, B, E-J, left=lingual view, right=labial view; C, D, left=occlusal view, middle=anterior view, right=profile view. Scale: A, C-J=5 mm; B=1 mm.
reported from Cenomanian deposits in Saskatchewan (Cumbaa et al., 2006; Underwood and Cumbaa, 2010). Reports of hybodont fossils are rare in Kansas, but specimens of *Meristodonoides* sp. have been reported from the Early Cretaceous Kiowa Shale as well as the Late Cretaceous Dakota Sandstone and Codell Sandstone in Kansas (Everhart, 2011).

Subcohort NEOSELACHII Compagno, 1977  
Order incertae sedis  
Family PTYCHODONTIDAE Jaekel, 1898  
Genus *PTYCHODUS* Agassiz, 1835  
*PTYCHODUS MORTONI* (Mantell, 1836)

**Fig. 3C**

*Description*—Teeth of this species are characterized by a high, conical cusp with occlusal ridges that radiate from the apex in all directions and terminate at the marginal area of the crown, which extends over a box-like root. FHSM VP-18529 (Fig. 3C), the largest of the two *P. mortoni* teeth, measures 12 mm in crown height, 15 mm in total tooth height, and shows a conspicuous wear facet on the crown. FHSM VP-18230, a more laterally positioned tooth, has a more elongate margin and measures 6 mm in crown height and 10 mm in total.

*Material*—FHSM VP-18529, one tooth; VP-18230, one tooth.

*Discussion*—Members of the genus *Ptychodus* were durophagous sharks with shell-crushing dentition (Welton and Farish, 1993). *Ptychodus mortoni* was a very large shark, with one individual estimated to be about 11 m in total body length (Shimada et al., 2010). The fossil record of *P. mortoni* consists of predominantly isolated teeth from Coniacian–Campanian deposits in North America, including Texas and Kansas (Welton and Farish, 1993; Shimada, 1996; Cappetta and Case, 1999; Shimada and Fielitz, 2006; Shimada et al., 2010), but associated tooth plates and other skeletal remains, including placoid scales and an upper right jaw fragment, have been reported (Shimada et al., 2010; Shimada, 2012). *Ptychodus mortoni* has also been reported from Africa (Angola) and Europe (United Kingdom, Belgium, and Italy) (for a summary of localities, see Blanco-Piñón et al., 2007, but note that their stratigraphic information is unreliable: Stinnesbeck et al., 2008; but see also and Blanco-Piñón and Garibay-Romero, 2008).

*PTYCHODUS WHIPPLEI* (Marcou, 1858)

***Fig. 3D***

*Description*—Teeth of *Ptychodus whipplei* have a distinctly high and well-developed cusp. The sides of the cusp are almost vertical with parallel transverse ridges that run part way down just the occlusal faces of the crown. The crown margin overhangs the box-like root and is ornamented with concentrically-oriented granules. FHSM VP-18531 (Fig. 3D) is 11 mm in crown height, 15 mm in total tooth height, and it the largest *P. whipplei* tooth in the collection.

*Material*—FHSM VP-18531, one tooth; VP-18532, four teeth.

*Discussion*—*Ptychodus whipplei* is endemic to the Western Interior Seaway of North America, but it has been widely reported from Turonian deposits formed within the
seaway, including Kansas, South Dakota, Iowa, Colorado, Wyoming, Texas, Arizona, Utah, and New Mexico (Cappetta, 1973; Edwards, 1976; Martin and Stewart, 1977; Evetts, 1979; Russell, 1988; Welton and Farish, 1993; Williamson et al., 1993; Cappetta and Case, 1999; Cicimurri, 2001, 2004; Hanks and Shimada, 2002; Shimada, 2006; Spielmann et al., 2009; Becker et al., 2010; Bice et al., 2013; McIntosh et al., 2013; Gorman et al., 2014). The geologically oldest reported specimens are from the Upper Cenomanian (Shimada, 1994), and *P. whipplei* occurs in rocks as young as the Lower Coniacian (Welton and Farish, 1993; Lucas and Johnson, 2002).

Order LAMNIFORMES Berg, 1958  
Family MITSUKURINIDAE Jordan, 1898  
Genus *ANOMOTODON* Arambourg, 1952  
*ANOMOTODON* sp.  
Fig. 3E, F

*Description*—Teeth of the genus *Anomotodon* have an elongate cusp with smooth labial and lingual faces. The lingual face is moderately convex. The cusp curves lingually and a well-developed cutting edge runs the length of each side of the cusp, continuing down the mesial and distal heels of the cusp. The root is bilobate and high with a well-developed lingual protuberance and a deep nutrient groove. Root lobes flatten towards the bottom of the root. FHSM VP-18533 (Fig. 3E) is a mesially positioned tooth and has a U-shaped root. It is the largest of the two *Anomotodon* sp. teeth and measures 9 mm in crown height and 9.5 mm in total height. FHSM VP-18534 (Fig. 3F) is a more distally positioned tooth and has compressed root lobes. The crown measures 6 mm in crown height and the total tooth height is 8 mm.

*Material*—FHSM VP-18533, one tooth; VP-18534, one tooth.

*Discussion*—Members of the genus *Anomotodon* have been reported from Late Cretaceous deposits in France, the United Kingdom, and Bulgaria as well as early Maastrichtian deposits in Syria (Bardet et al., 2000; Andreev and Motchurova-Dekova, 2010; Guinot et al., 2013). North American specimens have been reported from Campanian deposits in Alabama and Turonian deposits in New Mexico, U.S.A., and Coahuila, Mexico (Applegate, 1970; Russell, 1988; González-Barba, Espinosa-Chávez, 2005; Spielmann et al., 2009), but the *Anomotodon* sp. specimens reported here are the first reported from Kansas.

Genus SCAPANORHYNCHUS Woodward, 1889  
*SCAPANORHYNCHUS RAPHIODON* (Agassiz, 1843)  
Fig. 3G, I

*Description*—Teeth of *Scapanorhynchus raphiodon* have a narrow, pointed cusp with fine, longitudinal striations on the lingual surface. They possess a smooth, flat labial surface. A single pair of cusplets may be present, and both cusp and cusplets have a smooth, continuous cutting edge on each side. The root lobes are rounded and widely separated with a deep nutrient groove. Lateral teeth have broad cusps that are more labiolingually compressed. The largest tooth in the collection, FHSM VP-18535 (Fig. 3G), measures 20 mm in crown height and 30 mm in total tooth height.
Material—FHSM VP-18535, one tooth; VP-18536, one tooth; VP-18537, one tooth; VP-18538, 468 teeth; VP-18539, 43 teeth.

Discussion—Scapanorhynchus raphiodon is the most commonly cited species in the genus (Cappetta, 2012) and has been reported from Late Cretaceous deposits of Western Europe, Israel, and North America (Cappetta, 2012; Guinot et al., 2013; Retzler et al., 2013). Specimens of *S. raphiodon* have been reported in Cenomanian–Turonian deposits from South Dakota, Wyoming, Utah, New Mexico, Arizona, and Texas (Russell, 1988; Welton and Farish, 1993; Williamson et al., 1993; Cappetta and Case, 1999; Cicimurri, 2001, 2004; Spielmann et al., 2009; Becker et al., 2010). In Kansas, *S. raphiodon* teeth have been reported from the Greenhorn Limestone, Carlile Shale members, and the overlying Niobrara Chalk (Williston, 1900; Hattin, 1962; Hamm and Shimada, 2002; Everhart et al., 2003). Members of the genus *Scapanorhynchus* have also been reported from the Blue Hill Shale and Fort Hays Limestone and are likely to be *S. raphiodon* (Shimada, 1996, 2006).

Family ODONTASPIDIDAE Müller and Henle, 1839

Genus *ODONTASPIS* Agassiz, 1838

*ODONTASPIS* cf. *O. watinensis* (Cook et al., 2013)

Fig. 3J

Description—Members of the genus *Odontaspis* are characterized by a lingually convex cusp with a smooth surface and up to three pairs of tall, sharp cusplets (Cappetta, 2012). Teeth of *O. watinensis* have a single pair of thin cusplets and a distinct, recessed lingual neck. A sharp cutting edge runs along the cusp and is continuous with the cusplets. The root has a well-developed lingual protuberance and a nutrient groove on a root with a very high basal concavity. FHSM VP-18540 (Fig. 3J) measures 12 mm in total tooth height with a 9-mm-high crown.

Material—FHSM VP-18540, one tooth.

Discussion—*Odontaspis watinensis* has only been reported previously from early Turonian deposits in Alberta, Canada (Cook et al., 2013). FHSM VP-18540 overall resembles teeth of *O. watinensis*, but it lacks a well-defined nutrient groove, which may have been abraded. Therefore, I here tentatively identify it as *O. cf. O. watinensis*. If FHSM VP-18540 indeed belongs to *O. watinensis*, the specimen would make it the geologically youngest and southern-most reported specimen for the species.

Family OTODONTIDAE Glickman, 1964

Genus *CRETALAMNA* Glickman, 1958

*CRETALAMNA appendiculata* (Agassiz, 1843)

Fig. 4A, B

Description—Teeth of *Cretalamna appendiculata* are moderately large and have a central cusp and a pair of triangular cusplets. The main cusp has a convex labial face and a smooth lingual face. The broad, bilobate root has a weak lingual protuberance, often with a nutrient foramen present. Both the cusp and root are labiolorally compressed. The species can be distinguished from other lamnoids by the absence of a nutrient
Figure 4. Teeth of Otodontidae (Lamniformes), Archaeolamnidae (Lamniformes), and Cretoxyrhinidae (Lamniformes) from Codell Sandstone in Jewell County, Kansas. A, Cretalamna appendiculata (tooth; FHSM VP-18541); B, C. appendiculata (tooth; FHSM VP-18542); C, Archaeolamna cf. A. kopingensis (tooth; FHSM VP-18544); D, A. cf. A. kopingensis (tooth; FHSM VP-18545); E, A. cf. A. kopingensis (tooth; FHSM VP-18546); F, Cretoxyrhina mantelli (tooth; FHSM VP-18547); G, Cretodus crassidens (tooth; FHSM VP-18549); H, C. crassidens (tooth; FHSM VP-18550); I, Dallasiella cf. D. willistoni (tooth; FHSM VP-18552); J, D. cf. D. willistoni (tooth; FHSM VP-18553). K, D. cf. D. willistoni (tooth, FHSM VP-18554). Orientations: left=lingual view, right=labial view. Scale: all=5 mm.
Cretalamna appendiculata has a long stratigraphic range that extends from the Lower Cretaceous (Albian) to the Lower Eocene (Ypresian) (Cappetta, 2012). It has been reported from Cretaceous deposits nearly worldwide including the Middle East, Central Asia, Africa, Australia, and throughout Europe (Müller and Diedrich, 1991; Siverson, 1992, 1996; Mustafa, 2000; Antunes and Cappetta, 2002; Mustafa et al., 2002; Vullo, 2005; Kennedy et al., 2008; Andreev and Motchurova-Dekova, 2010; Cappetta, 2012; Retzler et al., 2013). In North America, Cretalamna appendiculata has been reported from Late Cretaceous deposits throughout the Western Interior Seaway in Canada, Nebraska, Utah, Texas, Colorado, and Kansas, including the underlying Turonian Fairport Chalk and Blue Hill Shale and the overlying Coniacian–Campanian Fort Hays Limestone and Smoky Hill Chalk (Martin and Stewart, 1977; Welton and Farish, 1993; Shimada, 1996, 2006; Cappetta and Case, 1999; Shimada et al., 2006b; Cumbaa et al., 2006; Shimada and Fieltz, 2006; Becker et al., 2010; Gallardo et al., 2012; Jansen et al., 2013; McIntosh et al., 2013). The 50 million year range and worldwide distribution of C. appendiculata suggests that C. appendiculata may represent a large species complex instead of a single species. If C. appendiculata is considered a species complex, the teeth described here may instead be assigned to Cretalamna ewelli, the Coniacian-aged, North American species (Siverson et al., 2014).

Family ARCHAEOLAMNIDAE Underwood and Cumbaa, 2010
Genus ARCHAEOLAMNA Siverson, 1992
ARCHAEOLAMNA cf. A. KOPINGENSIS (Davis, 1890)
Fig. 4C–E

Description—Teeth of Archaeolamna kopingensis are characterized by a tall, triangular median cusp with a small pair of cusplets that are slightly taller than they are wide. The cusplets point in a more lateral direction relative to the central cusp. The lingual face of the median crown is strongly convex and the labial face is slightly convex. A well-defined cutting edge is continuous between the median cusp and the cusplets. The teeth have a distinct lingual neck with a robust bilobate root. The lingual protuberance is well developed and may have a nutrient groove and one or more nutrient foramina. The largest A. cf. A. kopingensis tooth in the collection is FHSM VP-18544 (Fig. 4C) and measures 27 mm in total tooth height with a crown height of 19 mm.

Material—FHSM VP-18544, one tooth; VP-18545, one tooth; VP-18546, one tooth.

Discussion—Archaeolamna kopingensis has been reported from Albian to Maastrichtian deposits in numerous regions, including Australia, Western Europe, Central Asia, and Russia (Siverson, 1996; Vullo et al., 2007; Cook et al., 2008, 2013; Kennedy et al., 2008; Underwood and Cumbaa, 2010; Guinot et al., 2013; McIntosh et al., 2013). In North America, specimens of A. kopingensis have been reported from Cretaceous deposits in Alberta, Saskatchewan, Iowa, Nebraska, Colorado, and Kansas, including a partial skeleton from the Pierre Shale in Kansas (Shimada et al., 2006b; Cook
et al., 2008, 2011, 2013; Underwood and Cumbaa, 2010; Gallardo et al., 2012; Nagrodski et al., 2012; McIntosh et al., 2013; Meglej et al., 2013; Gorman et al., 2014).

Family CRETOXYRHINIDAE Glickman, 1958
Genus CRETOXYRHINA Glickman, 1958
CRETOXYRHINA MANTELLI (Agassiz, 1843)

Fig. 4F

Description—Teeth of *Cretoxyrhina mantelli* are typically robust, with a triangular crown. The crown has a sharp mesial and distal cutting edge. Distally-located teeth may have a pair of lateral cusplets in Cenomanian–Turonian specimens, but cusplets are less common in more geologically younger ones (Shimada, 1997a; Cappetta, 2012). The crown has a flat labial surface and a convex lingual surface. The root is broad and relatively flat, with rounded lobe ends. A prominent lingual protuberance is present with one or more nutrient foramina present. This taxon is represented in this collection by six incomplete teeth, the largest of which (FHSM VP-18547; Fig. 4F) measures 25 mm in total tooth height and 19 mm in crown height.

Material—FHSM VP-18547, one tooth; VP-18548, 5 teeth.

Discussion—The complete dental pattern of *Cretoxyrhina mantelli* has been described based on articulated specimens from the Niobrara Chalk in Kansas (Shimada, 1997a; Bourdon and Everhart, 2011). *Cretoxyrhina mantelli* was a large lamniform shark, with an estimated length of up to 7 m (Shimada et al., 2006a; Shimada, 1997b). The species is commonly reported from Upper Cretaceous in Europe, Africa, and the Middle East (Müller and Diedrich, 1991; Siverson, 1996; Mustafa, 2000; Antunes and Cappetta, 2002; Mustafa et al., 2002; Cappetta, 2012; Retzler et al., 2013). In North America, *C. mantelli* has been reported from Cenomanian–Santonian deposits in Alberta, Saskatchewan, Wyoming, South Dakota, Nebraska, Iowa, Colorado, Kansas, and Texas (Welton and Farish, 1993; Williamson et al., 1993; Shimada, 1997c, 1996; Cappetta and Case, 1999; Beeson and Shimada, 2004; Shimada and Fielitz, 2006; Shimada et al., 2006b; Cumbaa et al., 2006; Underwood and Cumbaa, 2010; Gallardo et al., 2012; Nagrodski et al., 2012; Bice et al., 2013; Cook et al., 2013; McIntosh et al., 2013; Gorman et al., 2014). In Kansas, *C. mantelli* has been reported from the underlying Graneros Shale, Heartland Shale, Lincoln Limestone, Jetmore Chalk, Pfeifer Shale, and Fairport Chalk and the overlying Fort Hays Limestone and Smoky Hill Chalk (Martin and Stewart, 1977; Shimada, 1996, 1997c; Beeson and Shimada, 2004; Shimada and Fielitz, 2006; Shimada and Nagrodski, 2010; Bice et al., 2013; McIntosh et al., 2013).

