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## Fossil vertebrates from a unique marine bonebed of the Upper Cretaceous Niobrara Chalk, western Kansas, U.S.A.: new insights into the Niobrara vertebrate paleoecology

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**Fossil vertebrates from a unique marine bonebed of the Upper Cretaceous Niobrara Chalk,  
western Kansas, U.S.A.: new insights into the Niobrara vertebrate paleoecology**

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

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By

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## Abstract

The Smoky Hill Chalk Member of the Niobrara Chalk is a sedimentary deposit formed in the Western Interior Seaway of North America during the Late Cretaceous. In this study, I examined a unique fossiliferous bonebed from an uncertain horizon within the Smoky Hill Chalk in Gove County, Kansas, U.S.A. Over 40,450 taxonomically identifiable specimens were collected, where they consisted of at least four chondrichthyans, 24 osteichthyans, and two tetrapods, including taxa such as *Nanocorax*, *Squalicorax*, *Rhinobatos*, pycnodontids, Lepisosteidae, *Protosphyraena*, *Pachyrhizodus*, ichthyodectiforms, plethodids, Albulidae, *Apateodus*, Ichthyotringidae(?), cf. *Stratodus*, *Cimolichthys*, *Enchodus*, Acanthomorpha, *Platecarpus*, and Hesperornithiformes. The diversity of these vertebrates suggests the presence of a very complex ecosystem when the bonebed formed, which is determined to be of the latest Santonian in age possibly about  $84.0 \pm 0.3$  Ma on the basis of biostratigraphic, geographic, and geologic evidence. Based on published literature and this new study, at least 117 vertebrate taxa are now known from the Smoky Hill Chalk of Kansas, comprising 18 chondrichthyans, 63 osteichthyans, and 36 tetrapods. Comparisons of faunal data from the bonebed with databases on vertebrate fossils from the Niobrara Chalk of Kansas in seven major museum collections indicate that the commonness of taxa by number of specimens in the bonebed and that in the museums are markedly different. The Niobrara fossil record based on museum collections appears to be biased towards large reptilian remains compared to osteichthyan fossils. In particular, this study indicates that *Enchodus* spp. were especially common when the bonebed formed. A major corollary from this study is that a more accurate reconstruction of the paleoecology of the Western Interior Seaway requires the need for more analyses on smaller vertebrate taxa.

## I. INTRODUCTION

Ecological research is often viewed in light of living systems. However, it can extend back in geologic time for prehistoric ecosystems and involves consideration of both the abiotic and biotic factors within them. Often, paleoecology entails the examination of environmental parameters that controlled the abundance and distribution of ancient life and their responses to changing environmental conditions (Raup and Stanley, 1978). There are many ways to infer prehistoric conditions from finding extinct organisms that require unique living conditions to identifying the general appearance and location of a rock sample to uncover the conditions needed for deposition. Paleontologists use fossil evidence to decipher ancient ecosystems. Due to the general scarcity of fossils, a majority of the biodiversity within extinct ecosystems remains unknown (Donovan and Paul, 1998). Understanding the depositional environment for fossil organisms offers insight into the living conditions when the organism was alive and is crucial when interpreting and deciphering ecological interactions (Rich, 1951; Frey, 1972).

Geologic history includes evidence for planetary change over extensive periods of time. During the Late Cretaceous period (100–66 Ma) and into the early Paleogene period approximately 60 Ma, the North American continent experienced intense geologic activity. Volcanism led to the uplift of the Rocky Mountains, and eustatic sea-levels fluctuated creating a continental seaway that connected both the Boreal Sea (or Arctic Ocean) to the north and the Tethys Ocean via the Gulf of Mexico to the south (Kauffman and Caldwell, 1993). This seaway, commonly referred to as the Western Interior Seaway, separated the landmass Laramidia on the west from Appalachia to the east and extended nearly 3,200 km (Kauffman and Caldwell, 1993; Fig. 1A). Sediments were deposited and accumulated along the seafloor through eustatic



transgressions and regressions. During periods of highest eustatic sea-levels, the Western Interior Seaway has been estimated to be 1,000 km wide and as deep as 760 m (Ogg et al., 2012).

Climatic shifts and further orogenies led to the disappearance of the Western Interior Seaway by the earliest Paleogene period, but mostly by the end of the Cretaceous period (Maastrichtian) (Ogg et al., 2012). Because there are no modern analogs to this distinct paleoenvironment, rocks formed in the seaway offer a glimpse into a potentially unique marine ecosystem and unexplored ecosystem dynamics from sea-level rise due to warm global climate.

One of the eustatic fluctuations in the Western Interior Seaway produced a relatively large increase in the sea-level rise, approximately 300 m above the modern sea-level. This cycle is known as the ‘Niobrara cycle,’ which lasted from 90.25 Ma to 81.5 Ma (Hattin, 1982). The prolonged intervals of transgressions and regressions during the ‘Niobrara cycle’ resulted in widespread long-term deposition of chalks and marls of the Niobrara Chalk now found in Kansas and a few other neighboring states such as Colorado and Nebraska in the U.S.A. (Hattin, 1982; Fig. 1B). Due to very little terrigenous detritus found within the formation where its sediments are dominated by pure carbonate mud, the paleoenvironment has been inferred to be relatively far from shore at the time of deposition (Hattin and Siemers, 1978). The Niobrara Chalk, that conformably underlies the Sharon Springs Shale Member of the Pierre Shale, consists of two stratigraphic members: the Fort Hays Limestone Member and Smoky Hill Chalk Member (Hattin, 1982; Fig. 1B). Whereas vertebrate fossils are known also from the Fort Hays Limestone (Shimada, 1996; Shimada and Everhart, 2003), the Smoky Hill Chalk is well known for diverse fossil marine vertebrates, such as sharks, bony fishes, marine reptiles, as well as a diverse group of terrestrial vertebrates such as pterosaurs, non-avian dinosaurs, and birds, besides diverse fossil invertebrates (e.g., Hattin, 1982; Russell, 1988, 1993; Stewart, 1990; Everhart, 2017).

Much of the understanding of the Niobrara paleoecology is based on specimens represented in museum collections. Russell (1993) surveyed a few museums with a large collection of Niobrara vertebrate specimens, and reported the following specimen representations of the Niobrara vertebrate fossil record by taxa: in descending order, fishes (57%), mosasaurs (24%), pterosaurs (12%), birds (3%), turtles (3%), and plesiosaurs (1%). However, whether these representations of taxa in Russell's (1993) study reflect the actual representations of the Niobrara ecosystem has not been examined yet.

FHSM VP-644 is a rock specimen collected from the Smoky Hill Chalk in western Kansas, and is housed in Fort Hays State University's Sternberg Museum of Natural History (FHSM) in Hays, Kansas (Fig. 2A). Although the exact stratigraphic horizon of this specimen within the stratigraphic member is uncertain, FHSM VP-644 is unique in that it is packed with numerous, small, disarticulated bones and teeth of fossil marine vertebrates that can be characterized as a 'bonebed' (Fig. 2B). Such high densities of fossils are rare within the Niobrara Chalk, and thus FHSM VP-644 offers insights into the taxonomic composition of small vertebrate taxa that are not well known in the Niobrara fossil record. The goal of this study is four-fold. First, I examine the taxonomic composition of the vertebrate fauna represented in the 'Niobrara bonebed.' Second, based on the geographic and faunal data, I determine the stratigraphic horizon, age, and depositional environment of the bonebed. Third, I make inferences about the paleoecology of the Western Interior Seaway of Kansas based on the taxonomic composition found in the bonebed. Fourth, I compare my faunal data with the Niobrara vertebrate fossil record represented in museum collections to examine and discuss potential biases in the Niobrara fossil record. I specifically test the following hypothesis: 'There is no difference in the composition of taxa by number of specimens between the bonebed and

museum collections.’ This study is significant because it examines remains of smaller vertebrate taxa that are less studied from the Niobrara Chalk and adds to the understanding of the paleoecology of the Western Interior Seaway during the Late Cretaceous.

## II. MATERIALS AND METHODS

The bonebed sample examined here, FHSM VP-644, was collected from the Smoky Hill Chalk Member of the Niobrara Chalk near Monument Rocks in Gove County, Kansas (Fig. 1), by G. F. Sternberg and curated by M. V. Walker in 1956. The bonebed does not contain any visible remains of macroinvertebrates, but the matrix is calcareous where it is quite possible much of it is made of microinvertebrates such as foraminifera and coccolithophores that form the bulk of the Niobrara chalk beds (e.g., see Hattin, 1982). FHSM VP-644 in the original condition (Fig. 2A) measured about 40 cm x 24 cm x 3 cm in maximum dimensions, weighted approximately 4 kg, and measured 2.2 L in volume. However, it was subsequently broken into five smaller sections for the purpose of this study (Fig. 2A). One section was saved intact for record, which retains the original catalog number FHSM VP-644, whereas all other parts, including collected fossils, stemming from other sections were subsequently given separate catalog numbers (see below). A total of about 3.6 kg (i.e., equivalent to 1.7 L volume-wise) of rock pieces were submerged under vinegar (5% acetic acid solution) to dissolve any calcium carbonate present. Whereas one of the larger sections has been saved only slightly dissolved (FHSM VP-19642: Fig. 2C), much of the remaining rock pieces were acid treated (e.g., FHSM VP-19643: Fig. 2D). Old vinegar was replaced weekly with new solution where approximately 106 L was used in total. During the process, disaggregated materials were collected periodically, washed with tap water to remove calcium acetate residue, and dried and screened with ca. 0.5 mm sieves to remove finer particles that were not analyzed in this study due to logistical reasons (ca. 1,100 mL of sediments preserved as FHSM VP-19646 and VP-19647). Larger (>5 mm) fossils could be picked easily using the naked eye (e.g., FHSM VP-19644 representing the

largest vertebrate elements recovered from the bonebed; Fig. 2E), but the vast majority of the fossils were microscopic that were sorted using a dissecting microscope. All identifiable vertebrate remains were taxonomically sorted in separate vials, where those specimens separated by vials received separate FHSM catalog lot numbers ranging from FHSM VP-19648 to FHSM VP-19723. Residual sediments containing numerous unidentifiable fragmentary bones and teeth were also kept for record (ca. 400 mL of fossiliferous sediments: FHSM VP-19645). It should be noted that FHSM VP-644 was previously referred to in some literature such as Beeson and Shimada (2004), Shimada and Fielitz (2006), and Allen and Shimada (2020); however, this present study represents the most comprehensive work on the Niobrara bonebed fauna that supersedes any of the previous reports on fossils from FHSM VP-644.

The taxonomic scheme follows largely of Nelson et al. (2016) for fishes, Konishi et al. (2012) for *Platecarpus*, and Aotsuka and Sato (2016) for Hesperornithiformes. In order to analyze the faunal composition, the number of specimens of each taxon was counted and compared with the relative abundance among taxa represented in major museum collections with fossils from the Niobrara Chalk. Besides the Vertebrate Paleontology collection of FHSM, they consisted of the following six collections in the U.S.: American Museum of Natural History (AMNH), Fossil Fish collection, New York, New York; Field Museum of Natural History (FMNH), Chicago, Illinois; Natural History Museum of Los Angeles County (LACM), California, U.S.A.; University of Kansas Museum of Natural History, Vertebrate Paleontology (KUVP), Lawrence, Kansas; U.S. National Museum of Natural History (Smithsonian Institution: NMNH), Washington, D.C.; and Yale Peabody Museum of Natural History (YPM), New Haven, Connecticut. An inventory database of all vertebrate fossil specimens from the Niobrara Chalk of Kansas (as of late 2020–early 2021) repositied by separate 'catalog lots' in each museum

collection was generated. Each catalog lot may consist of a single anatomical element, multiple isolated anatomical elements from multiple individuals of the same taxon, or multiple anatomical elements (i.e., 'associated materials') from a single individual. Whereas there is no known case of an associated material deliberately split into separate catalog lots, my data from the museum collections that were organized taxonomically consisted of enumeration of the total number of specimens per taxon that equated the minimum number of individuals for that taxon (Appendices 1, 2). Unless otherwise specifically noted in the caption for Appendix 1 for cases of multiple isolated anatomical elements being lumped together in a single catalog lot, each catalog lot in museum databases was considered to represent one individual animal. The abundance of individuals for each taxon from the bonebed was then compared with that of museum collections in order to examine any patterns and differences between the natural (bonebed) assemblage and artificial (museum) assemblage. It should be noted that my dataset is more inclusive and robust than Russell's (1993) survey that largely based only on the AMNH, KUVP, and YPM collections.

### III. SYSTEMATIC PALEONTOLOGY

Over 40,450 taxonomically identifiable specimens were collected from the bonebed, where identified taxa consist of at least four chondrichthyans, 24 osteichthyans, and two tetrapods. The collected specimens also included numerous small coprolites possibly of vertebrates in origin. Table 1 summarizes the taxa from the bonebed, and a brief description and discussion for each taxon are provided below.

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Lamniformes Berg, 1958

Family Anacoracidae Casier, 1947

Genus *Nanocorax* Cappetta, 2012

*Nanocorax microserratodon* (Shimada, 2008)

(Fig. 3A, B)

Material—FHSM VP-19648, one tooth; VP-19649, one tooth; VP-19650, eight teeth.

Description—Teeth of this taxon are small and measure up to 3 mm in total height. The crown has a triangular cusp that is steeply inclined distally with a gently convex distal heel. The mesial and distal cutting edges contains weak serrations. The labial crown is gently convex, and its base overhangs a broadly spread bilobed root with gently arched basal concavity. The labial and lingual faces of the root exhibit many pits, some of which are more prominent than others.

Discussion—Species of the genus *Nanocorax* were previously referred to as *Microcorax crassus* (Cappetta and Case, 1975b), *Squalicorax microserratodon* (Shimada, 2008), or *Pseudocorax* sp. (Shimada, 1997), but Cappetta (2012) erected the genus to place them. *Nanocorax microserratodon* has been reported only from the Smoky Hill Chalk of Kansas. The type specimen comes from the Coniacian portion of the stratigraphic member (Shimada, 2008).