Genus CRETODUS Sokolov, 1965
CRETODUS CRASSIDENS (Dixon, 1850)

Fig. 4G, H

Description—Teeth of *Cretodus crassidens* are high-crowned with a robust, highly convex lingual surface and a flat labial surface. Vertical, fold-like ridges are present only at the crown foot, with the rest of the crown characterized by smooth surfaces. Teeth of *C. crassidens* typically have a pair of triangular lateral cusplets. The large, U-shaped bilobate root has a shelf-like lingual protuberance that spans as wide as
the width of the central cusp. A weakly developed nutrient groove may be present on the lingual protuberance. All specimens of *C. crassidens* in the collection are incomplete. The largest specimen is FHSM VP-18549 (Fig. 4G) consisting of a complete root with a broken crown. Its root measures 37 mm in height, and the estimated total tooth height is 30 mm. *Material*—FHSM VP-18549, one tooth; VP-18550, one tooth; VP-18551, seven teeth.

*Discussion*—*Cretodus crassidens* is known from Cenomanian–Turonian deposits from Great Britain and Belgium as well as from Western Interior Seaway deposits in Texas, Kansas, Utah, and South Dakota (Welton and Farish, 1993; Williamson et al., 1993; Cappetta and Case, 1999; Cicimurri, 2001; Shimada, 2006; Becker et al., 2010). *Cretodus crassidens* has been reported from the Codell Sandstone and the underlying Fairport Chalk and Blue Hill Shale (Martin and Stewart, 1977; Shimada, 2006).

Genus *DALLASIella* Cappetta and Case, 1999

*DALLASIella* cf. *D. willistoni* (Cappetta and Case, 1999)

Fig. 4I–K

*Description*—The taxon is represented by 10 teeth in the collection. Teeth of *Dallasiella* cf. *D. willistoni* have a thick central cusp and a pair of small, triangular cusplets. The cusplets are oriented almost parallel to the central cusp and are well united to the central cusp at the crown base. The central cusp has a slightly convex labial surface and a more strongly convex lingual surface. A continuous cutting edge is present along the median cusp and cusplets. The lingual neck of teeth in *D. cf. D. willistoni* is narrow and the root lobes are labiolingually compressed and broad, from slightly U-shaped to almost flat. There is a well-developed lingual protuberance with a nutrient groove and a distinct nutrient foramen. The largest tooth in the collection (FHSM VP-18552; Fig. 4I) measures 6 mm in crown height and 9 mm in total height. 

*Material*—FHSM VP-18552, one tooth; VP-18553, one tooth; VP-18554, one tooth; VP-18555, seven teeth.

*Discussion*—Reports of *Dallasiella willistoni* from North America are limited and are found in Cenomanian through Turonian deposits. Specimens have been reported from Western Interior Seaway deposits from Alberta, Saskatchewan, Texas, Montana, and Kansas (Cappetta and Case, 1999; Siverson and Lindgren, 2005; Cumbaa et al., 2006; Cook et al., 2008, 2013; McIntosh et al., 2013). Teeth of *D. willistoni* may resemble those of small *Archaeolamna kopinensis*, but differ mainly with their compressed root lobes and a less developed nutrient groove (Underwood and Cumbaa, 2010). The teeth described here resemble those of *D. willistoni*; however, because they lack a deep nutrient groove, I here conservatively refer them to as *D. cf. D. willistoni* with the possibility that the observed shallow nutrient groove may be due to taphonomic abrasion or weathering.

Family ANACORACIDAE Casier, 1947

Genus *SQUALICORAX* Whitley, 1939

*SQUALICORAX* cf. *S. FALCATUS* (Agassiz, 1843)

Fig. 5A–J
**Description**—Teeth of *Squalicorax* cf. *S. falcatus* exhibit a wide morphological range, but in general have a triangular crown with a distal heel. The teeth have a convex lingual surface and flat labial surface. All cutting edges are finely serrated and present along the entire mesial and distal cutting edges of the crown, including the distal heel. Anterior teeth are slightly inclined distally, with lateral and posterior teeth more distally inclined. Teeth of *S. falcatus* have a high, rounded to rectangular bilobate root with short lobes. The largest tooth of *S. cf. S. falcatus* described here (FHSM VP-18556; Fig. 5A) measures 24 mm in total height and 21.5 mm in crown height. Three teeth in the collection show dental abnormalities, including labially curved crowns (FHSM VP-18563 and VP-18565; Fig. 5H, J) and a bifurcated crown (FHSM VP-18564; Fig. 5I).

**Material**—FHSM VP-18556, one tooth; VP-18557, one tooth; VP-18558, one tooth; VP-18559, one tooth; VP-18560, one tooth; VP-18561, one tooth; VP-18562, one tooth; VP-18563, one tooth; VP-18564, one tooth; VP-18565, one tooth; VP-18566, 616 teeth.

**Discussion**—Teeth in the collection identified as *Squalicorax* cf. *S. falcatus* generally resemble teeth of *S. falcatus*, but because teeth of *Squalicorax* spp. may appear to grade into one another, teeth identified as *Squalicorax falcatus* may actually include other members of the genus. The taxonomy of anacoracids is also considered problematic and is in need of revision (Siverson et al., 2007). Therefore, the materials are here referred to as *S. cf. S. falcatus*. Teeth of *S. cf. S. falcatus* are the most common chondrichthyan fossils in the collection. *Squalicorax* spp. in general were prominent scavengers in the Upper Cretaceous Western Interior Seaway in which their bite marks have been found on the bones of vertebrates or one or more teeth were associated with carcasses of other fossil vertebrates (Schwimmer et al., 1997a; Hanks and Shimada, 2002). *Squalicorax falcatus* has been reported from North American strata from the Cenomanian–Santonian throughout the Western Interior Seaway, including Saskatchewan, Wyoming, South Dakota, Nebraska, Iowa, Kansas, Colorado, Arizona, New Mexico, and Texas (Hattin, 1962; Case et al., 1990; Welton and Farish, 1993; Williamson et al., 1993; Shimada, 1996, 2006; Cappetta and Case, 1999; Cicimurri, 2001, 2004; Everhart et al., 2003; Beeson and Shimada, 2004; Shimada and Fielitz, 2006; Shimada et al., 2006b; Cumbaa et al., 2006; Spielmann et al., 2009; Cappetta, 2012; Bice et al., 2013; McIntosh et al., 2013; Gorman et al., 2014). In Kansas, remains of *S. falcatus* and *S. cf. S. falcatus* have been reported from the underlying Fairport Chalk and Blue Hill Shale as well as the overlying Fort Hays Limestone and Smoky Hill Chalk (Hattin, 1962; Martin and Stewart, 1977; Shimada, 1996, 2006; Beeson and Shimada, 2004; Shimada and Fielitz, 2006; McIntosh et al., 2013).

*SQUALICORAX* cf. *S. KAUPI* (Agassiz, 1843)

Fig. 5K

**Description**—Teeth of *Squalicorax kaupi* can be distinguished from other members of the genus by their high crown and more rounded, convex mesial cutting edge (Welton and Farish, 1993). The distal cutting edge is nearly vertical with a less well-defined distal heel. Both labial and lingual faces of the crown are weakly convex. The cutting edge is more coarsely serrated than *S. cf. S. falcatus*. FHSM VP-18567 (Fig. 5K) measures 12 mm in crown height and 16 mm in total height.
Material—FHSM VP-18567, one tooth.

Discussion—The tooth in the collection generally resembles *Squalicorax kaupi*, but as stated previously, because teeth of members of the genus may appear to grade into one another and the problematic taxonomy of anacoracid sharks, the tooth reported here is referred to as *S. cf. S. kaupi*. Teeth of *S. kaupi* are known from Late Cretaceous deposits spanning from the Coniacian to the Campanian, but the taxon is best represented in the Campanian (Cappetta, 2012). Fossils of this species have been reported from Coniacian through Maastrichtian deposits in Western Europe, Syria, Israel, Kazakhstan, and the Western Interior Seaway in Montana, Texas, Wyoming, Arkansas, and Kansas (Case, 1978; Case and Schwimmer, 1988; Welton and Farish, 1993; Cappetta and Case, 1999; Bardet et al., 2000; Shimada and Cicimurri, 2005; Vullo, 2005; Becker et al., 2006b; Shimada and Fielitz, 2006; Guinot et al., 2013; Retzler et al., 2013). Possible scavenging behavior has been reported for *S. kaupi*, including a tooth embedded in a mosasaur vertebra and a tooth tip embedded in a hadrosaur metatarsal (Schwimmer et al., 1997a). It has been suggested that *S. falcatus* was the preceding species in the same lineage as *S. kaupi*, with the potential speciation event occurring sometime during the Santonian and *S. kaupi* replacing *S. falcatus* by the end of the Santonian (Case et al., 1990; Shimada and Cicimurri, 2006; Cappetta, 2012). If the fossil reported here is in fact *S. kaupi*, it would be the geologically oldest reported *S. kaupi* to date and would extend the stratigraphic range of the species from at least the late Turonian through the Maastrichtian. It would also push back the possible speciation event between *S. falcatus* and *S. kaupi* from the Santonian to the Turonian or earlier.

*SQUALICORAX cf. S. PAWPAWENSIS* (Siverson et al., 2007)

Fig. 5L–U

Description—Teeth of *Squalicorax pawpawensis* have nearly symmetrical anterior teeth with an upright to slightly distally inclined triangular cusp. More laterally positioned teeth are more distally inclined. Teeth of *S. pawpawensis* can be recognized by their smaller size and the large but often irregular or poorly defined serrations that line the cutting edge (Siverson et al., 2007). The distal edge forms a sharp angle with a rounded distal heel that may have irregular serrations as well. The lingual face of the crown is convex, and the smooth labial face slightly overhangs the root. On more anterior teeth, the root is deeply V-shaped. The more posteriorly positioned teeth have a shallower curve to their root and an almost straight labial basal crown edge. The largest tooth here identified as *S. cf. S. pawpawensis* is FHSM VP-15868 (Fig. 5L) and measures 8 mm in crown height and 10 mm in total height.

Material—FHSM VP-18568, one tooth; VP-18569, one tooth; VP-18570, one tooth; VP-18571, one tooth; VP-18572, one tooth; VP-18573, one tooth; VP-18574, one tooth; VP-18575, one tooth; VP-18576, one tooth; VP-18577, one tooth; VP-18578, 29 teeth.

Discussion—Teeth in this collection generally resemble those of *Squalicorax pawpawensis* but, as stated previously, because of the problematic taxonomy of anacoracid sharks, the teeth here are referred to as *S. cf. S. pawpawensis*. *Squalicorax pawpawensis* was first reported from Late Albian deposits from the Pawpaw Formation in Texas (Siverson et al., 2007). Teeth conservatively reported as *S. cf. S. pawpawensis*
have been reported from Upper Cretaceous Western Interior Seaway deposits from Iowa and Kansas (Cook et al., 2013, referred to as *Squalicorax* sp. B; McIntosh et al., 2013; Gorman et al., 2014). If the specimens reported here are in fact *S. pawpawensis*, they would extend the stratigraphic range of the species from the Albian through the middle Turonian.

*SQUALICORAX* sp.

*Fig. 6*

**Description**—Teeth of *Squalicorax* sp. are relatively small compared to other anacoracid teeth. Mesially positioned teeth have a triangular, upright cusp, whereas the cusp is more distally inclined with a convex mesial cutting edge in distally positioned teeth. The lingual face of the crown is convex, and the labial face is flat to slightly convex. The cusp connects to a low distal heel at a shallow angle. Both the mesial and distal cutting edges carry well-defined, fine serrations. The roots are bilobate with a shallow basal concavity. More laterally positioned teeth have a wider root with a shallower basal concavity. Teeth of *Squalicorax* sp. have a distinct lingual protuberance with no nutrient groove or foramina present. The teeth of *Squalicorax* sp. in the collection measure between 6 mm and 10 mm in total height and 5 mm and 6 mm in crown height. More distally positioned teeth have a wider root with a shallower basal concavity. The mesial-most tooth represented in the sample (FHSM VP-18582; Fig. 6D) measures 8 mm in total root width, and the most distally positioned tooth (FHSM VP-18586; Fig. 6H) measures 12 mm in total root width.

**Material**—FHSM VP-18579, one tooth; VP-18580, one tooth; VP-18581, one tooth; VP-18582, one tooth; VP-18583, one tooth; VP-18584, one tooth; VP-18585, one tooth; VP-18586, one tooth; VP-18587, one tooth; VP-18588, one tooth; VP-18589, one tooth; VP-18590, one tooth.

**Discussion**—Teeth of *Squalicorax* sp. are smaller than those in the collection identified as *S. cf. S. falcatus* and *S. cf. S. kaupi*, but are similar in size to those identified as *S. cf. S. pawpawensis*. Teeth of *Squalicorax* sp. can be distinguished from *S. cf. S. pawpawensis* and other members of the genus by their low distal heel, the shallow angle at the transition between the distal heel and cusp, a curved labial basal crown edge that does not overhang the root, a shallower basal concavity, and fine, regularly distributed serrations that run the length of the mesial and distal cutting edges. Teeth of *Squalicorax* sp. that is likely conspecific with the form described here have been reported previously from Turonian deposits in Texas (Cappetta and Case, 1999, pl. 6, figs. 4–9).

ANACORACIDAE indet.

*Fig. 7A*

**Description**—Three isolated anacoracid vertebral centra are reported here. Centra from anacoracid sharks have visible concentric lamellae and are weakly amphicoelous. The width of the centra range from about 25% to 30% of the diameter, making them relatively thin for shark centra (Shimada and Cicimurri, 2005). Trunk centra in anacoracid sharks are circular and become more elongate toward the caudal region.
Figure 6. Teeth of *Squalicorax* sp. from Codell Sandstone in Jewell County, Kansas. A, *Squalicorax* sp. (tooth; FHSM VP-18579); B, *Squalicorax* sp. (tooth; FHSM VP-18580); C, *Squalicorax* sp. (tooth; FHSM VP-18581); D, *Squalicorax* sp. (tooth; FHSM VP-18582); E, *Squalicorax* sp. (tooth; FHSM VP-18583); F, *Squalicorax* sp. (tooth; FHSM VP-18584); G, *Squalicorax* sp. (tooth; FHSM VP-18585); H, *Squalicorax* sp. (tooth; FHSM VP-18586); I, *Squalicorax* sp. (tooth; FHSM VP-18587); J, *Squalicorax* sp. (tooth; FHSM VP-18588); K, *Squalicorax* sp. (tooth; FHSM VP-18589); L, *Squalicorax* sp. (tooth; FHSM VP-18590). Orientations: left=lingual view, right=labial view. Scale: all=5 mm.
Figure 7. Remains of Anacoracidae indet., Pseudocoracidae (Lamniformes), Lamniformes incertae sedis, Lamniformes indet., Rhinobatidae (Rajiformes), Ptychotrygonidae (Rajiformes), Sclerorhynchidae (Rajiformes), Mobulidae (Myliobatiformes) from Codell Sandstone in Jewell County, Kansas. A, Anacoracidae indet. (vertebra; FHSM VP-18593); B, Pseudocorax laevis (tooth; FHSM VP-18591); C, Paranomotodon sp. (tooth; FHSM VP-18596); D, Paranomotodon sp. (tooth; FHSM VP-18597); E, Paranomotodon sp. (tooth; FHSM VP-18598); F, Lamniformes indet. (vertebra; FHSM VP-18600); G, Lamniformes indet. (tooth; FHSM VP-18601); H, Rhinobatos incertus (tooth; presumed female; FHSM VP-18604); I, Rhinobatos incertus (tooth; presumed male; FHSM VP-18606); J, Ptychotrygon sp. (tooth; FHSM VP-18607); K, Ischyrhiza mira (rostral tooth; FHSM VP-18610); L, Ischyrhiza texana (rostral tooth; FHSM VP-18612); M, Cretomanta canadensis (tooth; FHSM VP-18613). Orientations: A, F, left=articular view, right=profile view; B-E, H-J, left=lingual view, right=labial view; G, left=lingual view, right=mesial view; K, left=dorsal view, right=profile view; L, left=anterior view, right=profile view; M, left=lingual view, right=profile view. Scale: A-G=5 mm, F=10 mm, H-M=1 mm.
The vertebrae reported here measure between 19 mm and 33 mm in diameter and between 3 mm and 11 mm in thickness.

**Material**—FHSM VP-18593, one vertebra; VP-18594, one vertebra; VP-18595, one vertebra.

**Discussion**—The vertebral centra reported here are compressed relative to the centra of other elasmobranchs, consistent with centra of the family Anacoracidae (Shimada and Cicimurri, 2005). Based on the diameter of the centra reported here and other reported *Squalicorax* skeletal remains from the Late Cretaceous in Kansas, the specimens reported here are in the same size range as the centra of *S. falcatus* (Shimada and Cicimurri, 2005).