Genus *Squalicorax* Whitley, 1939

*Squalicorax* cf. *S. pawpawensis* Siverson, Lindgren, and Kelley, 2007

(Fig. 3C)

Material—FHSM VP-19651, one tooth.

Description—FHSM VP-19651 measures about 1.5 mm in total tooth height and total tooth width. It has a triangular, distally inclined cusp with its tip directed slightly apically. Both mesial cutting and distal edges bear rather irregular serrations, and the labial crown base that is gently convex overhangs the root. The distal part is missing in FHSM VP-19651, but it is discernable that the root had a moderate basal concavity.

Discussion—FHSM VP-19651 is the same tooth originally illustrated and referred to as *Squalicorax volgensis* by Shimada and Fielitz (2006, fig. 2C). *Squalicorax pawpawensis* or *S.* cf. *S. pawpawensis* has been reported from the Albian of Texas (Siverson et al., 2007) as well as the Turonian of Kansas and Iowa (Nelms et al., 2014; Gorman et al., 2014; McIntosh et al., 2016; Bice and Shimada, 2016). Teeth in those reports generally exhibit a flat labial face, whereas the labial surface of FHSM VP-19651 is slightly convex. Therefore, whether FHSM VP-19651 is



conspecific to such previously described forms is uncertain, it indicates the presence of a previously unreported form of *Squalicorax* that may be closely allied to *S. pawpawensis*.

*Squalicorax* cf. *S. falcatus* (Agassiz, 1843)

(Fig. 3D, E)

Material—FHSM VP-19652, one tooth; VP-19653, one tooth; VP-19654, 21 teeth.

Description—Teeth from *Squalicorax* cf. *S. falcatus* from the Niobrara bonebed measure up to 15 mm tall and can be identified by having a broad triangular, relatively erect crown with a flat labial crown surface. Both the mesial and distal cutting edge are serrated rather regularly throughout their extent. The labial crown base only weakly overhangs the large bilobed root with a moderate basal concavity.

Discussion—The type specimen of *Squalicorax falcatus* comes from the Turonian of the U.K., where the validity of many previous reports of the species from elsewhere, including those from North America, remains questionable (Siverson et al., 2007). Nevertheless, teeth in many of such previous reports, including those from Cenomanian–Santonian deposits of the Western Interior Seaway do bear resemblance to *S. falcatus*, and thus have frequently been referred to as *S. cf. S. falcatus* (e.g., Hamm and Cicimurri, 2011; McIntosh et al., 2016; Ouroumova et al., 2016; Guzzo and Shimada, 2018). Several skeletal remains of *S. cf. S. falcatus* are known from the Niobrara Chalk, revealing that they typically ranged up to about 2 m in total length (Shimada and Cicimurri, 2005). The tooth illustrated in Figure 3E (FHSM VP-19653) is minute and morphologically peculiar, but it is interpreted to be a possible embryonic tooth of *S. cf. S. falcatus*.

Order Rajiformes Berg, 1940

Family Rhinobatidae Müller and Henle, 1838

Genus *Rhinobatos* Linck, 1790

*Rhinobatos incertus* Cappetta, 1973

(Fig. 3F, G)

Material—FHSM VP-19655, one tooth (male); VP-19656, one tooth (female); VP-19957, 217 teeth.

Description—Teeth of *Rhinobatos* measure up to 1 mm in height and width. Teeth are sexually dimorphic (Case et al., 1990; Welton and Farish, 1993), where the crown apex of male teeth is sharply pointed (e.g., Fig. 3F), whereas that of female teeth is blunt and rounded (Fig. 3G). The labial surface ranges from flat to slightly convex and the base overhangs the bilobed root with slight semicircular concavity. The lingual surface has three (mesial, distal, and medial) protuberances separated by grooves.

Discussion—The genus *Rhinobatos* (guitarfish) has a wide geologic range from the Lower Cretaceous (Berremian) to Recent (Cappetta, 2012). *Rhinobatos incertus* is the most common species of the genus reported from the Cretaceous of North America (e.g., Welton and Farish, 1993; Underwood and Cumbaa, 2010; Ouroumova et al., 2016), where in Kansas, it has been documented from the late Albian to early Campanian, including the Smoky Hill Chalk (Everhart, 2007). One example from the bonebed described here was illustrated as *Rhinobatos* sp. by Shimada and Fielitz (2006, fig. 2E).

Class Actinopterygii Woodward, 1891

Subclass Neopterygii Regan, 1923

Order Pycnodontiformes Berg, 1940

Family Pycnodontidae Agassiz, 1833

Genus *Palaeobalistum* Blainville, 1818

cf. *Palaeobalistum* sp.

(Fig. 4A–C)

Material—FHSM VP-19660, one molariform tooth; VP-19661, one molariform tooth; VP-19662, 24 molariform teeth; VP-19663, one pair of incisiform teeth; VP-19664, two incisiform teeth.

Description—Two forms of teeth of this taxon are recognized: molariform and incisiform teeth. Most molariform teeth, that generally measure up to about 1.5 mm in maximum dimension, have a triangular occlusal surface bounded by one or more sharp rims (e.g., Fig. 4A), some of which may be heavily jagged (e.g., Fig. 4B). The crown base is hollow, but some teeth also preserve a conical dentine root with a large pulp cavity. One pair of incisiform teeth tentatively identified as cf. *Palaeobalistum* sp. recovered from the bonebed (Fig. 4D) is about 2 mm tall. Each tooth has a flattened crown with truncate with sharp edges and an elongate columnar root.

Discussion—*Palaeobalistum* is known patchily from the Albian to the early Eocene in North America, South America, northwestern Africa, and Europe (see Shimada et al., 2006, and references therein). Teeth referable to *Palaeobalistum* are relatively common in the Cenomanian–Turonian Western Interior Seaway deposits (Shimada et al., 2006; Nagrodski et al.,

2012; Ouroumova et al., 2016). One example of a molariform tooth from the bonebed described here was illustrated as *Palaeobalistum* sp. by Shimada and Fielitz (2006, fig. 2F), but this present work represents the first formal description of this taxon from the Niobrara Chalk. Another pycnodont taxon, *Nursallia*, that also lived during the Late Cretaceous, shares somewhat similar tooth morphology as *Palaeobalistum* (Kriwet, 2005, fig. 40B–D), and it is possible that the materials described here may actually belong in part or entirely to that genus. Therefore, the taxon is here conservatively referred to as ‘cf. *Palaeobalistum* sp.’

Pycnodontidae indet.

(Fig. 4D)

Material—FHSM VP-19665, one molariform tooth; VP-19666, two molariform teeth.

Description—Specimens of Pycnodontidae indet. described here are all represented by molariform teeth that measure about 1 mm in greatest dimension. In occlusal view, the teeth are oval in shape where the center of the crown is raised to form a smooth blunt cusp.