**Family PSEUDOCORACIDAE** Cappetta, 2012

**Genus PSEUDOCORAX** Priem, 1897

**PSEUDOCORAX LAEVIS** (Leriche, 1906)

**Fig. 7B**

**Description**—The taxon is represented by two teeth in the collection (e.g., Fig. 7B). They are labiolingually compressed with a distally inclined cusp that has a convex lingual face and a flat labial face. The teeth have smooth and sharp cutting edges continuous with a distal heel, and a notch is present between the distal heel and the cusp. The bilobed root has a V-shaped basal concavity and a lingual protuberance with a distinct nutrient groove. The two teeth are small, measuring 5 mm and 3 mm in total height and 3.5 mm and 2 mm in respective crown height.

**Material**—FHSM VP-18591, one tooth; VP-18592, one tooth.

**Discussion**—Teeth of *Pseudocorax laevis* have been reported from Turonian through mid-Campanian deposits in Western Europe, Alabama, and Kansas (Leriche, 1906; Applegate, 1970; Vullo, 2005; Shimada and Fielitz, 2006; Hamm and Shimada, 2007; Shimada, 2009; Cappetta, 2012). In North America, another *Pseudocorax* species, *P. granti*, has been reported, that is similar morphologically and with a similar geographical range to *P. laevis* (Hamm and Shimada, 2007). The specimens reported here resemble Leriche’s (1906) original description of *P. laevis* based on the labiolingually compressed crown and the strongly bilobate root with a distinct nutrient groove. The distinction between *P. laevis* and *P. granti* is weakly founded and the taxa may be conspecific, with *P. laevis* having priority (Hamm and Shimada, 2007).

**Family incertae sedis**

**Genus PARANOMOTODON** Herman in Cappetta and Case, 1975

**PARANOMOTODON** sp.

**Fig. 7C–E**

**Description**—Teeth of *Paranomotodon* sp. have a high, triangular cusp that is erect in anterior teeth and more distally inclined in lateral teeth. The lingual surface of the crown is smooth and convex. The labial surface of the crown is moderately convex and a basal depression may be present. Teeth of *Paranomotodon* sp. have a distinct margin or heel on the mesial and distal side of the crown, with a sharp cutting edge running continuously along each length of the crown. The root has a well-developed lingual
protuberance with a nutrient groove (Cappetta, 2012). The root has a moderately concave basal edge with narrow root lobes. The largest tooth of *Paranomotodon* sp. (FHSM VP-18596; Fig. 7C) in the collection measures 10 mm in crown height and 13 mm in total height.

**Material**—FHSM VP-18596, one tooth; VP-18597, one tooth; VP-18598, one tooth; VP-18599, eight teeth.

**Discussion**—The genus *Paranomotodon* was previously attributed to the family Alopidae Bonaparte, 1838, but has since been considered an indeterminate lamniform at the familial level (Cappetta, 2012). Teeth identified as *Paranomotodon* sp. have been reported from the Cenomanian–Maastrichtian, in Europe, Russia, northern and western Africa, Japan, and North America (Williamson et al., 1993; Vullo, 2005; Cappetta, 2012; Guinot et al., 2013). In North America, *Paranomotodon* sp. has been reported from Turonian through Campanian formations in Texas, Kansas, and New Mexico (Russell, 1988; Welton and Farish, 1993; Shimada, 1996; Spielmann et al., 2009).

**LAMNIFORMES indet.**

Fig. 7F, G

**Description**—One vertebra and 271 isolated incomplete teeth belong to Lamniformes but lack sufficient diagnostic features to assign to a particular lamniform taxa. The vertebra (FHSM VP-18600; Fig. 7F), that measures 38 mm in diameter and 17 mm in thickness, is amphicoelous and exhibits concentric lamellae. FHSM VP-18601 (Fig. 7G) is a single tooth with a narrow, erect, lingually curved, 7-mm-high crown that has strongly convex lingual and labial faces, separated by a dull, sigmoidal cutting edge. Most of its root is missing, but a distinct tooth neck and a massive lingual protuberance without nutrient groove are present. All other tooth specimens (FHSM VP-18602 and VP-18603) represent fragmentary cusps and roots.

**Material**—FHSM VP-18600, one vertebra; VP-18601, one tooth; VP-18602, 260 fragmentary teeth; VP-18603, 10 fragmentary teeth.

**Discussion**—The vertebral centrum (Fig. 7F) is conservatively assigned here as a lamnoid vertebra. The width of the centra is about 50% of the diameter, indicating that it most likely did not belong to an anacoracid shark that tends to have more compressed centra (Shimada and Cicimurri, 2005). The centrum generally resembles those of *Cretoxyrhina mantelli* or *Cretalamna appendiculata*, and based on size it could belong to either taxon (Shimada, 1997b, 2007). FHSM VP-18601 (Fig. 7G) overall resembles teeth of the genus *Johnlongia* Siverson, 1996, but because of the absence of distinct nutrient groove that characterizes the genus, it is conservatively referred to as Lamniformes indet. Incomplete teeth represented in FHSM VP-18602 and VP-18603 exhibit a wide range of morphology suggesting that they come from multiple lamniform taxa, such as *Cretoxyrhina mantelli*, *Cretalamna appendiculata*, and *Cretodus crassidens*; however, they are too fragmentary for decisive taxonomic assignment.

Order RAJIFORMES Berg, 1940
Family RHINOBATIDAE Müller and Henle, 1838
Genus *RHINOBATOS* Linck, 1790
*RHINOBATOS INCERTUS* (Cappetta, 1973)
Fig. 7H, I

Description—Teeth of *Rhinobatos incertus* are small, generally no more than 2 mm in any dimension. They have mesiodistally wide crowns with no cutting edge. The labial crown face is rounded and extends over the root. The lingual face of the crown has a rounded, robust protuberance that extends below the cusp with a pair of smaller protuberances flanking the mesial and distal sides of the medial protuberance. The root is situated directly below the crown and has a flat attachment surface with root lobes separated by a deep nutrient groove. Teeth of *R. incertus* display strong sexual heterodonty. FHSM VP-18604 (Fig. 7H) and VP-18605 are presumed female teeth, with a flat, low crown. FHSM VP-18606 (Fig. 7I) and VP-18607 are presumed male teeth, with a more sharply pointed crown. The largest tooth of this species in the collection (FHSM VP-18604; Fig. 7H) measures 1.5 mm in crown height and 2 mm in total height.

Material—FHSM VP-18604, one tooth; VP-18605, four teeth, VP-18606, one tooth; VP-18607, two teeth.

Discussion—Members of the family Rhinobatidae, commonly known as guitarfishes, have a ray-like body that is dorsoventrally flattened with pectoral fins attached to the head, a wedge-shaped snout, and a tail that is not clearly distinguished from their body (Welton and Farish, 1993). Teeth of *Rhinobatos incertus* have been reported from Late Cretaceous Western Interior Seaway deposits throughout North America, including Alberta, Saskatchewan, South Dakota, Colorado, Kansas, and Texas (Cappetta, 1973; Stewart, 1990; Welton and Farish, 1993; Cicimurri, 2001; Everhart et al., 2003; Everhart, 2007b; Underwood and Cumbaa, 2010; Gallardo et al., 2012; Nagrodski et al., 2012; Cook et al., 2013). In Kansas, *R. incertus* had a considerably consistent presence from the Albian through the Campanian, including the underlying Graneros Shale, Lincoln Limestone, Blue Hill Shale, Codell Sandstone, and the Smoky Hill Chalk (Everhart, 2007b).

Family PTYCHOTRYGONIDAE Kriwet et al., 2009
Genus *PTYCHOTRYGON* (Jaekel, 1894)

*PTYCHOTRYGON* sp. (Fig. 7J)

Description—The genus *Ptychotrygon* is characterized by small, broad teeth with a low, rounded crown. The crown is subtriangular from an oral view with a transverse crest and two transverse labial ridges. The labial face extends beyond the root forming an apron. The lingual face may have a depression where the labial apron of the succeeding tooth rests in life. The root has a flat basal attachment surface and is split by a central groove. Each root lobe has a triangular attachment face. The largest tooth in the collection (FHSM VP-18607; Fig. 7J) measures 1 mm in total crown height, 1.5 mm in total tooth height, and 2.5 mm in total tooth width.

Material—FHSM VP-18607, one tooth; VP-18608, three teeth.

Discussion—Members of the genus *Ptychotrygon* have been reported from Albian to Maastrichtian strata in Europe, the Middle East, northern Africa, and North America (Lauginiger and Hartstein, 1983; Williamson et al., 1993; Mustafa et al., 2002; Vullo et al., 2007; Cappetta, 2012). The genus was common in the Western Interior Seaway and
has been reported from Alberta, South Dakota, Utah, Colorado, Nebraska, Kansas, Arkansas, New Mexico, and Texas (Russell, 1988; Welton and Farish, 1993; Williamson et al., 1993; Beavan and Russell, 1999; Cappetta and Case, 1999; Hanks and Shimada, 2002; Everhart et al., 2003; Becker et al., 2006b, 2010; Shimada et al., 2006b; Spielmann et al., 2009; Jansen et al., 2013). The teeth reported here generally resemble those of *P. triangularis*, but are missing the three transverse ridges that characterize the species (see Welton and Farish, 1993). The underlying Graneros Shale and Blue Hill Shale in Kansas both report *P. triangularis* (Everhart et al., 2003; Jansen et al., 2013), lending further evidence that the teeth reported here may belong to the species, but due to the morphological ambiguity, the teeth are conservatively referred to as *Ptychotrygon* sp.

**Family SCLERORHYNCHIDAE Cappetta, 1974**

**Genus ISCHYRHIZA Leidy, 1856b**

**ISCHYRHIZA MIRA** (Leidy, 1856b)  
Fig. 7K

*Description*—The taxon is represented by three rostral teeth in the collection. Rostral teeth of *Ischyrhiza mira* have long crowns with smooth anterior and posterior cutting edges that extend from the crown apex to the base. The crown is dorsoventrally flattened and slightly convex on the dorsal and ventral faces. The root is longer than the crown and expands basally. A longitudinal furrow divides root lobes, which have bulges and may appear scalloped. The largest rostral tooth in the collection, FHSM VP-18610 (Fig. 7K), has a crown height of 5 mm. The specimen has an incomplete root, but based on previous descriptions of the rostral teeth of *I. mira* (Welton and Farish, 1993, pg. 141, figs. 1–6c; Cappetta, 2012, pg. 377, fig. 365K, L), it has an estimated total tooth height of about 10 mm.

*Material*—FHSM VP-18610, one tooth; VP-18611, two teeth.

*Discussion*—*Ischyrhiza mira* was present in the Western Interior Seaway and has been reported from Turonian through Maastrichtian rocks in Texas, New Mexico, Arkansas, and as far north as Alberta (Russell, 1988; Welton and Farish, 1993; Beavan and Russell, 1999; Becker et al., 2006b; Spielmann et al., 2009). The species has also been reported from Late Cretaceous formations in North America along the Atlantic coast, including New Jersey, Delaware, and Georgia (Cappetta and Case, 1975b; Lauginiger and Hartstein, 1983; Case and Schwimmer, 1988; Cappetta, 2012). Members of the family Sclerorhynchidae have both rostral and oral teeth and generally resemble the modern sawfish (Pristidae Berg, 1958) (Welton and Farish, 1993; Cappetta, 2012). The rostral teeth are set laterally along a long, dorsoventrally flattened rostrum, referred to as a saw (Cappetta, 2012). The saw may have been used to probe into the substrate to find shelled invertebrate prey (Welton and Farish, 1993).

**ISCHYRHIZA TEXANA** (Cappetta and Case, 1975b)  
Fig. 7L

*Description*—The taxon is represented here by one rostral tooth. The rostral tooth of *Ischyrhiza texana* has a shorter, posteriorly directed crown relative to *I. mira*. Both anterior and posterior crown faces have a cutting edge, with enameloid ridges along the
grown foot. The root is rectangular to square in basal view with a wide basal attachment surface and large, rounded lobes. The tooth in the collection (FHSM VP-18612; Fig. 7L) measures 1.5 mm in total height, and the crown measures 0.5 mm in height.

**Material**—FHSM VP-18612, one tooth.

**Discussion**—According to Welton and Farish (1993), teeth of *Ischyrhiza texana* are restricted to Turonian–Coniacian rocks in the Western Interior Seaway, but reports of *I. cf. I. texana* teeth from the Cenomanian of Nebraska may extend the range of the species back to the Cenomanian (Jansen et al., 2013). Teeth of another sclerorhynchid with similar tooth morphology, *I. avonicola*, have been reported from Turonian–Coniacian deposits in Texas, but they may best be referred to as *I. texana* (Welton and Farish, 1993). *Ischyrhiza avonicola* is restricted to Campanian through Maastrichtian deposits (Welton and Farish, 1993).

Order MYLIOBATIFORMES Compagno, 1973
Family MOBULIDAE Gill, 1893
Genus *CRETOMANTA* Case et al., 1990
*CRETOMANTA CANADENSIS* (Case et al., 1990)

**Description**—There is one tooth of *Cretomanta canadensis* in the collection (FHSM VP-18613, Fig. 7M), that measures 1.75 mm in total height and 0.75 mm in crown height. The tooth has a hook-shaped crown that curves lingually. The labial face is convex with a prominent bulge, and there are no cutting edges. A depressed collar surrounds the basal portion of the crown, distinguishing it from the root that is massive and bulbous without any nutrient pore or furrow. The root expands lingually, and the entire lingual face forms a lingual protuberance.

**Material**—FHSM VP-18613, one tooth.

**Discussion**—Teeth of *Cretomanta canadensis* are common in Cenomanian deposits in the Western Interior Seaway (Cumbaa et al., 2010), but they have been reported from Turonian and Coniacian strata as well. Teeth assigned to *C. canadensis* have been reported from Saskatchewan, South Dakota, Wyoming, Colorado, Nebraska, Kansas, and Texas (Case et al., 1990; Shimada and Martin, 1993; Welton and Farish, 1993; Cappetta and Case, 1999; Cicimurri, 2001, 2004; Hanks and Shimada, 2002; Everhart et al., 2004; Shimada et al., 2006b; Cumbaa et al., 2006, 2013; Underwood and Cumbaa, 2010; Nagrodski et al., 2012; Gallardo et al., 2012; Jansen et al., 2013). Cappetta and Case (1990) suggested that the relatively small and simple teeth of *Cretomanta canadensis* indicate the taxon was a planktivore (Cappetta and Case, 1999). However, its exact taxonomic identity remains uncertain (Shimada and Martin, 2008).

**ELASMOBRANCHII indet.**

**Description**—The four of the five specimens (not figured) represent fragmentary elasmobranch vertebral centra, whereas the one other specimen is a small but nearly complete centra, measuring 4 mm in anteroposterior thickness and 9 mm in diameter. They are amphicoelous and composed of calcified cartilage, but lack any other specific characters to suggest specific taxonomic identification.
Material—FHSM VP-18614, five vertebral centra.

Discussion—Elasmobranch centra are common in the Cretaceous fossil record because, like the teeth, they are calcified and likely to be preserved (Welton and Farish, 1993). Elasmobranch vertebrae have cartilaginous neural and hemal arches which rarely preserve in the fossil record (Welton and Farish, 1993), as is the case with the centra reported here. The vertebrae reported here are too small or fragmented to identify beyond belonging to Elasmobranchii.

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Cope, 1887
Superorder NEOPTERYGII Regan, 1923
Order PYCNODONTIFORMES Berg, 1940
Family PYCNODONTIDAE Agassiz, 1833
Genus MICROPYCNODON Hibbard and Graffham, 1945
MICROPYCNODON cf. M. KANSASENSIS (Hibbard and Graffham, 1941)

Fig. 8A

Description—The taxon is represented by a single prearticular tooth with an abraded and broken root and measures 2.5 mm in total height and 1.5 mm in crown height (Fig. 8A). The tooth has an oval outline when viewed occlusally and a blunt, conical cusp. Faint striations run from the crown base to about two-thirds of the way up the crown. The crown base is constricted and sits atop a columnar root.

Material—FHSM VP-18615, one tooth.

Discussion—Pycnodont fishes were laterally compressed, deep-bodied fishes that inhabited shallow marine waters worldwide from the Triassic through the Eocene (Nursall, 1996). Fossil remains of the pycnodont species *Micropycnodon kansasensis* have been primarily reported from the Coniacian–Santonian Niobrara Chalk in Kansas (Hibbard and Graffham, 1941, 1945; Dunkle and Hibbard, 1946; Russell, 1988; Stewart, 1990; Shimada, 1996; Shimada and Fieltz, 2006; Everhart, 2007a). *Micropycnodon kansasensis* has also been reported from Cenomanian through Turonian deposits in Colorado, New Mexico, Kansas, South Dakota, and Saskatchewan (Cicimurri, 2001; Cumbaa et al., 2006, 2010, 2013; Shimada et al., 2006b; Shimada and Martin, 2008; Spielmann et al., 2009; Gallardo et al., 2012; Nagrodski et al., 2012).

Genus ANOMOEODUS (Forir, 1887)
ANOMOEODUS sp.

Fig. 8B

Description—Members of the genus *Anomoeodus* have teeth arranged in dental plates. The tooth of *Anomoeodus* sp. reported here (Fig. 8B) is a large, oblong tooth that is mediolaterally elongated. The anterior face of the crown has a more sigmoidal curve than the posterior face. The root is incomplete and appears to be almost completely abraded. The tooth measures 2 mm in total height and 10 mm long in the labial-lingual direction.

Material—FHSM VP-18616, one tooth.
Figure 8. Remains of Pycnodontidae (Pycnodontiformes), Aspidorhynchidae (Aspidorhynchiformes), Pachycormidae (Pachycormiformes), Plethodidae (Tseltatiiformes), Ichthyodectidae (Ichthyodectiformes), Pachyrhizodontidae (Elopiformes), Enchodontidae (Aulopiformes), Ichthyotringidae (Aulopiformes), Aulopiformes indet., and Osteichthyes indet. from Codell Sandstone in Jewell County, Kansas. A, Micropycnodon cf. M. kansasensis (tooth, FHS VP-18615); B, Anomoeodus sp. (tooth, FHS VP-18616); C, Belonostomus sp. (jaw fragment, FHS VP-18617); D, Protosphyraena sp. (tooth, FHS VP-18618); E, Protosphyraena sp. (hypural fragment, FHS VP-18620); F, Plethodidae indet. (tooth, FHS VP-18621); G, Xiphactinus audax (tooth, FHS VP-18622); H, X. audax (premaxilla, FHS VP-18624); I, X. audax (vertebra, FHS VP-18625); J, Pachyrhizodus minimus (tooth, FHS VP-18627); K, P. minimus (hypurals, FHS VP-18628); L, Pachyrhizodus sp. (tooth, FHS VP-18629); M, Pachyrhizodus sp. (jaw fragment, FHS VP-18630); N, Pachyrhizodus sp. (vertebra, FHS VP-18631); O, Enchodus cf. E. gladiolus (tooth, FHS VP-18635); P, E. cf. E. gladiolus (palatine bone, FHS VP-18636); Q, E. cf. E. petrosus (tooth, FHS VP-18637); R, E. cf. E. petrosus (tooth, FHS VP-18638); S, E. cf. E. petrosus (tooth, FHS VP-18639); T, E. cf. E. petrosus (palatine bone, FHS VP-18642); U, E. cf. E. petrosus (jaw fragment, FHS VP-18644); V, E. cf. E. shumardi (palatine bone, FHS VP-18646); W, Apatodus sp. (tooth, FHS VP-18647); X, Aulopiformes indet. (tooth, FHS VP-18653); Y, Osteichthyes indet. (vertebra, FHS VP-18648); Z, Osteichthyes indet. (fin rays, FHS VP-18651). Orientations: A, J, Q, R, left=profile view, middle=lingual view, right=profile view; B, C, top=profile view, bottom=dorsal view; D, G, left=profile view, right=mesial view; E, F, K, O, P, S, T-X, Z, left and right=profile view; H, left=ventral view, right=anterior view; I, N, Y, left=articual view, right=profile view; L, left=lingual view, right=labial view; M, top=dorsal view, bottom=profile view. Scale: A, F, J, W, X=1 mm; B-E, G-I, K-V, Y, Z=5 mm.
Discussion—Reports of the genus *Anomoeodus* range from the Jurassic–Eocene, and over 25 species have been described to date (Shimada and Everhart, 2009). Members of the genus have been reported from Cretaceous deposits in western Europe, including England, France, Spain, and Germany (Kriwet, 1999, 2002; Vullo, 2005; Licht and Kogan, 2011). In North America, *Anomoeodus* has been reported from Maryland, Georgia, Kansas, Arkansas, Texas, and Wyoming (Berry, 1939; Hussakof, 1947; Case and Schwimmer, 1988; Russell, 1988; McKinzie, 2002; Shimada, 2006; Shimada and Everhart, 2009). The species *A. barberi* has been reported from Kansas from both the underlying Blue Hill Shale (Turonian) and the overlying Smoky Hill Chalk (Campanian), but without an intact or partially intact tooth plate (Shimada, 2006; Shimada and Everhart, 2009), it is difficult to assign a species to FHSM VP-18616.

Order ASPIDORHYNCHIFORMES Bleeker, 1859
Family ASPIDORHYNCHIDAE Nicholson and Lydekker, 1889
Genus *BELONOSTOMUS* Agassiz, 1834

*BELONOSTOMUS* sp.  
Fig. 8C

Description—FHSM VP-18617 is represented by a long, narrow jaw fragment (Fig. 8C). It is broken at both ends and consists of two long rows of teeth. The fragment tapers anteriorly and forms a V-like cross section. The V-shaped cross section suggest that the fragment may be the presymphysial bone (see Bardack, 1968). The teeth all missing or broken, are widely spaced in rows of twelve on each side of the jaw fragment. The base of the teeth are circular or slightly elliptical is cross section. The specimen measures 28 mm in maximum preserved length, and it is 7 mm wide at the wider, posterior end. The bases of the broken teeth all measure less than 1 mm.

Material—FHSM VP-18617, one jaw fragment.

Discussion—Members of the genus *Belonostomus* were small, long-snouted, fusiform fishes (Bardack, 1968; Everhart, 2009a; Cumbaa et al., 2013) that ranged from Late Jurassic to Late Cretaceous deposits worldwide, including shallow, coastal waters in North America, Italy, Chile, India, Morocco, and Lebanon (Sahni et al., 1984; Brito and Suárez, 2003; Forey et al., 2003; Martill et al., 2011). In North America, *Belonostomus* is reported from Albian–Maastrichtian deposits, including Kansas, Texas, Saskatchewan and Alberta (Bardack, 1968; Whetstone, 1978; Russell, 1988; Wilson and Chalifa, 1989; Cumbaa et al., 2006, 2013; Everhart, 2009a; Sues et al., 2010).

Order PACHYCORMIFORMES Berg, 1940
Family PACHYCORMIDAE Woodward, 1895
Genus *PROTOSPHYRAENA* (Leidy, 1857a)

*PROTOSPHYRAENA* sp.  
Fig. 8D, E

Description—Teeth of Protosphyraena are triangular or arrowhead-shaped and laterally compressed. They have smooth, sharp medial and distal cutting edges. The labial and lingual faces are gently convex with fine, vertical striations. The largest
Protosphyraena sp. tooth in the collection (FHSM VP-18618; Fig. 8D) measures 12 mm in total height. The hypural bone fragment shows shallow ridges and is 30 mm in length and 13 mm thick (Fig. 8E).

**Material**—FHSM VP-18618, one tooth; VP-18619, two teeth; VP-18620, one hypural bone fragment.

**Discussion**—The genus Protosphyraena resembled modern billfish with a sharp, sword-like rostrum and long, crescent-shaped pectoral fins and is known from various parts of the world, including Europe and North America (Woodward, 1908; Applegate, 1970; Stewart, 1988; Diedrich, 2001). The oldest North American report of a Protosphyraena fossil is from the Cenomanian Graneros Shale in Kansas (Everhart et al., 2004). Specimens of Protosphyraena have been reported throughout the Western Interior Seaway from the Cenomanian–Campanian in Alberta, Saskatchewan, South Dakota, Colorado, Iowa, and Kansas (Witzke, 1981; Russell, 1988; Cumbaa and Tokaryk, 1999; Cicimurri, 2001; Liggett et al., 2005; Shimada et al., 2006b; Cumbaa et al., 2006, 2013; Shimada and Fielitz, 2006; Parris et al., 2007; Shimada and Martin, 2008; Gallardo et al., 2012; Nagrodski et al., 2012). Species of Protosphyraena cannot be distinguished based on teeth alone and without any rostral materials or preserved fins, the specimens here are referred to only as Protosphyraena sp. (Cumbaa et al., 2006; Shimada and Fielitz, 2006).

Order TSELFATIIFORMES Nelson, 1994
Family PLETHODIDAE Loomis, 1900
PLETHODIDAE indet.

**Description**—The taxon is represented by a single tooth in the collection (Fig. 8F). It is small, measuring 1.5 mm in total height. It is curved and have a smooth, conical crown with a circular crown base. The pronounced lingual curve of the tooth differentiates it from other osteichthyan material in the collection.

**Material**—FHSM VP-18621, one tooth.

**Discussion**—Plethodid teeth are not diagnostic at the species level (Shimada et al., 2006b), so the material reported here is referred to as Plethodidae indet. Plethodids have a worldwide distribution in Albian–Campanian deposits (Applegate, 1970; Chalifa and Lewy, 1991; Chanet, 1997; Taverne, 1999, 2000a, 2000b, 2001a, 2001b, 2002, 2003). In the Western Interior, plethodids have been reported from Late Cretaceous deposits in Iowa, Colorado, Saskatchewan, Nebraska, and Kansas, including the underlying Fairport Chalk and Blue Hill Shale and the overlying Smoky Hill Chalk and Pierre Shale (Martin and Stewart, 1977; Witzke, 1981; Russell, 1988; Carpenter, 1990; Fielitz and Shimada, 1999; Carpenter, 2003; Shimada and Schumacher, 2003; Beeson and Shimada, 2004; Shimada, 2006; Shimada and Fielitz, 2006; Shimada et al., 2006b; Cumbaa et al., 2006, 2013; Shimada and Martin, 2008; Gallardo et al., 2012; Bice et al., 2013; Jansen et al., 2013; McIntosh et al., 2013; Gorman et al., 2014)

Order ICHTHYODECTIFORMES Bardack and Sprinkle, 1969
Family ICHTHYODECTIDAE Crook, 1892
Genus XIPHACTINUS Leidy, 1870
XIPHACTINUS AUDAX (Leidy, 1870)
Description—Teeth of *Xiphactinus audax* are large and conical, appearing oval-shaped or circular in cross section. The robust teeth have longitudinal, crack-like striations that run their length. The largest tooth in the collection (FHSM VP-18622; Fig. 8G) measures 22.5 mm in total preserved height. The partial premaxilla (FHSM VP-18624; Fig. 8H) measures 66 mm long anteroposteriorly and 27 mm thick. The premaxillary teeth extend ventroanteriorly and are broken off, measuring 17 mm and 15 mm in diameter at their base. Vertebral centra of *X. audax* are large and strongly biconcave. The dorsal edges of the centra are flattened, with a pair of dorsal depressions where the base of the neural arches inserts. The centra are perforated by a small notochordal canal. FHSM VP-18625 (Fig. 8I) is the largest vertebra of *X. audax* in the collection and measures 45 mm in diameter and 28 mm deep. The presence of ventral depressions for hemal arches on the specimen indicates that it was a caudal vertebra.

Material—FHSM VP-18622, one tooth; VP-18623, eight teeth; VP-18624, one partial premaxilla; VP-18625, one vertebra; VP-18626, one vertebra fragment.

Discussion—*Xiphactinus audax* is one of the largest Cretaceous teleosts known that reached up to 5 m in total length (Bardack, 1965; Shimada and Everhart, 2004). It fed on a variety of other fishes and fossil evidence suggests that it was fed upon by large sharks such as *Cretoxyrhina mantelli* (Bardack, 1965; Shimada, 1997d; Shimada and Everhart, 2004). *Xiphactinus audax* occurs in Cenomanian–Campanian deposits within the Western Interior Seaway from Saskatchewan, Manitoba, South Dakota, Nebraska, Colorado, Kansas, Texas, Arkansas, and as far east as the eastern Gulf Coastal Plain in Alabama (Cope, 1872; Bardack, 1965; Martin and Stewart, 1977; Russell, 1988; Schwimmer et al., 1997b; Cumbaa and Tokaryk, 1999; Everhart et al., 2003; Liggett et al., 2005; Shimada, 2006; Shimada and Fielitz, 2006; Shimada et al., 2006b; Shimada and Martin, 2008; Bice et al., 2013; Cumbaa et al., 2013). A morphologically similar species, *X. vetus* Leidy, 1856a, ranges from the Campanian to Maastrichtian and is restricted to the middle Atlantic Coastal Plain of North America and coastal Gulf of Mexico (Schwimmer et al., 1997b; Everhart et al., 2003, 2004). Along with the differences in their temporal and geographic ranges, teeth of *X. vetus* are laterally compressed and can therefore be distinguished from teeth of *X. audax*, that are more circular in cross section (Schwimmer et al., 1997b).

Order ELOPIFORMES Greenwood, Rosen, Weitzman, and Meyers, 1966
Family PACHYRHIZODONTIDAE Cope, 1872
Genus *PACHYRHIZODUS* Dixon, 1850

*PACHYRHIZODUS MINIMUS* (Stewart, 1899)

Fig. 8J, K

Description—The taxon in the collection is represented by one tooth (Fig. 8J) and one pair of fused hypurals (Fig. 8K). The tooth is small, measuring 2.5 mm in total height, and is lingually curved and smooth, with a conical crown. A transparent enamaloid cap covers the tooth tip and no evidence of a pulp cavity is present at the tooth base. The fused hypurals are fan-shaped and blade-like, with smooth lateral surfaces. A prominent ridge runs anteroposteriorly through the middle of the fused hypural, with
shallow ridges originating along the center ridge and extending posterodorsally and posterovertrally. The fused hypural measures 23 mm long anteroposteriorly and 28 mm wide dorsoventrally at the widest point.

**Material**—FHSM VP-18627, one tooth; VP-18628, one fused hypurals.

**Discussion**—*Pachyrhizodus minimus* is the smallest member of the genus in North America, measuring up to about 80 cm in total length (see Applegate, 1970, fig. 189). *Pachyrhizodus minimus* is reported from Cenomanian–Campanian deposits throughout the Western Interior Seaway, including Kansas, Nebraska, Colorado, Iowa, South Dakota, and Saskatchewan (Cumbaa and Tokaryk, 1999; Hanks and Shimada, 2002; Carpenter, 2003; Everhart et al., 2003; Beeson and Shimada, 2004; Liggett et al., 2005; Shimada and Fielitz, 2006; Shimada et al., 2006b; Cumbaa et al., 2006, 2013; Shimada and Martin, 2008; Nagrodski et al., 2012; Gallardo et al., 2012; Jansen et al., 2013; Gorman et al., 2014).

**PACHYRHIZODUS** sp.

Fig. 8L–N

**Description**—The tooth (FHSM VP-18629; Fig. 8L) and the tooth embedded in the jaw fragment (FHSM VP-18630; Fig. 8M), that measure 12.5 and 6 mm in total height respectively, are characterized by a smooth, conical crown with a gentle lingual curve. There is a distinct pulp cavity present with a swollen, bony root in the teeth. The vertebral centra reported here are relatively short in the anteroposterior direction and are strongly biconcave. The anterior and posterior surfaces have distinct, concentric growth rings. The bases of neural and hemal spines remain on several specimens. The largest intact vertebrae in the collection (FHSM VP-18631; Fig. 8N) measures 15 mm in diameter and 7 mm in dorsoventral height.

**Material**—FHSM VP-18629, one tooth; VP-18630, one jaw fragment; VP-18631, one vertebra; VP-18632, nine fragmentary vertebrae.

**Discussion**—The genus *Pachyrhizodus* is known worldwide from Cretaceous deposits in Europe, North America, Australia, and New Zealand (Stewart, 1900; Bartholomai, 1969; Forey, 1977; Wiffen, 1983). In North America, four *Pachyrhizodus* species have been reported: *P. minimus*, *P. caninus* Cope, 1872, *P. kingi* Cope, 1872, and *P. leptopsis* Cope, 1874 (Shimada and Fielitz, 2006). Larger members of *Pachyrhizodus* could reach up to 2 m in total length (Applegate, 1970; Stewart and Bell, 1994). The teeth and vertebrae reported here are from a species larger than *P. minimus*, but without more skeletal material, the specimens are referred to conservatively as *Pachyrhizodus* sp.