Discussion—Pycnodonts are extinct, generally deep-bodied fishes that lived from the Late Triassic through the middle Eocene primarily in shallow marine deposits (e.g., Kriwet, 2005; Poyato-Ariza, 2005). In the Smoky Hill Chalk, two other pycnodont species are known: *Micropycnodon kansasensis* and *Hadrodus marshi* (Shimada and Fielitz, 2006). Molariform teeth of *M. kansasensis* are characterized by a circular crown in occlusal view, often with many small tubercles (e.g., Cronin and Shimada, 2019), whereas *H. marshi* is a large pycnodont with its premaxillary incisiform teeth measuring over 6 cm in height (Gregory, 1950). Therefore,

specimens of Pycnodontidae indet. described here are significant, because it indicates the presence of yet another pycnodont species in the Niobrara Chalk.

Infraclass Holostei Müller, 1845

Order Lepisosteiformes Hay, 1926

Family Lepisosteidae Cuvier, 1825

Lepisosteidae indet.

(Fig. 4E)

Material—FHSM VP-19658, one tooth; VP-19659, 15 teeth.

Description—Teeth of this taxon are mostly smooth and slightly compressed labiolingually, measuring 4 mm in total height. An arrowhead-shaped crown apex with distinct smooth mesial and distal cutting edges rests on a largely conical, elongate tooth base. The base of each tooth is hollow.

Discussion—Lepisosteids include the present-day gars, and the family is known to have existed since the Albian (Grande, 2010). A skeletal remain of ‘*Lepisosteus* sp.’ was documented from the Smoky Hill Chalk as the first marine occurrence of the genus by Wiley and Stewart (1977), but they proposed that the skeletal remain could represent a stomach content of a larger fish transported from the freshwater environment to the marine environment where it became fossilized. That specimen is now referred to as ‘Lepidosteidae indet.’ (Grande, 2010). Although whether the isolated teeth described here is conspecific with the lepisosteid taxon described by Wiley and Stewart (1977) is uncertain, their occurrence marks the second report of Lepidosteidae from the Smoky Hill Chalk.

Order Pachycormiformes Berg, 1940

Family Pachycormidae Woodward, 1895

Genus *Protosphyraena* Leidy, 1857

*Protosphyraena* sp.

(Fig. 4F)

Material—FHSM VP-19668, one tooth; VP-19669, one tooth.

Description—Teeth of *Protosphyraena* are triangular, erect, and labiolingually compressed, where larger of the two teeth measures about 7 mm tall and 3 mm in basal width. Their mesial and distal margins are gently convex and form cutting edges. Both labial and lingual faces are smooth and gently convex.

Discussion—*Protosphyraena* is an extinct fish group with an elongate rostrum like billfishes (Everhart, 2017). In Kansas, the genus is relatively common in the Smoky Hill Chalk (Stewart, 1988), but it is also known stratigraphically as low as the mid-Cenomanian (Graneros Shale and basal Greenhorn Limestone) (e.g., see Shimada et al., 2006 and references therein; Shimada and Martin, 2008). Whereas the species '*P.*' *gladius* has been assigned to the genus *Bonnerichthys* (Friedman et al., 2010), three species of *Protosphyraena* are known from the Smoky Hill Chalk based primarily on their pectoral fins: *P. nitida*, *P. pernicioso*, and *P. tenuis*. Because species-level characterization of teeth for this genus is not investigated, I conservatively refer the specimens from the bonebed to *Protosphyraena* sp.

Non-teleostean(?) Actinopterygii incertae sedis

(Fig. 4G)

Material—FHSM VP-19667, one tooth.

Description—FHSM VP-19667 measures about 4 mm tall and is somewhat reminiscent of teeth of *Lepisosteus* sp. in that it is characterized by an arrowhead-like crown tip that rests on a conical, elongate tooth base. However, the specimen differs from them by its shaft being posteriorly curved rather than being erect as well as its cutting edge on the crown tip is confined to the posterior margin.

Discussion—The taxonomic identification of FHSM VP-19667 is highly tentative. It is based on the resemblance to teeth assigned to as ‘non-teleostean(?) Actinopterygii incertae sedis’ from the mid-Cenomanian of Colorado by Shimada et al. (2006). Despite its tenuous taxonomic assignment, FHSM VP-19667 is important because it warrants the possibility that there may be another unreported osteichthyan fish in the Niobrara fossil record.

Infraclass Teleostei Müller 1845

Order Elopiformes Greenwood, Rosen, Weitzman, and Meyers, 1966

Family Pachyrhizodontidae Cope, 1872

Genus *Pachyrhizodus* Dixon, 1850

*Pachyrhizodus caninus* Cope, 1872

(Fig. 4H)

Material—FHSM VP-19670, one tooth; VP-19671, two teeth.

Description—All three teeth from the bonebed are incomplete, but they are robust, gently curved, conical teeth with smooth surfaces. FHSM VP-19670 preserves the bony tooth base showing a prominent pulp cavity with an estimated total tooth height of 8 or 9 mm. The other two specimens (FHSM VP-19671) are represented by partial crown tips that also show well-developed pulp cavity.

Discussion—*Pachyrhizodus caninus*, that ranged from the late Cenomanian(?) to the mid-Campanian in North America, was a large fish that reached at least 2.3 m in total length and fed on other fishes (Shimada, 2015). Approximately ten specimens of this species from the Smoky Hill Chalk have been formally documented in literature (Shimada and Fielitz, 2006). Whereas many of them are partial skeletal remains, a nearly complete skeleton is also known (Hakel and Stewart, 2003).

*Pachyrhizodus minimus* Stewart, 1899

(Fig. 4I)

Material—FHSM VP-19672, one tooth; VP-19673, 1,870 teeth.

Description—Teeth of this species, that measure up to about 4 mm, are rather structurally simple, characterized by gently curved, smooth hook-like teeth. The tooth base is gently concave and a small opening for a pulp cavity is present at the center.

Discussion—*Pachyrhizodus minimus* was the smallest species of the genus *Pachyrhizodus* in North America, that measured up to about 80 cm (e.g., see Applegate, 1970, fig. 189). Remains of the species have been reported widely from the Cenomanian–Campanian deposits of the Western Interior Seaway (see Bice and Shimada, 2006, and references therein).



Teeth of *P. minimus* are the second most common identifiable vertebrate remains recovered from the bonebed, next to teeth of *Enchodus*.

Order Ichthyodectiformes Bardack and Sprinkle, 1969

Family Saurodontidae Cope, 1871

Saurodontidae indet.

(Fig. 4J)

Material—FHSM VP-19674, one tooth; VP-19675, 39 teeth.

Description—Teeth of this taxon, that measures up to about 5 mm in height, are triangular, erect, and labiolingually compressed and have gently convex mesial and distal margins forming cutting edges. They resemble teeth of *Protosphyraena* but are more robust by exhibiting more inflated labial and lingual faces compared to *Protosphyraena* teeth.

Discussion—Three species of Saurodontidae are known from the Smoky Hill Chalk of Kansas: *Prosaurodon pygmaeus* (Loomis, 1900), *Saurocephalus lanciformis* Harlan, 1824, and *Saurodon leanus* Hays, 1830 (Shimada and Fielitz, 2006). They are primarily represented by partial skeletons or skulls, but morphological differences in teeth among the three species are not investigated. Hence, the species assignment for the specimens described here is premature, and they are conservatively presented as Saurodontidae indet. here.