Order AULOPIFORMES Rosen, 1973
Suborder ENCHODONTOIDEI Berg, 1940
Family ENCHODONTIDAE Woodward, 1901
Genus ENCHODUS Agassiz, 1835
**ENCHODUS** cf. *E. GLADIOLUS* (Cope, 1872)

Fig. 8O, P

**Description**—The tooth identified as *Enchodus* cf. *E. gladiolus* (FHSM VP-18635; Fig. 8O) is tall and laterally compressed with fine striations on the labial and
lingual faces. It measures 10 mm in total height and has a sigmoidal shape when viewed laterally. Both the mesial and distal cutting edges have smooth cutting edges. Although absent on the tooth in the collection, teeth of *E. gladiolus* may have a posteroapical barb (Goody, 1976). The lingual face is more convex than the labial face. There is no evidence of a pulp cavity present on the tooth. The taxon is also represented by a palatine bone (FHSM VP-18636; Fig. 8P), measuring 35 mm long and 9 mm deep. The palatine bone is anteroposteriorly elongate and the anterior end is the base of a palatine tooth that broke off. Palatine bones of *E. gladiolus* tend to be four times as long as they are deep. The palatine tooth base is directed anteroventrally.

*Material*—FHSM VP-18635, one tooth; VP-18636, one palatine bone.

*Discussion*—Members of the genus *Enchodus* were predatory fish that most likely fed on fast swimming cephalopods (Stewart and Carpenter, 1990) and evidence suggests that they were preyed upon by other teleosts and plesiosaurs (Stewart and Carpenter, 1990; Shimada and Everhart, 2003). *Enchodus gladiolus* is known from Cenomanian through Maastrichtian deposits throughout the Western Interior Seaway, including the Northwest Territories, Saskatchewan, Wyoming, Nebraska, Colorado, Iowa, Arkansas, and Kansas (Goody, 1976; Fielitz, 1996, 2002; Cumbaa and Tokaryk, 1999; Everhart et al., 2003; Beeson and Shimada, 2004; Shimada and Fielitz, 2006; Shimada et al., 2006b; Cumbaa et al., 2006, 2013; Shimada and Martin, 2008; Gallardo et al., 2012; Bice et al., 2013; Jansen et al., 2013; Gorman et al., 2014). Of the four known North American *Enchodus* species (*E. dirus*, *E. gladiolus*, *E. petrosus*, and *E. shumardi*), the material reported here most closely resembles that of *E. gladiolus*, particularly the relatively elongate palatine bone (Goody, 1976; Fielitz, 2004). Without other skeletal elements, it is difficult to definitively identify the specimens as *E. gladiolus* as described by Goody (1976), so the material is conservatively reported as *E. cf. E. gladiolus* here.

**ENCHODUS** cf. *E. PETROSUS* (Cope, 1874)

*Fig. 8Q–U*

*Description*—Teeth identified as *Enchodus* cf. *E. petrosus* are long and straight to slightly sigmoidal, with flat, smooth labial faces and convex, striated lingual faces (Fig. 8Q–S). The palatine teeth are asymmetrical and have lateral and anterior cutting edges and the dentary teeth have mesial and distal cutting edges. The largest, most complete tooth identified as *E. cf. E. petrosus* (FHSM VP-18637; Fig. 8Q) measures 26 mm in total height. Palatine bones identified as *E. cf. E. petrosus* are also included in the collection, the largest of which (FHSM VP-18642; Fig. 8T) measures 30 mm long and 14 mm deep. All palatine bones have broken tooth bases present and some have scalloped tooth replacement scars. Where palatine tooth bases are preserved, they point anteroventrally. Palatine bones of *E. petrosus* are about twice as long as they are deep (Goody, 1976). Jaw fragments with broken teeth (e.g., Fig. 8U) are also reported in which the tooth bases show evidence of cone shaped teeth or robust teeth with convex lingual faces and flat labial faces.

*Material*—FHSM VP-18637, one tooth; VP-18638, one tooth; VP-18639, one tooth; VP-18640, 43 teeth; VP-18641, 52 teeth; VP-18642, one palatine bone; VP-18643, 11 palatine bones; VP-18644, one jaw fragment; VP-18645, five jaw fragments.
Discussion—Materials identified as *Enchodus* cf. *E. petrosus* are the most common osteichthyan materials in the collection. *Enchodus petrosus* was the largest member of the genus with an estimated standard length of 1.1 m (Goody, 1976). *Enchodus petrosus* has been reported from the Turonian–Maastrichtian deposits from Atlantic Plain localities such as Alabama, Georgia, New Jersey, and Delaware, and Western Interior Seaway localities such as New Mexico, Wyoming, South Dakota, Kansas, Arkansas, and Texas. The record from Kansas includes the Blue Hill Shale and Smoky Hill Chalk (Applegate, 1970; Goody, 1976; Case and Schwimmer, 1988; Everhart et al., 2003; Beeson and Shimada, 2004; Shimada and Fielitz, 2006; Parris et al., 2007). The material reported as *E.* cf. *E. petrosus* most closely fits the description of *E. petrosus*, particularly the robust, straight teeth and the palatine bones that are about one half as deep as they are long (Goody, 1976). As with *E.* cf. *E. gladiolus*, without other skeletal elements, it is difficult to assign the material reported here to *E. petrosus* as described by Goody (1976), so the material is conservatively reported as *E.* cf. *E. petrosus*.

**ENCHODUS** cf. *E. SHUMARDI* (Leidy, 1856c)

**Fig. 8V**

Description—The taxon is represented by a single palatine bone. It is anteroposteriorly shorter, but relatively deeper, than palatine bones of the other *Enchodus* reported here, measuring 6 mm long and 4 mm deep. A broken tooth base is present on the palatine bone, set at right angle to the palatine bone and pointing ventrally.

Material—FHSM VP-18646, one palatine bone.

Discussion—*Enchodus shumardi* has been reported from Cenomanian–Maastrichtian deposits throughout the Western Interior Seaway, including Saskatchewan, Manitoba, Alberta, Montana, South Dakota, Nebraska, Colorado, Kansas, and Texas, (Goody, 1976; Russell, 1988; Wilson and Chalifa, 1989; Cumbaa and Tokaryk, 1999; Beeson and Shimada, 2004; Shimada and Fielitz, 2006; Cumbaa et al., 2006, 2013; Shimada and Martin, 2008; Gallardo et al., 2012; Nagrodski et al., 2012; Bice et al., 2013; Jansen et al., 2013). In Kansas in particular, remains of *E. shumardi* have been reported from the Fairport Chalk and Blue Hill Shale as well as the Fort Hays Limestone (Shimada and Everhart, 2003; Shimada, 2006; McIntosh et al., 2013). The small palatine bone reported here (Fig. 8V) resembles the description of palatine bones of *E. shumardi* and falls within the known stratigraphic range of the species (Goody, 1976; Parris et al., 2007). Along with a shorter palatine bone than other *Enchodus* species, Goody (1976) also describes *E. shumardi* as having a palatine tooth longer than the palatine bone. Without the palatine tooth present, it is difficult to confidently assign the specimen to *E. shumardi*, and it is therefore referred to as *E.* cf. *E. shumardi*.

Suborder **ICHTHYOTRINGOIDEI** Goody, 1969
Family **ICHTHYOTRINGIDAE** Jordan, 1905
Genus **APATEODUS** (Woodward, 1901)
**APATEODUS** (?) sp.

**Fig. 8W**
Description—FHSM VP-18647 (Fig. 8W) is small, measuring 3.5 mm in total tooth height. Like other reported *Apateodus* teeth, the specimen is triangular with sharp mesial and distal cutting edges that come to a sharp point at the apex (Fielitz and Shimada, 2009; Nagrodski et al., 2012; Gorman et al., 2014). The tooth has a slight lingual curve, convex labial and lingual faces, and a small pulp cavity at the base.

Material—FHSM VP-18647, one tooth.

Discussion—Remains of *Apateodus* are not widely reported from the Western Interior Seaway, but several specimens that are somewhat complete and consist of some cranial and pectoral girdle elements have been reported from the Turonian of England and the Maastrichtian of Belgium (Kruizinga, 1924; Leriche, 1929; Goody, 1969). Isolated teeth and skeletal elements attributed to *Apateodus* have been reported from Late Cretaceous through Paleocene deposits from various locations worldwide, including Germany, Russia, India, and Bolivia (Jaillard et al., 1993; Prasad and Godinot, 1994; Nessov, 1995; Ladwig, 2000; Rana et al., 2005; Silva and Gallo, 2011). In North America, *Apateodus* remains have been reported from Cenomanian–Campanian deposits in Alberta, Manitoba, Colorado, and Kansas (Nicholls, 1988; Wilson and Chalifa, 1989; Shimada and Fielitz, 2006; Fielitz and Shimada, 2009; Nagrodski et al., 2012). The relatively sparse reports of *Apateodus* remains from the Western Interior Seaway may indicate that it was a minor component of the paleofauna in the seaway (Fielitz and Shimada, 2009). The isolated tooth reported here generally resembles those reported *Apateodus*, but is conservatively reported as *Apateodus* (?) sp. due to its isolated find.

AULOPIFORMES indet.

Fig. 8X

Description—The teeth reported here are slender and laterally compressed with fine, vertical striations extending from the base almost to the apex of the teeth. The teeth are sigmoidal in lateral view with a mesially recurved tip. They have a convex lingual face and flatter labial face. There is a sharp cutting edge on the mesial face, and a short posteroapical barb forms a short distal cutting edge. The teeth have a circular cross-section at the base which becomes more elliptical toward the tip. The larger (FHSM VP-18633; Fig. 8X) of the two teeth measures 6 mm in total length.

Material—FHSM VP-18633, one tooth; VP-18634, one tooth.

Discussion—The slender, compressed, sigmoidal teeth with a posteroapical barb reported here generally resemble those of other North American Late Cretaceous auropiform fishes, in particular those of the genera *Enchodus* and *Cimolichthys* Leidy, 1857b (Goody, 1970, 1976), but they differ from the two genera in distinct ways. The teeth have a thin base and lack a posterior cutting edge, making them unlikely to belong to *Cimolichthys* (Kriwet, 2003). The teeth also have a distinct pulp cavity, which differentiates them from members of the genus *Enchodus*. Teeth of *Enchodus* spp. have a very compressed pulp cavity or none at all (Goody, 1976; Kriwet, 2003). Without any additional associated skeletal elements, it is difficult to assign a taxonomic rank beyond Auropiformes to the teeth reported here.

OSTEICHTHYES indet.

Fig. 8Y, Z
Description—Specimens reported here consist mainly of bony vertebral centra. FHSM VP-18648 (Fig. 8Y) preserves a neural spine and measures 35 mm in total length and 6 mm in centrum diameter. The other vertebrae reported here vary in size, with the largest intact centrum (in FHSM VP-18649; not figured) measuring 21 mm in diameter and 20 mm in depth, and the smallest intact centrum (in FHSM VP-18650; not figured) measuring 1 mm in diameter and 1 mm in depth. The fin ray fragment (FHSM VP-18651; Fig. 8Z) is represented by several long, slender fin rays running parallel across the length of the fragment. FHSM VP-18651 measures 40 mm long and 17 mm in height.

Material—FHSM VP-18648, one vertebra; VP-18649, 44 vertebrae; VP-18650, 14 vertebrae; VP-18651, one fragmentary set of fin rays.

Discussion—Vertebrae of osteichthyan fishes have a biconcave shape with dorsal depressions for the insertion of the neural arch and lateral or ventral depressions for the insertion of ribs or hemal arches (Kardong, 2006). Sometimes, the bases of the neural and hemal arches fossilize attached to the centrum (Welton and Farish, 1993; Kardong, 2006). The vertebrae and fin rays reported here are isolated finds and lack any distinguishing characteristics that would differentiate them from one another and are therefore conservatively referred to only as Osteichthyes indet.

Class REPTILIA Laurenti, 1768
Order TESTUDINES Linnaeus, 1758
TESTUDINES indet.

Description—FHSM VP-18652 (Fig. 9A) is a single shell fragment that has a flat dorsal surface with striations and pits covering the surface. The ventral side is also covered with striations and pits, but has a more irregular surface texture with distinct ridges. The shell fragment measures 27 mm in the maximum dimension and up to 7 mm in thickness.

Material—FHSM VP-18652, one body shell fragment.

Discussion—Marine turtles were common in the Western Interior Seaway during the Late Cretaceous, but little is known about the turtle inhabitants of the Seaway due to a scarcity of complete fossils (Russell, 1988; Everhart, 2005). As is true today, sea turtles in the Western Interior Seaway likely had broad-ranging omnivorous diets, feeding on algae, plants, fishes, and sea jellies (Benton, 2005; Everhart, 2005; Sørensen et al., 2013; Kear, 2006). Marine turtles were also prey to large predators like Cretuxyrhina mantelli, whose teeth have been found embedded in turtle fossils (Shimada and Hooks, 2004). Turtle bones have also been reported with striated tooth marks, indicating scavenging by a member of the genus Squalicorax (Becker et al., 2006a). Remains of turtles have been reported from Late Cretaceous deposits throughout the Western Interior Seaway, including marine deposits in Saskatchewan, Alberta, South Dakota, Kansas, Nebraska, Arizona, and New Mexico (Russell, 1988; Everhart, 2005; Cumbaa et al., 2006, 2013; Spielmann et al., 2009; Sues et al., 2010; Meglei et al., 2013). The marine environment present during the deposition of the Codell Sandstone and a lack of any other terrestrial fossils suggests that this fossil likely originated from a marine turtle, but it is possible that the shell fragment originated from a terrestrial turtle whose remains washed out to sea.
Figure 9. Remains of Testudines and Mosasauridae from Codell Sandstone in Jewell County, Kansas. A, Testudines indet. (shell fragment, FHSM VP-18652); B, Mosasauridae indet. (tooth, FHSM VP-18653); C, Mosasauridae indet. (tooth, FHSM VP-18654); D, Mosasauridae indet. (tooth, FHSM VP-18655); E, Mosasauridae indet. (tooth, FHSM VP-18656); F, Mosasauridae indet. (tooth, FHSM VP-18657); G, Mosasauridae indet. (tooth, FHSM VP-18658); H, Mosasauridae indet. (tooth, FHSM VP-18659); I, Mosasauridae indet. (tooth, FHSM VP-18660); J, Mosasauridae indet. (tooth, FHSM VP-18661); K, Mosasauridae indet. (tooth, FHSM VP-18662); L, Mosasauridae indet. (tooth, FHSM VP-18663); M, Mosasauridae indet. (tooth, FHSM VP-18664); N, Mosasauridae indet. (tooth, FHSM VP-18665); O, Mosasauridae indet. (tooth, FHSM VP-18666); P, Mosasauridae indet. (tooth, FHSM VP-18667); Q, Mosasauridae indet. (tooth, FHSM VP-18668); R, Mosasauridae indet. (jaw bone, FHSM VP-18669); S, Mosasauridae indet. (vertebra, FHSM VP-18670); T, Mosasauridae indet. (vertebra, FHSM VP-18671); U, Mosasauridae indet. (vertebra, FHSM VP-18672); V, Mosasauridae indet. (vertebra, FHSM VP-18673). Orientations: A, top=ventral view, bottom=dorsal view; B-K, left and right=profile views, L-R, left=lingual, right=labial; S-V, left=anterior view, middle=ventral view, right=posterior view. Scale: A-Q, S-V=5 mm; R=10 mm.
Without any diagnostic skeletal elements, a terrestrial origin of this fragment cannot be ruled out.

Order SQUAMATA Oppel, 1811
Superfamily MOSASAUROIDEA Camp, 1923
Family MOSASURIDAE Gervais, 1853
MOSASURIDAE indet.

Fig. 9B–V

Description—The taxon is represented by 16 isolated teeth, one fragmentary jaw bone, and four isolated prococelous vertebrae. The teeth range from 6 mm to 22 mm in total height. The apex of each tooth curves posteriorly. The teeth have striations that run vertically as well as unserrated anterior and posterior cutting edges. The largest jaw fragment (pieced together from three fragments; Fig. 9R) tapers anteriorly and measures 80 mm long and 20 mm deep at the deepest posterior end. Four other fragments could not be pieced together but show broken teeth in tooth sockets. Three of the four vertebra (FHSM VP-18670, VP-18672, and VP-18673; Fig. 9S, U, V) are caudal vertebrae, the largest of which (FHSM VP-18672) measures 35 mm in condylar width, 34 mm in condylar height, and 36 mm in total length. The dorsal surface of the caudal vertebrae is convex and the ventral surface has paired, shallow depressions located posteriorly. FHSM VP-18671 (Fig. 9T) is a partial trunk vertebra with a prezygapophysis.

Material—FHSM VP-18653, one tooth; VP-18654, one tooth; VP-18655, one tooth; VP-18656, one tooth; VP-18657, one tooth; VP-18658, one tooth; VP-18659, one tooth; VP-18660, one tooth; VP-18661, one tooth; VP-18662, one tooth; VP-18663, one tooth; VP-18664, one tooth; VP-18665, one tooth; VP-18666, one tooth; VP-18667, one tooth; VP-18668, one tooth; VP-18669, one jaw bone (in multiple pieces); VP-18670, one vertebra; VP-18671, one vertebra; VP-18672, one vertebra; VP-18673, one vertebra.

Discussion—The oldest mosasauroids are known from Cenomanian deposits in Israel (Polcyn et al., 1999), but the Turonian was an important time for the diversification of the now extinct group of aquatic squamates (Bell and VonLoh, 1998; Bardet et al., 2008). Mosasaurs were widely distributed during the Turonian (Antunes, 1964; Páramo, 1994; Páramo-Fonseca, 2000; Bardet et al., 2003b, 2008; Kear, 2003). The earliest mosasaur remains reported from North America are Turonian in age, and by the mid-Turonian, three subfamilies of Mosasauridae could be found in the Western Interior Seaway: Mosasaurinae Williston, 1897, Plioplatecarpinae Dollo, 1884, and Tylosaurinae Williston, 1897 (Polcyn et al., 2008). Remains of Turonian mosasaurs have been reported from Texas, South Dakota, Wyoming, New Mexico, and Kansas, including the Fairport Chalk and Blue Hill Shale (Martin and Stewart, 1977; Russell, 1988; Bell and VonLoh, 1998; Bell and Polcyn, 2005; Polcyn and Bell, 2005; Shimada, 2006; Spielmann and Lucas, 2006; Polcyn et al., 2008). Mosasaur remains have also been reported from the Codell Sandstone Member in Kansas, including Tylosaurinae and Russelllosaurina remains in Jewell County, Kansas, at the same locality as the fossils reported here (Polcyn et al., 2008). FHSM VP-18661–VP-18668 are relatively small for mosasaur teeth, but they are reported here as “Mosasauridae indet.” because of their morphological similarity to the other teeth referred to as Mosasauridae indet. in the collection
(posteriorly curved apex, cutting edges, and striations) and may represent juvenile mosasaur teeth (Michael J. Everhart, personal communication, 2013).

Order PLESIOSAURIA Blainville, 1835
PLESIOSAURIA indet.
Fig. 10

Description—The material identified as Plesiosauria indet. includes two nearly complete teeth, two tooth fragments, and one fragmentary propodial. The teeth are conical elongated, and posteriorly curved, and have longitudinal ridges that run the length of the tooth. The largest tooth (FHSM VP-18674; Fig. 10A) measures 29 mm in total height. The teeth and tooth fragments are also all finely striated, but none of the teeth reported here have any preserved roots. The propodial (FHSM VP-18678; Fig. 10E), that has a flattened, broad shape, measures 78 mm long and 12 mm wide at the mesial end, and 2 mm wide at the distal end.

Material—FHSM VP-18674, one tooth; VP-18675, one tooth; VP-18676, one tooth fragment; VP-18677, one tooth fragment; VP-18678, one propodial fragment.

Discussion—Plesiosaurs were a group of marine reptiles that first appeared in the Triassic (Storrs, 1997). They had four powerful, paddle-like limbs to propel them underwater, sometimes to depths great enough that they experienced decompression syndrome when surfacing (Rothschild and Storrs, 2003; Benton, 2005). Plesiosaurs had a world-wide distribution, with specimens reported from the Middle East, Australia, New Zealand, Japan, Morocco, and South America (Persson, 1960; Welles and Gregg, 1971; Sato and Tanabe, 1998; Bardet et al., 2000, 2003a; Sato and Storrs, 2000; Kear, 2003; Gasparini et al., 2014). The presence of plesiosaurs is well documented in the Late Cretaceous Western Interior Seaway, including deposits in Saskatchewan, Manitoba, Wyoming, Montana, South Dakota, Iowa, Utah, Nebraska, Arizona, New Mexico, and Kansas (Welles, 1952, 1962; Witzke, 1981; Hattin et al., 1987; Tokaryk, 1987; Russell, 1988; Martin et al., 1998; Storrs, 1999; Schumacher and Everhart, 2005; Cumbaa et al., 2006; Albright, III et al., 2007; O’Keefe and Chiappe, 2011; Meglei et al., 2013). Plesiosaur remains have not previously been reported from the Codell Sandstone, but several taxa have been reported from the Fairport Chalk (Hattin et al., 1987; Russell, 1988; Schumacher and Everhart, 2005; Schumacher et al., 2013) and probable plesiosaur remains have been reported from the Blue Hill Shale (Everhart, 2009b). The materials reported here are not diagnostic beyond the order Plesiosauria, but they represent the first plesiosaur remains reported from the Codell Sandstone in Kansas.

VERTEBRATA indet.
Fig. 11

Description—The collection contains nine bone fragments and 23 coprolites. The bone fragments (FHSM VP-18679; not figured) are small and lack any diagnostic features to distinguish even between fish or reptilian bone material. Four of the coprolites (FHSM VP-18680–VP-18682; Fig. 11A–C) have an amphipolar spiral shape, the largest of which measures 51 mm along its longer axis and 31 mm along its shorter axis. The rest of the coprolites (FHSM VP-18683–VP-18687; e.g., Fig. 11D–F) are irregular ellipsoidal
Figure 10. Remains of Plesiosauria from Codell Sandstone in Jewell County, Kansas. A, Plesiosauria indet. (tooth, FHSM VP-18674); B, Plesiosauria indet. (tooth, FHSM VP-18675); C, Plesiosauria indet. (tooth fragment, FHSM VP-18676); D, Plesiosauria indet. (tooth fragment, FHSM VP-18677); E, Plesiosauria indet. (propodial fragment, FHSM VP-18678). Orientations: left and right=profile views. Scale: A-D=5 mm; E=10 mm.
Figure 11. Coprolites of Vertebrata indet. from Codell Sandstone in Jewell County, Kansas. A, Vertebrata indet. (coprolite, FHSM VP-18680); B, Vertebrata indet. (coprolite, FHSM VP-18681); C, Vertebrata indet. (coprolite, FHSM VP-18682); D, Vertebrata indet. (coprolite, FHSM VP-18684); E, Vertebrata indet. (coprolite, FHSM VP-18685); F, Vertebrata indet. (coprolite, FHSM VP-18686). Scale: A-B=10 mm; C-F=5 mm.
or spherical coprolites. The smallest coprolite in the collection (FHSM VP-18686; Fig. 11F) is of an irregular ellipsoidal shape, measuring 12 mm along its longer axis and 7 mm along its shorter axis. None of the coprolites has any discernable skeletal remains of prey items.

**Material**—FHSM VP-18679, nine bone fragments; FHSM VP-18680, one coprolite; VP-18681, one coprolite; VP-18682, two coprolites; VP-18683, one coprolite; VP-18684, one coprolite; VP-18685, one coprolite; VP-18686, one coprolite; VP-18687, 15 coprolites.

**Discussion**—The bone fragments lack enough distinguishing characteristics to confidently assign them to a more specific group of vertebrates, so they are conservatively referred to as Vertebrata indet. here. The producer of the coprolites cannot easily be determined either. The large size of the coprolites indicates that they belong to vertebrates (Savrda and Bottjer, 1993). The spiral coprolites, identified as amphipolar by the evenly spaced coils that run the length of the coprolite (as defined by Neumayer, 1904), likely belong to a chondrichthyan or osteichthyan, which have valvular intestines that have been shown to produce intestinal contents and fecal matter in a spiral shape (Stewart, 1978b; McAllister, 1985). It is also unlikely that any of the coprolites belong to a mosasaur, as mosasaur remains are likely to contain densely packed, undigested skeletal remains of prey items (Lindgren et al., 2010; Eriksson et al., 2011).
DISCUSSION

TAXONOMIC REMARKS

Previous reports of vertebrate macrofossils from the Codell Sandstone in Kansas include scattered reports of chondrichthians (Ptychodus whipplei, Cretalamna appendiculata, and Meristodonoides sp.), teleosteans, and russellosaurine mosasaur remains (Hattin, 1962; Russell, 1988; Polcyn et al., 2008; Everhart, 2011). This present report is significant because it constitutes the first collective study of vertebrate remains from the Codell Sandstone in Kansas. Table 1 summarizes the taxa reported here as well as their assumed space utilization in the water column, assumed food source, and inferred size. In total, the fossil collection examined in this present study consists of 1,841 specimens from at least 38 taxa, including a minimum of 22 elasmobranchs, 13 osteichthians, and three reptilians.

The Codell Sandstone was deposited in Kansas at the end of the Turonian, and this timeframe is supported by the taxa reported here, twenty-two of which have been previously reported from the Turonian of Kansas: Meristodonoides sp., Ptychodus whipplei, Scapanorhynchus raphiodon, Cretalamna appendiculata, Archaeolamna cf. A kopingensis, Cretoxyrhina mantelli, Cretodus crassidens, Dallasiella cf. D. willistoni, Squalicorax cf. S. falcatus, S. cf. S. pawpawensis, Rhinobatos incertus, Ptychotrygon sp., Anomoeadus sp., Belonostomus sp., Plethodidae indet., Xiphactinus audax, Pachyrhizodus minimus, Enchodus cf. E. gladiolus, E. cf. E. petrosus, and E. cf. E. shumardi, as well as members of Testudines, Mosasauridae, and Plesiosauria (Russell, 1988; Everhart et al., 2003; Shimada, 2006; Everhart, 2007b, 2011; McIntosh et al., 2013). Members of the genus Protosphyraena and Pachyrhizodus have been reported from other Late Cretaceous deposits in Kansas, including underlying Cenomanian deposits and overlying Coniacian–Santonian deposits as well as Turonian deposits in North America outside of Kansas (Stewart, 1988; Cicimurri, 2001; Everhart et al., 2004; Shimada and Fielitz, 2006; Giersch et al., 2010).

Five of the taxa reported here have never been reported previously from Kansas: Anomotodon sp., Odontaspis cf. O. watinensis, Squalicorax sp., Ischyrhiza mira, and I. texana. This Codell assemblage also extends the stratigraphic range of several fish species. For example, this collection contains the oldest example of Squalicorax cf. S. kaupi, the oldest example of Ptychodus mortoni from North America, as well as the oldest examples of Pseudocorax laevis, Paranomotodon sp., Micropycnodon cf. M. kansasensis, and Apateodus sp. reported from formations in Kansas, although older reports of these species have been made in Colorado (Shimada et al., 2006b; Nagrodski et al., 2012). This collection also contains the geologically youngest record of S. cf. S. pawpawensis in the Western Interior Seaway.

PALEOECOLOGICAL REMARKS

The Codell Sandstone in Kansas was deposited at a shallow, near-shore environment as the eastern shoreline of the Western Interior Seaway migrated west due to its regression (Hattin, 1962). It has previously been described as a turbid, high energy
Table 1. List of vertebrate taxa from Codell Sandstone at Jewell County locality in Kansas along with sample sizes, presumed habitat, presumed feeding strategy, and presumed body size (habitat and feeding strategy from Goody, 1976; Welton and Farish, 1993; Nursall, 1996; Schwimmer et al., 1997; Shimada, 1997; Hamm and Shimada, 2002; Everhart, 2007; Wueringer et al., 2009; Shimada and Everhart, 2009; Cumbaa et al., 2010; Shimada et al., 2010; Martill et al., 2011; Cappetta, 2012; and Sørensen et al., 2013)

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Total Number of Specimens</th>
<th>Presumed Habitat</th>
<th>Presumed Feeding Strategy</th>
<th>Size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Pelagic</td>
<td>Benthic</td>
<td></td>
</tr>
<tr>
<td><strong>CHONDRICHTHYES</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Meristodonoides</em> sp.</td>
<td>4</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Psychodus mortoni</em></td>
<td>2</td>
<td>X</td>
<td>Durophagous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Psychodus whipplei</em></td>
<td>5</td>
<td>X</td>
<td>Durophagous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Anomotodon</em> sp.</td>
<td>2</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
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</tr>
<tr>
<td><em>Scapanorhynchus raphiodon</em></td>
<td>514</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Odontaspis</em> cf. <em>O. watinensis</em></td>
<td>1</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Cretalamna appendiculata</em></td>
<td>22</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Archeolamna</em> cf. <em>A. kopingsis</em></td>
<td>3</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Cretodus</em> crassidens</td>
<td>9</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Dallasiella</em> cf. <em>D. willistoni</em></td>
<td>10</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Squalicorax</em> cf. <em>S. falcatus</em></td>
<td>626</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Squalicorax</em> cf. <em>S. kaupi</em></td>
<td>1</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td><em>Squalicorax</em> cf. <em>S. pawpawensis</em></td>
<td>39</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Squalicorax</em> sp.</td>
<td>12</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Pseudocorax</em> laevis</td>
<td>2</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Anacoracidae</em> indet.</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Paranomotodon</em> sp.</td>
<td>11</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td>Lammiformes* indet.</td>
<td>272</td>
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<tr>
<td><em>Rhinobatos</em> incertus</td>
<td>8</td>
<td>X</td>
<td>Durophagous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Psychotrygon</em> sp.</td>
<td>4</td>
<td>X</td>
<td>Durophagous</td>
<td>Small</td>
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<tr>
<td><em>Ischyrhiza</em> mira</td>
<td>3</td>
<td>X</td>
<td>Durophagous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Ischyrhiza</em> texana</td>
<td>1</td>
<td>X</td>
<td>Durophagous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Cretomanta</em> canadensis</td>
<td>1</td>
<td>X</td>
<td>Planktivorous</td>
<td>Small</td>
</tr>
<tr>
<td>Elasmobranch* indet.</td>
<td>5</td>
<td></td>
<td></td>
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<tr>
<td><strong>OSTEICHTHYES</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Micropycnodon</em> cf. <em>M. kansasensis</em></td>
<td>1</td>
<td>X</td>
<td>Durophagous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Anomocodus</em> sp.</td>
<td>1</td>
<td>X</td>
<td>Durophagous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Belonostomus</em> sp.</td>
<td>1</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Protosphyraena</em> sp.</td>
<td>4</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td>Plethodidae* indet.</td>
<td>1</td>
<td>X</td>
<td>Durophagous</td>
<td>Small</td>
</tr>
<tr>
<td><em>Xiphactinus</em> audax</td>
<td>12</td>
<td>X</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
</tbody>
</table>
**Pachyrhizodus minimus** 2 X Piscivorous/Carnivorous Small
**Pachyrhizodus** sp. 12 X Piscivorous/Carnivorous Small
**Enchodus cf. E. gladiolus** 2 X Piscivorous/Carnivorous Small
**Enchodus cf. E. petrosus** 116 X Piscivorous/Carnivorous Large
**Enchodus cf. E. shumardi** 1 X Piscivorous/Carnivorous Small
**Apatoedus** sp. (?) 1 X Piscivorous/Carnivorous Small
**Aulopiformes indet.** 2 X Piscivorous/Carnivorous Small
**Osteichthyes indet.** 60

**REPTILIA**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Number</th>
<th>Diet</th>
<th>Size</th>
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</thead>
<tbody>
<tr>
<td>Testudines indet.</td>
<td>1</td>
<td>Omnivorous</td>
<td>Small</td>
</tr>
<tr>
<td>Mosasauridae indet.</td>
<td>21</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
<tr>
<td>Plesiosauria indet.</td>
<td>5</td>
<td>Piscivorous/Carnivorous</td>
<td>Large</td>
</tr>
</tbody>
</table>

**MISCELLANEOUS**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertebrata indet.</td>
<td>32</td>
</tr>
</tbody>
</table>

environment (Hattin, 1962), but when sediment size from the locality was analyzed, 16% were coarse to medium (between 1 and 0.25 mm in diameter) and 84% were fine grained (less than 0.25 mm in diameter). It is known that overall grain size increases from relatively low-energy, off-shore environments to relatively high-energy, near-shore environments (Tucker, 1991). The dominance of fine-grained sand could indicate that the fossil locality may have been a more low-energy environment than previously thought. The sea floor may have been affected by weak tidal currents that would primarily deposit fine-grained sediments. Whereas still a near-shore environment, the fossil locality may have been below the fair-weather wavebase, remaining relatively undisturbed during normal weather and wave-action (e.g., see Peters and Loss, 2012), and less turbid than previously described by Hattin (1962). The presence of vertebrate taxa generally associated with shallow, near-shore habitats at other Late Cretaceous localities, such as *Meristodonoides* sp., * Ptychodus whipplei, Cretodus crassidens, Rhinobatos incertus, Ptychotrygon* sp., *Ischyryzula mira, Ischyryzula texana*, and *Belonostomus* sp. (e.g., Welton and Farish, 1993; Shimada, 2006; Everhart, 2007b; Wueringer et al., 2009; Martill et al., 2011), further supports the near-shore condition that was present in Kansas during the deposition of the Codell Sandstone. However, the collection does not contain any unequivocal terrestrial remains suggesting that the location was away from the shoreline within the 'near-shore regime.'

floor (*Ptychodus mortoni*, *P. whipplei*, *Rhinobatos incertus*, *Ptychotrygon* sp., *Ischyrhiza mira*, *I. texana*, *Micropycnodon* cf. *M. kansasensis*, and *Anomoeodus* sp.). Nine taxa have crushing dentition that indicates a durophagous diet that consisted of primarily of hard-shelled invertebrates (*Ptychodus mortoni*, *P. whipplei*, *R. incertus*, *Ptychotrygon* sp., *Ischyrhiza mira*, *I. texana*, *Micropycnodon* cf. *M. kansasensis*, and *Anomoeodus* sp.). Members of the genus *Ischyrhiza* are considered to have been a more active, opportunistic feeder than other sclerorhynchid taxa (Wueringer et al., 2009), but they were considered durophagous in this report due to previous reports or oral teeth that suggest durophagy (Welton & Farish, 1993). The rest of the taxa reported were likely piscivorous, except *Cretomanta canadensis*, which may have had a planktivorous diet (Cappetta and Case, 1999), and the turtle, which was likely omnivorous, feeding on both animal and plant material (Benton, 2005; Sørensen et al., 2013). Thirteen of the taxa were large organisms with an estimated total body length greater than 2 m (*Ptychodus mortoni*, *P. whipplei*, *Scapanorhynchus raphiodon*, *A. cf. A. kopingensis*, *Cretalamna appendiculata*, *Cretoxyrhina mantelli*, *Cretodus crassidens*, *Squalicorax* cf. *S. falcatus*, *S. cf. S. kaupi*, *Protosphyraena* sp., *X. audax*, *E. cf. E. petrosus*, *Mosasauridae* indet., and *Plesiosauria* indet.).