Family Ichthyodectidae Crook, 1892

Genus *Ichthyodectes* Cope, 1870

*Ichthyodectes ctenodon* Cope, 1870

(Fig. 4K)

Material—FHSM VP-19676, one tooth; VP-19677, one tooth.

Description—The larger and better-preserved tooth (Fig. 4K) of the two for this taxon from the bonebed is about 10 mm in preserved height. This species has robust, straight to slightly curved conical teeth with smooth crown surfaces and with a circular to slightly ovoid base.

Discussion—The genus *Ichthyodectes* is known from the Cenomanian–Campanian deposits of the Western Interior Seaway (Bardack, 1965; Cumbaa et al., 2010; McIntosh et al., 2016; Everhart, 2017). In the Smoky Hill Chalk, it is represented by a single species, *I. ctenodon*, known primarily from many partial skeletal remains (Shimada and Fielitz, 2006). The species measured up to about 3 m in total length (Everhart, 2017).

Order Tselfatiiformes Nelson, 1994

Family Plethodidae Loomis, 1900

Genus *Dixonangomius* Taverne, 2000

*Dixonangomius* sp.

(Fig. 4L)

Material—FHSM VP-19678, one left dentary.

Description—The specimen represents the anterior portion of the left dentary, measuring about 5 mm in preserved anteroposterior length. The anterior margin is straight and deep where the ventral margin is directed ventroposteriorly, indicative of a very deep jaw. The lateral surface

of the jaw exhibits two large and two small sensory canals. The occlusal surface is gently convex longitudinally and exhibits numerous, well-defined, finely pitted alveoli for tooth attachments.

Discussion—The very deep mandible based on the straight, deep anterior margin and ventroposteriorly directed ventral margin is consistent with the dentary of *Dixonangomius* sp. known from the Smoky Hill Chalk of Kansas (Taverne, 2000; Shimada and Fielitz, 2006). One notable difference is the size where the corresponding preserved portion of FHSM VP-19678 (5 mm in length) in the previously reported dentary specimen from the chalk (KUVVP 12008) measures about 7 cm in length (see Taverne, 2000, fig. 8). Whether they represent conspecific individuals of two different ontogenetic stages is uncertain, but FHSM VP-19678 at least indicates the presence of very small individuals of this genus in the Smoky Hill Chalk.

#### Plethodidae indet.

(Fig. 4M, N)

Material—FHSM VP-19679, one right dentary; VP-19680, 13 jaw fragments; VP-19681, one tooth; VP-19682, one tooth.

Description—The specimens of this taxon consist of jaw fragments and isolated teeth. The jaw specimens are identified based on the presence of numerous, well-defined, finely pitted alveoli for tooth attachments. The best preserved jaw fragment (Fig. 4M) that measures up to about 3.5 mm in preserved length, is anteroposteriorly elongate with a short anterior margin and a slit-like sensory canal near the anterior end on the lateral side. The teeth collected from the bonebed measure about 1 mm in height. They resemble teeth of *Pachyrhizodus minimus* by

having curved conical teeth with a smooth crown surface, but they are slenderer and their lingually-directed curvature is more pronounced than those of *P. minimus*.

Discussion—One of the most unique faunal characteristics of the Smoky Hill Chalk in Kansas is the diversity of plethodid fishes, where at least 14 species belonging to 12 genera are known (Taverne and Gayet, 2005; Shimada and Fielitz, 2006). The depth of the dentary bones in FHSM VP-19678 (Fig. 4L) and VP-19679 (Fig. 4M) strongly suggests that there are at least two plethodid taxa represented in the bonebed. The exact taxonomic identification for FHSM VP-19679 is difficult, but it should be noted that multiple jaw fragments and isolated teeth referred to ‘Plethodidae indet.’ may be represented by multiple plethodid taxa, meaning that the actual plethodid diversity present in the bonebed may be actually higher than two documented here.

Order Albuliformes Forey, Littlewood, Ritchie, and Meyer, 1996

Suborder Alubuloidei Greenwood, Rosen, Weitzman, and Meyers, 1966

Family Albulidae Bleeker, 1859

Albulidae indet.

(Fig. 4O)

Material—FHSM VP-19683, one vomerine tooth plate.

Description—The vomerine specimen has an outline of an anteriorly tapering elongate trapezoid, measuring about 2 mm in length and slightly less than 1 mm in width. It is characterized by a number of coarsely pitted, poorly defined, shallow alveoli for tooth attachments, where one dome-like tooth is also preserved in the specimen.

Discussion—Albulidae ranges geologically from the Cenomanian through Recent (see Shimada et al., 2006, and references therein). FHSM VP-19683 is the same albulid specimen illustrated and reported by Shimada and Fielitz (2006, fig. 2G), who cited Beeson and Shimada (2004). The specimen is significant because it represents the sole example of Albulidae in the entire Niobrara fossil record (see also ‘Notes’ in Shimada and Fielitz, 2006, p. 201).

Order Aulopiformes Rosen, 1973

Suborder Ichthyotringoidei Goody, 1969

Family Ichthyotringidae Jordan, 1905

Genus *Apateodus* Woodward, 1901

*Apateodus* sp.

(Fig. 5A)

Material—FHSM VP-19684, one tooth; VP-19685, two teeth.

Description—Although all three specimens are fragmentary, their maximum estimated total tooth height is about 4 mm. They are represented by spearhead-shaped, labiolingually compressed teeth where labial side is slightly more inflated than the lingual side and exhibits some faint longitudinal striations. The mesial and distal margins form sharp cutting edges.

Discussion—*Apateodus* with one of the characteristics being the presence of longitudinal striations on the teeth has been found nearly worldwide from Albian–Maastrichtian marine deposits (see Newbrey and Konishi, 2015, and references therein). At least one decisive species of the genus, *A. busseni* Fielitz and Shimada, 2009, and another undescribed aulopiform species referred to as ‘cf. *Apateodus*’, are known from the Smoky Hill Chalk of Kansas (Fielitz and

Shimada, 2009, 2020). Whereas the tooth specimens described here are more similar to teeth of *A. busseni* than to those in Fielitz and Shimada's (2020) 'cf. *Apateodus*', whether or not the specimens from the bonebed belong to *A. busseni* is uncertain. Therefore, they are here simply referred to as *Apateodus* sp.

Ichthyotringidae(?) indet.

(Fig. 5B)

Material—FHSM VP-19686, one tooth.

Description—FHSM VP-19686 is represented by a fang-like tooth that measures 2.5 mm in height and slightly less than 1 mm in basal width. One surface (presumed lingual side) is highly convex and the other surface (preserved labial side) is flat, forming pronounced mesial and distal cutting edges that slightly curve labially near the apex. The tooth surfaces are mostly smooth but some very faint longitudinal striations are discernable.

Discussion—FHSM VP-19686 is somewhat reminiscent of teeth of 'cf. *Apateodus*' from the Smoky Hill Chalk of Kansas described by Fielitz and Shimada (2020). However, unlike teeth of Fielitz and Shimada's (2020) 'cf. *Apateodus*', FHSM VP-19686 has less pronounced longitudinal striations and labially curved tooth apex. The exact taxonomic identity of FHSM VP-19686 is uncertain, but I tentatively and conservatively assign it to Ichthyotringidae(?) indet.