The most abundant chondrichthyan taxa by sample size in the collection are the lamniform sharks *Squalicorax* cf. *S. falcatus* (626 specimens) and *Scapanorhynchus raphiodon* (514 specimens). The most abundant bony fish in the collection is *Enchodus* cf. *E. petrosus* (116 specimens). Most of the fishes and reptiles reported here, including all three of the most abundant taxa, appear to have been active predators, with piercing, clutching, or slicing dentition to feed on pelagic fishes and cephalopods (Welton and Farish, 1993; Schwimmer et al., 1997; Shimada, 1997; Hamm and Shimada, 2002; Cumbaa et al., 2010; Sørensen et al., 2013). They include *Meristodonoides* sp., *Anomotodon* sp., *Odontaspis* cf. *O. watinensis*, *Cretalamna appendiculata*, *Archaeolamna* cf. *A. kopingensis*, *Cretoxyrhina mantelli*, *Cretodus crassidens*, *Dallasiella* cf. *D. willistoni*, *Pseudocorax laevis*, *Paranomotodon* sp., *Belonostomus* sp., *Protosphyraena* sp., *Xiphactinus audax*, *Pachyrhizodus minimus*, *Pachyrhizodus* sp., *Enchodus* cf. *E. gladiolus*, *Enchodus* cf. *E. shumardi*, *Apateodus* (?) sp., *Aulopiformes* indet., *Mosasauridae* indet., and *Plesiosauria* indet. Members of the genus *Squalicorax* with serrated teeth, on the other hand, may have been scavengers, commonly feasting on vertebrate remains that died in the sea or were washed out to sea (Schwimmer et al., 1997a).

Whereas the exact diet of some taxa are uncertain due to their uncertain taxonomic identity (e.g., *Cretomanta canadensis* and *Testudines* indet.), the fossil assemblage described here also contains fishes with blunt and rounded dentition suited for crushing invertebrate shells. These fishes were likely benthic and include ptychodontid sharks *Ptychodus mortoni* and *P. whipplei* (Welton and Farish, 1993; Shimada et al., 2010). Ptychodontid sharks likely lived and fed along the sea floor, feeding on clams that lived buried within the substrate (Everhart, 2005). Other benthic, durophagous fishes include the guitarfish *Rhinobatos incertus* and the pycnodontid fishes *Micropycnodon* cf. *M. kansasensis* and *Anomoeodus* sp. (Nursall, 1996; Everhart, 2007a; Cumbaa et al., 2013). Other primarily benthic elasmobranchs, *Ptychotrygon* sp. and the sawfishes *Ischyrhiza mira* and *I. texana*, also had blunt, durophagous dentition and were
likely opportunistic feeders that fed on invertebrates on the sea floor, but may have also ventured into the pelagic zone to catch fishes (Wueringer et al., 2009). Plethodids had durophagous dentition as well, but unlike the other durophagous fishes identified here, it likely lived within the pelagic zone (Shimada et al., 2006b).

The ecosystem of the Western Interior Seaway during the Late Cretaceous probably resembled the ecosystem of the modern-day Gulf of Mexico (Everhart, 2005). The food web for the Western Interior Seaway, summarized in Everhart (2005), began with phytoplankton, such as coccolithophores and diatoms, the primary producers of the ecosystem that converted sunlight, carbon dioxide, nitrogen, and other nutrients into biological materials (Everhart, 2005). The primary consumers were likely zooplankton or benthic protozoans, such as agglutinated foraminiferans (Hattin, 1962), single-celled organisms that fed on the algae. The primary consumers were consumed by secondary consumers, including small fishes, crustaceans, and cephalopod larvae (Everhart, 2005). Filter feeders, such as the inoceramid bivalves, some ammonites, such as Baculites sp., and possibly Cretomanta canadensis (i.e., an alleged planktivorous ray), would likely have been secondary consumers in the ecosystem as well, feeding on both phytoplankton and zooplankton in the water column (Everhart, 2005; Kruta et al., 2011). Tertiary consumers would have been small to medium-sized fishes and macroinvertebrates, such as plethodids, ammonites, and squid, that fed on the small fishes, smaller ammonites, and crustaceans present (Everhart, 2005; Landman et al., 2010; Sørensen et al., 2013). The durophagous fishes reported here would have likely been tertiary consumers as well, feeding on hard-shelled crustaceans, inoceramids, and other mollusks on the sea floor. Smaller members of Enchodus and Pachyrhizodus likely would have fed on the smaller fishes and cephalopods as well. Large bony fishes, such as Xiphactinus audax, Enchodus cf. *E. petrosus*, pelagic sharks, plesiosaurs, and small mosasaurs, would have fed on the medium-sized fishes present (Walker, 1982; Walker and Everhart, 2006; Sørensen et al., 2013). At the very top of the food web, the apex predators would have been large sharks and mosasaurs. Large sharks (e.g., Cretoxyrhina mantelli) have been known to feed on smaller mosasaurs and large predatory bony fishes (e.g., *X. audax*) (Shimada, 1997d). Mosasaurs fed on a variety of vertebrates, including sharks, teleosts, birds, and even other mosasaurs (Cicimurri and Everhart, 2001). *Squalicorax* spp. were likely scavengers, recycling the dead biological material present in the ecosystem (Schwimmer et al., 1997a). Where invertebrate fossils are generally rare in the Codell Sandstone (Hattin, 1962), no invertebrate remains were specifically collected for the purpose of this present study. However, the presence of many large, high trophic-level consumers indicates that there was likely a high abundance of prey items at lower trophic levels to support the top-level predators in the ecosystem (Everhart, 2005; Sørensen et al., 2013). The taphonomic biases that favor the discovery of fossils of larger organisms with hard body parts may lead to smaller organisms being less abundant in collections, but it would be a mistake to assume that a lack of microinvertebrate fossils indicates they were not abundant in the ecosystem. These primary producers and primary consumers would have to have been present, and likely in large numbers, to sustain the secondary and higher-level consumers that have been reported here (e.g., Levinton, 2001; Sørensen et al., 2013).
FAUNAL ANALYSIS

Some Late Cretaceous marine vertebrate faunas in Kansas remain undescribed formally (e.g., the Fairport Chalk fauna: McIntosh et al., 2013). However, with this present report, there are sufficient occurrence data by taxa from each Upper Cretaceous stratigraphic unit in the Midwest, including Kansas, Nebraska, Colorado, to examine patterns of change of marine vertebrate community assemblages in the Western Interior Seaway through time, particularly in reference to sea-level changes using lithological differences as proxy (see Materials and Methods above for explanations and references). In this study, Assemblages 1, 3, and 5 are faunas from siliciclastic, near-shore deposits, whereas Assemblages 2 and 4 are the faunas from carbonate, off-shore rocks (Fig. 1A). The taxa included in each community assemblage as well as their presumed diet and body size are summarized in Appendix 1. For the purpose of this study, the examined taxa are at the generic level, although some taxa at higher taxonomic levels are included where specific generic identifications are not made (note: thus, expressions such as ‘generic richness’ and ‘generic diversity’ in this study assume that those higher-level taxa serve as an adequate proxy to genera). With the exception of pelagic, durophagous Plethodidae taxa reported primarily from the Niobrara Chalk (Bananogmius, Martinichthys, Thryptodus, Niobrara, Zanclites, Pentanogmius, Pseudothryptodus, Plethodus, Pseudoanogmius, Dixonanogmius, and Plethodidae indet.) (Fielitz and Shimada, 1999; Shimada et al., 2006b; Shimada and Martin, 2008), the benthic, non-durophagous shark Scyliorhinus arlingtonensis and eel Urenchelys abditus (Wiley and Stewart, 1981; Sørensen et al., 2013), and the pelagic, durophagous reptiles Coniasaurus crassidens and Globidens dakotensis (Massare, 1987; Caldwell and Cooper, 1999), durophagous taxa were also interpreted to be benthic taxa and non-durophagous taxa were interpreted to be pelagic taxa; therefore, diet preference was used as a proxy for habitat preference as well. The goals of this analysis of Late Cretaceous faunas are to test the hypotheses that there is a relationship between taxonomic diversity and paleoenvironment, preferred diet (durophagous and non-durophagous) and paleoenvironment, and body size (small, <2m or large, >2m) and paleoenvironment.

Previous research on paleo-communities provides a framework to generate expectations of how the assemblages may differ. Some extant marine communities show the greatest fish diversity at shallow to intermediate depths, with diversity decreasing at greater depths (Day and Pearcy, 1968; Angel, 1997; Smith and Brown, 2002; Zintzen et al., 2012). In terms of habitat and diet preference, it has been suggested that durophagous or benthic vertebrate fossils are more prevalent in near-shore marine formations (Edwards, 1976). These near-shore habitats would have had abundant sunlight that could have reached the seafloor to support primary producers and consumers in the substrate, oxygen would have been well circulated, and organic material from the pelagic zone could have easily reached the sea floor (Speight and Henderson, 2010). Benthic fish species richness has been observed to peak in shallow depths (Zintzen et al., 2012), and pelagic osteichthyan fish diversity has been observed to increase as depth increases (Smith and Brown, 2002). Patterns of vertebrate body size distribution in marine systems are not well characterized, but observations of extant marine osteichthyans show a positive correlation between body size and increasing depth (Smith and Brown, 2002). This observation suggests that larger osteichthyans, and their larger predators (Scharf et al., 2000), would have inhabited deeper waters. For this analysis, I expect that the near-
shore community assemblages will generally resemble one another but will differ significantly from the off-shore community assemblages, based on diet, preferred habitat, and organism size. I also expect to see more taxonomic diversity in near-shore environments than off-shore environments. Near-shore environments will likely be dominated by benthic, durophagous organisms, whereas the off-shore environments will be predominantly inhabited by pelagic organisms. I also expect that off-shore assemblages will have a greater proportion of larger taxa than the near-shore assemblages.

A total of 140 marine taxa have been reported from all five community assemblages (Appendix 1). Assemblage 1 contains 37 taxa total: 20 chondrichthyan taxa, 12 osteichthyan taxa, and five reptilian taxa. Ten taxa in Assemblage 1 are durophagous, and 27 are non-durophagous (Fig. 12A), and 12 are considered 'large' and 25 'small' (Fig. 13A). Assemblage 2 has 61 taxa total: 21 chondrichthyan taxa, 24 osteichthyan taxa, and 16 reptilian taxa. Fifteen of the taxa are durophagous and 46 non-durophagous (Fig. 12B), and 22 are considered 'large' and 39 'small' (Fig. 13B). Assemblage 3, including the fauna in the Codell Sandstone reported here, consists of 41 taxa total: 22 chondrichthyan taxa, 13 osteichthyan taxa, and six reptilian taxa. Fourteen of the taxa in Assemblage 3 are durophagous and 27 are non-durophagous (Fig. 12C), and 15 are considered 'large' and 26 'small' (Fig. 13C). Assemblage 4 has 79 taxa total: 12 chondrichthyan taxa, 48 osteichthyan taxa, and 19 reptilian taxa. This assemblage includes Aethocephalichthys with an unknown diet, but 20 of the taxa in Assemblage 4 are durophagous and 58 non-durophagous (Fig. 12D) whereas 15 are considered 'large' and 53 'small' (Fig. 13D). Assemblage 5 includes 27 taxa total: three chondrichthyan taxa, 14 osteichthyan taxa, and 10 reptilian taxa. Two taxa in Assemblage 5 are durophagous whereas 26 are non-durophagous (Fig. 12E), and 16 are considered 'large' and 12 'small' (Fig. 13E).

When comparing the biodiversity in each community assemblage using generic richness, a distinct pattern is discerned. Assemblages 2 and 4 (off-shore faunas) have a higher number of taxa reported than Assemblages 1, 3, and 5 (near-shore faunas) (Fig. 14). Several factors could contribute to this trend. The off-shore environments could have more complex ecosystems, with pelagic and benthic food webs intertwined and supporting a large number of taxa (Sørensen et al., 2013). On the other hand, near-shore, shallow environments could experience disturbances, like excess light, excess ultraviolet light, or turbulent wave action, which could decrease species richness (Grey, 2002; Speight and Henderson, 2010). However, the perceived pattern could also reflect biases in the fossil record. Assemblages 2 and 4 have more published reports than the other near-shore community assemblages where this increased sampling may have inherently led to an increase in the number of genera reported (e.g., see Gotelli and Colwell, 2001). The distance from shore may also affect the rate of burial where strong currents and wave action may disrupt fossilization of organisms. If the near-shore environments were higher energy and experienced greater currents and wave action as described for other Late Cretaceous deposits in Kansas (Hattin, 1962), then a lower rate of fossilization may explain the fewer reported taxa for Assemblages 1, 3, and 5.

Another pattern is detected when comparing class-level diversity changes during the Late Cretaceous. As the proportion of reptilian taxa changes over time, inverse changes can be seen in the proportion of chondrichthyan taxa (Fig. 15). As the proportion

Figure 13. Relative proportions between “small” (>2 m) and “large” (<2 m) vertebrate taxa in examined lithology-based community assemblages from Kansas, Nebraska, and Colorado. A, Assemblage 1. B, Assemblage 2. C, Assemblage 3. D, Assemblage 4. E, Assemblage 5.
Changes in total marine vertebrate diversity in examined lithology-based community assemblages from Kansas, Nebraska, and Colorado.

of marine reptiles present increased from about 14% to about 26% of the community assemblage between Assemblage 1 and Assemblage 2, the proportion on chondrichthyan taxa present decreased, from about 54% to about 34%. The proportion of reptiles present then decreased in Assemblage 3 to about 15%, whereas the proportion of Assemblage 3 comprised of chondrichthyanas returned to about 54%. In Assemblage 4, chondrichthysans made up only 15% of the vertebrates present, and the proportion of reptiles increased to about 24%. In Assemblage 5, the proportion of chondrichthysans decreased again to about 11% and reptiles made up about 37% of the vertebrates present. The proportion of bony fish present did not generally follow the pattern of either chondrichthysans or marine reptiles. The proportion of osteichthyan taxa increased slightly from Assemblage 1 to Assemblage 2, from 32% to 39% of the taxa present in the assemblages. The proportion of osteichthyan taxa present then decreased in Assemblage 3 back to about 32%.