Family Dercetidae Pictet, 1850

Genus *Stratodus* Cope, 1872

cf. *Stratodus* sp.

(Fig. 5C)

Material—FHSM VP-19687, one tooth; VP-19688, 19 teeth.

Description—Teeth of this taxon are slender and conical with generally sigmoidal curvature and smooth surface. The transverse cross-section at any given point is generally circular including the tooth base that exhibits a prominent pulp cavity. FHSM VP-19687 is the largest, best-representative specimen that has an estimated total height of about 7.5 mm.

Discussion—*Stratodus* is an uncommon taxon from the Smoky Hill Chalk, formally known only from a few partial skeletal remains (Shimada and Fielitz, 2006). Beeson and Shimada (2004) reported the occurrence of *Stratodus* from the bonebed, but the identification was subsequently dismissed by Shimada and Fielitz (2006). Whereas specimens described herein are different from samples identified as *Stratodus* by Beeson and Shimada (2004), the materials in this study are tentatively and conservatively identified as ‘cf. *Stratodus* sp.’ especially because the morphological characterization and variation range of *Stratodus* are not well documented yet.

Suborder Enchodontoidei Berg, 1940 (sensu Nelson, 1994)

Superfamily Cimolichthyoidea Nelson, 1994

Family Cimolichthyidae Goody, 1969

Genus *Cimolichthys* Leidy, 1857

*Cimolichthys nepaholica* (Cope, 1872)

(Fig. 5D)

Material—FHSM VP-19689, one tooth; VP-19690, 12 teeth.

Description—Teeth of this taxon from the bonebed measure up to 11 mm in height and 6 mm in basal width. The tooth is triangular and gently curved lingually and distally. The lingual face is strongly convex and the labial face only slightly convex, where fine vertical striations are present throughout both surfaces. In basal view, the enameloid crown base is generally D-shaped to oval, and the dentine that fills the enameloid cap bears a small pit-like pulp cavity in the middle. Smooth but prominent mesial and distal cutting edges are present.

Discussion—*Cimolichthys nepaholica* has been recorded from the upper Cenomanian through the Campanian throughout the Western Interior Seaway (e.g., Russell, 1988; Martin et al., 1998; Nagrodski et al., 2012). The species is relatively common in the Smoky Hill Chalk in Kansas represented by many skeletal remains (Shimada and Feilitz, 2006). *Cimolichthys nepaholica* measured up to about 2 m in total length, and the fossil record shows that the taxon fed on squid and smaller bony fishes (see Everhart, 2017, and references therein).

#### Family Enchodontidae Woodward, 1901

Genus *Enchodus* Agassiz, 1835

*Enchodus gladiolus* (Cope, 1872)

(Fig. 5E, F)

Material—FHSM VP-19691, one palatine bone; VP-19692, nine palatine bones; VP-19693, one tooth; VP-19694, ca. 3,100 teeth.

Description—Specimens of this taxon from the bonebed are represented by isolated palatine bones and teeth. Palatine bones are anteroposteriorly elongate, and the largest specimen (Fig. 5E) measures 19 mm in anteroposterior length. The anterior end is robust represents the



base of a palatine tooth that is directed anteroventrally, whereas the posterior end tapers posteriorly with a straight ventral margin. Teeth of this taxon from the bonebed measure up to about 7 mm and are characterized by a triangular crown with a sigmoidal flexure. The lingual face is more convex than the labial face, where numerous fine vertical striations are present on both sides. They possess a well-defined cutting edge along the entire mesial margin as well as near the apex along the distal margin that may be represented by a small barb. The tooth base is filled with dentine, and a prominent pit-like pulp cavity is present at the middle.

Discussion—Remains of *Enchodus gladiolus* and those that have been referred to as *E. cf. E. gladiolus* are known from Cenomanian–Maastrichtian deposits of North America (Goody, 1976; Shimada et al., 2006; Parris et al., 2007). This species is well documented from the Smoky Hill Chalk of Kansas (Fielitz, 2002; Shimada and Fielitz, 2006). This species is known only from partial remains. However, *E. gladiolus* was likely a medium-sized enchodontid based on the fact that its palatine bones are typically smaller than those of *E. petrosus* (that can exceed 5 cm in anteroposterior length: Everhart, 2017, Fig. 5.11) but larger than *E. shumardi* (see below for estimated total lengths of *E. petrosus* and *E. shumardi*).

*Enchodus petrosus* Cope, 1874

(Fig. 5G, H)

Material—FHSM VP-19695, one palatine bone; VP-19696, ca. 1,825 palatine bones; VP-19697, one tooth; VP-19698, ca. 32,850 teeth.

Description—Specimens of this taxon from the bonebed consist of isolated palatine bones and teeth. Palatine bones are anteroposteriorly short, where the largest samples from the

bonebed measure about 8 mm in anteroposterior length. The palatine tooth, if preserved, at the anterior end of the palatine bone is robust and directed ventrally. Many teeth of this taxon from the bonebed are incomplete but the estimated maximum height is about 2 cm. They are triangular, elongate, and straight or slightly curved lingually with a strongly convex lingual face and a gently convex labial face. Both lingual and labial faces are ornamented with numerous fine vertical striations, where the lingual face also generally exhibits several prominent vertical grooves. The mesial and distal cutting edges are straight. The dentine fills the tooth base, and a prominent pit-like pulp cavity is present at the center.

Discussion—Remains of *Enchodus petrosus* and those that have been referred to as *E. cf. E. petrosus* are known from Turonian–Maastrichtian deposits of North America (Goody, 1976; Shimada et al., 2006; Parris et al., 2007; Bice and Shimada, 2016). It is the largest species within the genus *Enchodus* that measured slightly over 1 m in length (Goody, 1976). *Enchodus petrosus* is well represented in the Niobrara fossil record based on partial skeletal remains (Shimada and Fielitz, 2006), and it is the most common taxon by number of specimens identified from the bonebed, exceeding 34,500 specimens of teeth and palatine bones combined. Remains of *E. petrosus* from the bonebed are appreciably smaller in size compared to conventional specimens of the species reported from the Smoky Hill Chalk (e.g., Everhart, 2017, fig. 5.9, 5.11), but they are interpreted to be from juveniles.

*Enchodus shumardi* Leidy, 1856

(Fig. 5I, J)

Material—FHSM VP-19699, one palatine bone; VP-19700, 30 palatine bones; VP-19701, one tooth; VP-19702, 52 teeth.

Description—Specimens of this taxon from the bonebed are represented by isolated palatine bones and teeth. Palatine bones are anteroposteriorly short, where the largest sample from the bonebed measures about 6 mm in anteroposterior length. The palatine tooth, if preserved, at the anterior end of the palatine bone is gracile and directed ventrally. Most teeth of this taxon from the bonebed are incomplete but the estimated maximum height is about 11 mm. They are triangular, elongate, and straight with a strongly convex lingual face and a gently convex labial face. Both lingual and labial faces are either relatively smooth or ornamented with numerous fine vertical striations. The mesial and distal cutting edges are straight. The dentine fills the tooth base with a prominent pit-like pulp cavity at its center.

Discussion—Remains of *Enchodus shumardi* and those that have been referred to as *E.* cf. *E. shumardi* are common in Cenomanian–Maastrichtian deposits of the Western Interior Seaway (see Bice and Shimada, 2016, and references therein). Although no complete skeletons are known for this species, *E. shumardi* from the Smoky Hill Chalk of Kansas is known primarily from incomplete cranial elements (Shimada and Fielitz, 2006). Based on the sizes of previously reported specimens (see Bice and Shimada, 2016, and references therein) as well as specimens collected from the bonebed, *E. shumardi* is inferred to be a small species within the genus *Enchodus*, generally measured no more than 20 cm in total length.

*Enchodus* spp.

(Not figured)

Material—FHSM VP-19703, numerous jaw fragments.

Description—Specimens in this catalog lot are represented by fragmentary palatine, maxillary, and mandibular bones, that are all less than 8 mm in maximum preserved dimension. One or more tooth bases may be preserved.

Discussion—This catalog lot is an ad hoc category to accommodate specimens that can be identified to the genus *Enchodus*, but too fragmentary for decisive species identification. Therefore, they most likely consist of remains from multiple species of *Enchodus* described above. The Smoky Hill Chalk is known to yield one additional species of *Enchodus*, *E. dirus* (Leidy, 1857) (Shimada and Fielitz, 2006), and one cannot deny the possibility that the species could be represented in such fragmentary materials that are not specifically identifiable.

#### Order Acanthomorpha Rosen, 1973

##### Acanthomorpha indet.

(Fig. 5K)

Material—FHSM VP-19704, one fin spine; VP-19705, 185 fin spines.

Description—Specimens identified represents fin spines, measuring no more than 5 mm in maximum preserved length. Although the distal end of them are typically broken off, the widening proximal end bears a distinct opening of attachment for the endoskeletal radial (= pterygiophore).

Discussion—Acanthomorpha is a diverse group of teleosts, geologically ranging from the Cenomanian to Recent (Rosen and Patterson, 1969; Nelson et al., 2016). Remains of acanthomorph fishes are sporadically reported from the deposits of the Western Interior Seaway

(Stewart, 1996; Cumbaa et al., 2006). *Ferrifrons rugosus* Jordan, 1924, known from the Smoky Hill Chalk (Shimada and Fielitz, 2006) is a probable acanthomorph fish (Arratia and Chorn, 1998), but whether the materials from the bonebed belongs to this taxon is uncertain. Nevertheless, specimens described here solidifies the presence of acanthomorphs during the deposition of the Smoky Hill Chalk.

Teleostei indet. ‘Type A’

(Fig. 5L)

Material—FHSM VP-19706, one tooth; VP-19707, 12 teeth.

Description—Teeth of this taxon, that measure up to about 4 mm in height and 1.5 mm in basal width, are triangular and may be gently curved lingually. The labial face is slightly more convex than the lingual face. Both surfaces are smooth, whereas the mesial and distal margins form cutting edges. The tooth base is represented by the edge of the enameloid because the dentine does not fill all the way to the tooth base.

Discussion—Several morphotypes of teleost teeth have been reported from the Cenomanian–Turonian deposits of Kansas and adjacent states. Shimada et al. (2006) described one morphotype as ‘Teleost A’ with a wide morphological range, where one sigmoidal form (Shimada et al., 2006, fig. 14.11) somewhat resembles teeth of cf. *Stratodus* sp. described here, whereas another form of ‘Teleost A’ (Shimada et al., 2006, fig. 14.12) is also appreciably similar to their ‘Teleost B’ (Shimada et al., 2006, fig. 14.13, 14.14). A review of these morphotypes, particularly those referred to as types or species ‘A’ and ‘B,’ is warranted, including subsequent studies (e.g., Shimada and Martin, 2008; Nagrodski et al., 2012; Gallardo et al., 2013;

Ouroumova et al., 2016). However, for the purpose of this paper, I consider the sigmoidal form of ‘Teleost A’ depicted by Shimada et al. (2006, fig. 14.11) to be conspecific with cf. *Stratodus* sp. described here, and identified the materials described here as conspecific with the other form of ‘Teleost A’ illustrated by Shimada et al.’s (2006, fig. 14.12). Whether this taxon belongs to any known fish taxon in the Niobrara fossil record is uncertain because tooth morphology of many osteichthyans is not well documented for comparisons, but this suggests that this taxon existed in the Western Interior Seaway at least from the mid-Cenomanian through the Santonian.

Teleostei indet. ‘Type C’

(Fig. 5M)

Material—FHSM VP-19708, one tooth; VP-19709, four teeth.

Description—Teeth of this taxon are characterized by conical crowns with prominent longitudinal striations throughout the crown surface. They are up to about 3 mm in height and may be slightly curved lingually. The dentine fills the enameloid cap, where a circular pulp cavity is present at the middle of the tooth base.

Discussion—Teeth of this taxon are readily distinguishable from any other teleostean dental morphotypes because of their prominent longitudinal striations. This taxon has been reported from various Cenomanian–Turonian deposits of the Western Interior Seaway (Shimada et al. 2006; Shimada and Martin, 2008; Nagrodski et al., 2012; Gallardo et al., 2013; Nelms et al., 2014; Gorman et al., 2014; Ouroumova et al., 2016; Johnson-Ransom and Shimada, 2016; Guzzo and Shimada, 2018). The recognition of this taxon from the Smoky Hill Chalk marks the geologically youngest record for this species.

Teleostei indet. ‘Type F’

(Fig. 5N)

Material—FHSM VP-19710, one tooth; VP-19711, three teeth.

Description—Teeth of this taxon consist of tall, labiolingually compressed, relatively erect (but with a slightly curved apex), triangular crown with smooth surfaces, measuring up to about 5 mm in height. The labial face is more convex than the lingual face, where the mesial and distal peripheries of the crown are slightly compressed labiolingually that forms part of smooth cutting edges. The tooth base with limited dentine filling forms a slightly inflated D-shape.

Discussion—Previously, five dental morphotypes of unidentified teleosteans have been described from Cenomanian–Turonian deposits of the Western Interior Seaway (e.g., Shimada et al., 2006; Nagrodski et al., 2012), where the last morphotype was designated as ‘Type E’ by Jansen et al. (2013). The specimens described here represents another morphotype and designated as Type F. As discussed above, teleostean teeth that have been assigned to Type A and Type B require review, where I note that a tooth illustrated as ‘Type A’ by Nagrodski et al. (2012, fig. 4P) may actually be conspecific with teeth of Type F from the bonebed described here (but to clarify, note that Nagrodski et al.’s ‘Type A’ is not conspecific with Type A from the bonebed described in this paper). If so, this taxon ranged at least from the late Cenomanian through the Santonian in the Western Interior Seaway.

Teleostei indet. ‘Type G’

(Fig. 5O)

Material—FHSM VP-19712, one tooth.