Osteichthyan taxa had a noticeably greater presence in Assemblage 4, increasing to 61% of the assemblage. The proportion of osteichthyan taxa then decreased in Assemblage 5 to 54%. Osteichthyan taxa did not appear to follow either chondrichthysans or reptilians in patterns of diversity. The inverse relationship between the proportions of chondrichthyan and reptilian taxa present may have been due to their similar ecological roles. Common sharks (particularly lamniforms), mosasaurus, and plesiosaurus are largely pelagic predators, feeding on fishes and cephalopods (see above). When the proportions of only lamniform sharks and carnivorous marine reptiles (mosasaur, excluding durophagous *Globidens,* and plesiosaurs) present in each community assemblage are graphed, the same inverse pattern is more clearly exhibited (Fig. 16). In Assemblage 1, 24% of the taxa present are lamniform sharks and 9% carnivorous marine reptiles. In Assemblage 2, the
proportion of taxa reported as lamniforms decreased to 19%, and carnivorous marine reptiles increased to 19%. In Assemblage 3, the proportion of lamniforms in the assemblage increased to 29%, and carnivorous mosasaurs and plesiosaurs decreased to 9%. The proportion of taxa reported as lamniform sharks decreased to 10% in Assemblage 4, and only slightly increased to 11% in Assemblage 5. The proportion of carnivorous marine reptiles present increased to 17% in Assemblage 4, and then increased again to 30% in Assemblage 5. Because lamniform sharks and carnivorous mosasaurs and plesiosaurs would have been relatively similar ecologically, a greater diversity of lamniform sharks in an ecosystem may increase competition and exclude mosasaurs and plesiosaurs and vice versa.

Figure 15. Changes in relative proportions of class-level marine vertebrate diversity in examined lithology-based community assemblages from Kansas, Nebraska, and Colorado.
When the ecological composition of the Upper Cretaceous community assemblages was examined, it was expected that the near-shore community assemblages would have greater proportions of durophagous organisms and greater proportions of small organisms than the off-shore assemblages. The dietary preferences of the taxa (i.e., durophagous vs. non-durophagous) in the five community assemblages were compared using a contingency table and chi-squared analysis (Table 2). *Aethocephalicthys* was excluded from the dietary analysis because of its uncertain diet; therefore, Assemblage 4 included 78 taxa instead of the total of 79 taxa. The result was not significant and was not consistent with a strong association between the community assemblages and dietary preference ($x^2=6.71$, df=4, $p=0.15$).

The prediction that there would be a relationship between dietary preference and assemblages (a proxy for distance from shore) was not supported by the fossil data, and even though near-shore Assemblage 5 had noticeably fewer durophagous taxa than the other community assemblages, no significant difference in the proportions of durophagous and non-durophagous vertebrates could be detected (Table 2). Off-shore environments supported durophagous organisms (and therefore benthic organisms) as well as near-shore environments. The lack of significant changes in benthic paleocommunities may have been due to relatively homogenous water conditions, such as temperature, salinity, and oxygen levels, which may have remained stable in the portion of the Western Interior Seaway analyzed here. In terms of dissolved oxygen levels, distance from shore may not have had a large effect. Sediments of the off-shore Fort Hays Limestone were shown to be well circulated and well oxygenated, with enough oxygen to support benthic ecosystems far from shore (Frey, 1972). In addition, whereas
the northern part of the Western Interior Seaway was less oxygenated during the Cenomanian and Turonian, the southern part was more

Table 2. Contingency table for test of differentiation in diet of taxa present in Late Cretaceous Western Interior Seaway (numbers in parentheses are total number of taxa in each habitat).

<table>
<thead>
<tr>
<th>Community Assemblage</th>
<th>Presumed Diet</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Durophagous</td>
<td>Non-Durophagous</td>
</tr>
<tr>
<td>Assemblage 1</td>
<td>0.27 (10)</td>
<td>0.73 (27)</td>
</tr>
<tr>
<td>Assemblage 2</td>
<td>0.25 (15)</td>
<td>0.75 (46)</td>
</tr>
<tr>
<td>Assemblage 3</td>
<td>0.34 (14)</td>
<td>0.66 (27)</td>
</tr>
<tr>
<td>Assemblage 4</td>
<td>0.26 (20)</td>
<td>0.74 (58)</td>
</tr>
<tr>
<td>Assemblage 5</td>
<td>0.07 (2)</td>
<td>0.92 (26)</td>
</tr>
</tbody>
</table>

Chi Square: 6.71  \( df=4 \)  \( p=0.15 \)

Numbers in parentheses are total number of taxa in each habitat

dynamic and well-mixed and may have been able to support more off-shore benthic communities (Simons et al., 2003). There could also have been a trade-off with a transition to a near-shore environment that could account for the lack of significant differences between assemblages. Near-shore shallow environments, which may have more sunlight through the water and on the substrate to sustain primary producers, could cause disturbances, like increased wave action, excess light, or ultraviolet light, which could decrease species richness of prey items in the substrate (Speight and Henderson, 2010). Increased turbidity can also negatively affect benthic ecosystems, as suspension feeding animals may have their food-filtering mechanism clogged (Frey, 1972). Even with greater resources available, the near-shore environments may have experienced increased physical disturbances that inhibited diversity of durophagous, benthic vertebrates.

Changes in sea level were not associated with changes in overall vertebrate body size either. I compared the sizes of the taxa (i.e., small vs. large) in the five community assemblages using a contingency table and chi-squared analysis (Table 3). My analysis suggests that there is no statistically significant association between the assemblages and vertebrate body sizes \( \chi^2=6.65, \ df=4, \ p=0.16 \).

Assemblage 5 had the largest proportion of large taxa, but this finding is likely a result of biases toward larger taxa in the fossil record. Larger fossils are easier to detect and collect, and larger taxa are often over-represented in poorly sampled collections. As the least-sampled community assemblage, it is not surprising that Assemblage 5 has the most large taxa. The bias toward discovering and reporting larger fossils may have also led to durophagous taxa being underrepresented in Assemblage 5, with any small teeth of small durophagous taxa (e.g. members of Rajiformes, Pycnodontidae, and Plethodidae) left undiscovered and unreported. Even with the greater proportion of large taxa in Assemblage 5, the lack of any significant relationship between body size and assemblage was unexpected.

Body sizes of extant bony fishes have previously been shown to increase as depth increases, but that same study found that extant chondrichthyan body size correlated negatively with depth (Smith & Brown, 2002). These opposing associations between
depth and total body size may have been affecting the results. When osteichthyan and chondrichthyan body sizes were analyzed separately, this more complex relationship between body size and depth was not observed. No statistically significant relationship between the community assemblages and chondrichthyan body size ($\chi^2=2.06, df=4, p=0.72$) or osteichthyan body size ($\chi^2=4.46, df=4, p=0.35$) was found (Table 4 and 5).

Accurately reconstructing the depth of the Western Interior Seaway has been a challenge (Hattin, 1962; Sageman and Arthur, 1994), but using microfossil evidence, such as Foraminifera, and markers of wave action in the rock formations, the maximum depth of the Seaway has been estimated at different times and locations (Hattin, 1962, 1982; Eicher, 1969; Everhart, 2005). It has been suggested that, over the scope of this analysis, the greatest depth of the Western Interior Seaway was from about 600 m to 900 m deep, reached during the Cenomanian Greenhorn Cyclothem, when fauna in Assemblage 2 inhabited the Seaway (Eicher, 1969). The vertebrate taxa from Assemblage 4, the other off-shore community assemblage, would have lived when the Western Interior Seaway’s greatest depth was about 200 m (Hattin, 1982; Everhart, 2005). By comparison, during the deposition of the Carlile Shale, the maximum depth of the Western Interior Seaway would have been at most around 90 m (Hattin, 1962). Total maximum body size of pelagic fishes, both chondrichthyan and osteichthyan, have been shown to have a relationship with depth, but these differences were measured over a large depth gradient, between 0 and 6,200 m (Smith and Brown, 2002). With a suggested maximum depth of 600 to 900 m, the depth range of the Western Interior Seaway may not have been great enough to be able to detect significant differences in vertebrate size. Even with the inherent limitations of the fossil record, which make it difficult or impossible to randomly and extensively sample paleocommunities, the addition of the taxa from the Codell Sandstone provide a more complete picture of vertebrate communities from the central Western Interior Seaway. Based on the community assemblages investigated here, over the 18-million-year scope of this analysis, marine paleoecological dynamics in the Western Interior Seaway appeared to have remained stable. The ecological composition of vertebrate communities examined here suggests that as sea levels changed possibly by as much as 800 m in the Western Interior Seaway during the Late Cretaceous, benthic and pelagic vertebrate paleocommunities appear to have persisted quite well regardless of different lithological environments. The central

Table 3. Contingency table for test of differentiation in total body size of taxa present in Late Cretaceous Western Interior Seaway (numbers in parentheses are total number of taxa in each habitat).

<table>
<thead>
<tr>
<th>Community Assemblage</th>
<th>Presumed Size</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Assemblage 1</td>
<td>0.68 (25)</td>
<td>0.32 (12)</td>
</tr>
<tr>
<td>Assemblage 2</td>
<td>0.64 (39)</td>
<td>0.36 (22)</td>
</tr>
<tr>
<td>Assemblage 3</td>
<td>0.63 (26)</td>
<td>0.37 (15)</td>
</tr>
<tr>
<td>Assemblage 4</td>
<td>0.67 (53)</td>
<td>0.33 (26)</td>
</tr>
<tr>
<td>Assemblage 5</td>
<td>0.42 (12)</td>
<td>0.57 (16)</td>
</tr>
</tbody>
</table>

Chi Square: 5.80 \(df=4\) \(p=0.21\)
Western Interior Seaway was likely consistently oxygenated and very productive in order to support the complex ecosystems described here.

Table 4. Contingency table for test of differentiation in total body size of chondrichthyan taxa present in Late Cretaceous Western Interior Seaway (numbers in parentheses are total number of taxa in each habitat).

<table>
<thead>
<tr>
<th>Community Assemblage</th>
<th>Presumed Size</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Assemblage 1</td>
<td>0.75</td>
<td>0.25</td>
</tr>
<tr>
<td>Assemblage 2</td>
<td>0.71</td>
<td>0.29</td>
</tr>
<tr>
<td>Assemblage 3</td>
<td>0.68</td>
<td>0.32</td>
</tr>
<tr>
<td>Assemblage 4</td>
<td>0.58</td>
<td>0.42</td>
</tr>
<tr>
<td>Assemblage 5</td>
<td>0.33</td>
<td>0.67</td>
</tr>
</tbody>
</table>

Chi Square: 2.06  
$\text{df} = 4$  
$p = 0.72$

Table 5. Contingency table for test of differentiation in total body size of osteichthyan taxa present in Late Cretaceous Western Interior Seaway (numbers in parentheses are total number of taxa in each habitat).

<table>
<thead>
<tr>
<th>Community Assemblage</th>
<th>Presumed Size</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Assemblage 1</td>
<td>0.83</td>
<td>0.17</td>
</tr>
<tr>
<td>Assemblage 2</td>
<td>0.92</td>
<td>0.08</td>
</tr>
<tr>
<td>Assemblage 3</td>
<td>0.77</td>
<td>0.23</td>
</tr>
<tr>
<td>Assemblage 4</td>
<td>0.90</td>
<td>0.10</td>
</tr>
<tr>
<td>Assemblage 5</td>
<td>0.73</td>
<td>0.27</td>
</tr>
</tbody>
</table>

Chi Square: 4.04  
$\text{df} = 4$  
$p = 0.40$

CONCLUSION

This report demonstrates that Kansas was home to a rich community of marine vertebrates during the deposition of the Codell Sandstone in the Western Interior Seaway during the middle Turonian. This report constitutes the first collective study of the fossil vertebrate assemblage from the stratigraphic unit and consists of at least 38 taxa, with at least 22 elasmobranchs, 13 osteichthyans, and three reptilians. The general ecological roles of the taxa discussed here provide a snapshot of the marine community present at the time of deposition. Benthic fishes, such as Ptychodus mortoni, P. whipplei, Rhinobatos incertus, Ptychotrygon sp., Ischy rhiza mira, I. texana, Micropycnodon cf. M. kansasensis, and Anomoeodus sp. swam along the sea floor, crushing hard-shelled invertebrate prey with their blunt, rounded teeth. Relatively small pelagic sharks, such as Anomotodon, Odontaspis cf. O. watinensis, Dallasiella cf. D. willistoni, Pseudocorax laevis, and Paranomotodon sp., and smaller, carnivorous fishes, such as Belonostomus
sp., *Pachyrhizodus minimus*, *Pachyrhizodus* sp., *Enchodus* cf. *E. gladiolus*, *E*. cf. *E. shumardi*, and *Apateodus* sp. inhabited the open waters of the Seaway, feeding on other fishes, and cephalopods. Large predators, including *Scapanorhynchus raphiodon*, *Archaeolamna* cf. *A. kopingensis*, *Cretalamna appendiculata*, *Cretoxyrhina mantelli*, *Cretodus crassidens*, *Protosphyraena* sp., *Xiphactinus audax*, *Enchodus* cf. *E. petrosus*, mosasaurs, and plesiosaurs, were the top of their food webs, eating any other animal they could. When an animal died in the Seaway, their remains could be scavenged by the at least four members of the genus *Squalicorax*. The Late Cretaceous vertebrate faunas reported from Kansas, Colorado, and Nebraska, including this present study, suggest that marine vertebrate communities in the central Western Interior Seaway were relatively stable ecologically during the Late Cretaceous. Biodiversity appeared to have increased as sea levels rose and decreased as the Seaway regressed, but vertebrate paleocommunity structure did not appear to be affected significantly at the genus level investigated here. Near-shore assemblages did not have significantly greater proportions of benthic, durophagous organisms than off-shore assemblages. An inverse relationship between the proportions of lamniform sharks and carnivorous reptilian taxa present in each community assemblage was detected, which may have been due to competition for their similar ecological roles. Whether far from shore in calm, deep waters or close to shore in turbid, high-energy habitats, the Western Interior Seaway was likely well oxygenated and highly productive, supporting complex benthic and pelagic paleocommunities of sharks, bony fish, and marine reptiles, both large and small, even as sea levels fluctuated possibly by as much as 800 m.
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Appendix 1. List of vertebrate taxa from Upper Cretaceous marine deposits in Kansas, Nebraska, and Colorado with presumed feeding strategy, presumed body size, and their presence (X-marks) in each lithology-based community assemblage (see Materials and Methods for references used to compile the data).

<table>
<thead>
<tr>
<th>Taxa Reported</th>
<th>Durophagous (D) or Non-Durophagous (ND)</th>
<th>Large (L) or Small (S)</th>
<th>Community Assemblage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 2 3 4 5</td>
</tr>
<tr>
<td>Meristodonoides</td>
<td>ND</td>
<td>S</td>
<td>X X</td>
</tr>
<tr>
<td>Hybodontidae indet.</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Polyacrodus</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Ptychodus</td>
<td>D</td>
<td>L</td>
<td>X X X</td>
</tr>
<tr>
<td>Chiloscyllium</td>
<td>D</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Ptychodus</td>
<td>D</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Cretorectolobus</td>
<td>D</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Pararhincodon</td>
<td>D</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Scyliorhinus</td>
<td>D</td>
<td>S</td>
<td>X X</td>
</tr>
<tr>
<td>Carcharhiniformes indet.</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Anomotodon</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Scapanorhynchus</td>
<td>ND</td>
<td>L</td>
<td>X X</td>
</tr>
<tr>
<td>Carcharias</td>
<td>ND</td>
<td>S</td>
<td>X X</td>
</tr>
<tr>
<td>Odontaspis</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Eostriatolamia</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Johnlongia</td>
<td>ND</td>
<td>S</td>
<td>X X</td>
</tr>
<tr>
<td>Cretalamna</td>
<td>ND</td>
<td>L</td>
<td>X X X</td>
</tr>
<tr>
<td>Cardiobodon</td>
<td>ND</td>
<td>L</td>
<td>X X</td>
</tr>
<tr>
<td>Archaeolamna</td>
<td>ND</td>
<td>L</td>
<td>X X X</td>
</tr>
<tr>
<td>Telodontaspis</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Cretorhynchos</td>
<td>ND</td>
<td>L</td>
<td>X X X</td>
</tr>
<tr>
<td>Cretodus</td>
<td>ND</td>
<td>L</td>
<td>X X</td>
</tr>
<tr>
<td>Dallasiella</td>
<td>ND</td>
<td>S</td>
<td>X X</td>
</tr>
<tr>
<td>Squalicorax (Large)</td>
<td>ND</td>
<td>L</td>
<td>X X X</td>
</tr>
<tr>
<td>Squalicorax (Small)</td>
<td>ND</td>
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<td>X X X</td>
</tr>
<tr>
<td>Pseudocorax</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
<tr>
<td>Microcorax</td>
<td>ND</td>
<td>S</td>
<td>X</td>
</tr>
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