Description—FHSM VP-19712 is a dome-shaped tooth that measure about 1 mm in height, width, and length. A transparent enameloid cap is present on the tooth apex, and the remaining crown surface is ornamented with vertical striations. Its nearly circular base is filled with dentine with a small pit in the middle.

Discussion—This crushing-type tooth is a new dental morphotype recognized from deposits of the Western Interior Seaway. It could represent a peripheral tooth of a known teleostean species or even one of the taxa described above, but until more comparative teleostean dental data become available, it is presented here as a distinct taxon.

Teleostei indet. (multiple taxa)

(Fig. 5P)

Material—FHSM VP-19713, one vertebra; VP-19714, numerous vertebrae; VP-19715, eight jaw fragments.

Description—Vertebrae and jaw fragments are represented by different sizes and shape. Some fragmentary vertebral specimens are suggestive of originally having the diameter of as large as about 15 mm in their articular view, but the vast majority of them are smaller than that depicted in Figure 5P, which has an articular diameter of about 5 mm. Jaw fragments are up to about 5 mm in preserved length and bear one or more teeth that are rather poorly preserved for decisive taxonomic identification.



Discussion—This is an ad hoc category to accommodate numerous isolated vertebrae and several jaw fragments of teleosteans that most certainly belong to multiple taxa, that may include one or more teleostean taxa described above. However, these specimens are lumped together here because of their taxonomic uncertainty.

Class Reptilia Linnaeus, 1758

Subclass Diapsida Osborn, 1903

Order Squamata Opper, 1811

Superfamily Mosasauoidea Camp, 1923

Family Mosasauridae Gervais, 1852

Subfamily Plioplatecarpinae Dollo, 1884

Genus *Platecarpus* Cope, 1869

*Platecarpus tympaniticus*(?)

(Fig. 6A, B)

Material—FHSM VP-19716, one tooth; VP-19717, one tooth; VP-19718, three teeth.

Description—Teeth of this taxon from the bonebed measure up to about 13 mm in height and 6.5 mm in basal width. They all have a conical, lingually (or posteriorly) curved crown with many longitudinal striations. Prominent anterior and posterior (or mesial and distal) carinae are present on the apical three-quarters of the crown but become faint or disappear near the crown base. The tooth base is filled with dentine with a flat surface and a circular to oval central pore.

Discussion—The genus *Platecarpus* is one of the most common mosasaur taxa in the fossil record of Smoky Hill Chalk (Russell, 1967; Everhart, 2001). It is generally accepted to be

monospecific, represented by *P. tympaniticus* Cope, 1869, that reached at least 5.5 m in total length and is stratigraphically restricted to the Santonian–early Campanian portion within the Smoky Hill Chalk (Konishi and Caldwell, 2011; Konishi et al., 2012; Everhart, 2017). Because the specimens described here are isolated teeth, their attribution to this species is tentative.

Class Aves Linnaeus, 1758

Subclass Ornithurae Haeckel 1866

Order Hesperornithiformes Fürbringer 1888

Hesperornithiformes indet.

(Fig. 6C, D)

Material—FHSM VP-19719, one tooth; VP-19720, one tooth; VP-19721, 88 teeth.

Description—Teeth vary morphologically but are generally no more than 3 mm in height. They are labiolingually compressed and, whereas the basal one-third of the crown base is erect, the apical two-thirds of the tooth shows a rather sharp posterior curvature or bent that leads to an acutely pointed apex, giving an overall hook-like appearance. The labial face is more convex than the lingual face, where in anteroposterior view, the labial face curves lingually near the apex and is slightly constricted at the tooth base, whereas the lingual face is straight. Many fine vertical striations are present on both labial and lingual surfaces. Much of the anterior crown margin forms a blunt carina, but a carina is only weakly present and commonly confined to towards the tooth base or at the bent of the crown. The tooth base is characterized by funnel-shaped dentine filling where an oval pore is present at the deepest central point.

Discussion—The specimens described here are identified based on the close resemblance with hesperornithiform teeth illustrated by Dumont et al. (2016, particularly fig. 1B).

Hesperornithiforms are characterized as toothed, foot-propelled, pursuit diving seabirds that fed on small fishes (Martin and Tate, 1976; Bell et al., 2019; Wilson, 2019). Furthermore, the fossil record shows that hesperornithiforms were fed by mosasaurs and possibly plesiosaur (Martin and Bjork, 1987; Martin et al., 2016). Although hesperornithiform remains have been commonly reported from various Upper Cretaceous deposits of the Western Interior Seaway, including the Smoky Hill Chalk of Kansas, as well as in Europe and Asia (Rees and Lindgren, 2005; Aotsuka and Sato, 2016; Everhart, 2017, and references therein), the collection of hesperornithiform teeth from the bonebed described here represents arguably the richest horizon in terms of the number of hesperornithiform specimens in the fossil record.

Vertebrata(?) incertae sedis

(Fig. 6E)

Material—FHSM VP-19722, one coprolite with *Enchodus* tooth; VP-19723, numerous coprolites.

Description—The specimens are represented by white to light brown phosphatic pebbles measuring up to about 1 cm in greatest dimension, including the prominent light-colored oblong piece near the bottom right corner of Figure 2C. Some contains fragmentary bones and teeth of bony fishes, including a crown tip of a bony fish (*Enchodus?*) tooth illustrated in Figure 6E.

Discussion—Fecal remains represented by phosphatic pebbles are common in deposits of the Western Interior Seaway (see Shimada et al., 2006, and references therein). Whereas smaller

phosphatic pebbles (<4 mm in greatest dimension) may be produced by invertebrates, larger pebbles (>4 mm), especially if remains of vertebrates are observed as inclusions, are generally attributed to vertebrates in origin (Savrda and Bottjer, 1993). Although some of the phosphoric pebbles could be from invertebrates, at least some of them are considered to be derived from vertebrates based on their sizes and vertebrate inclusions.

## IV. DISCUSSION

### A. Age and depositional environment of the Niobrara bonebed

The Smoky Hill Chalk was deposited in Kansas within the Niobrara depositional cycle spanning from the late Coniacian through early Campanian (Hattin, 1982). The locality of the bonebed is catalog as ‘near Monument Rocks’ in Gove County, where much of the Smoky Hill Chalk exposed in that region of Kansas represents the upper half of the stratigraphic member (Hattin, 1982; Bennett, 1990, 2000). That stratigraphic range is broadly known as the ‘Upper Chalk’ that roughly corresponds to Hattin’s (1982) Marker Units (MU) 11–23, ranging from the mid-Santonian through the lower Campanian (Everhart, 2011, fig. 3; Fig. 1B). Williston (1897) characterized the Upper Chalk as the ‘*Hesperornis* bed’ because of frequent occurrences of hesperornithiform bird remains (Everhart, 2011), and the abundance of hesperornithiform teeth from the bonebed in this study does not contradict with the interpretation that the bonebed originated somewhere in the Upper Chalk. In addition, the occurrence of *Platecarpus* from the bonebed also suggests that the bonebed horizon was not from lower in the chalk but within the Santonian–early Campanian portion of the Smoky Hill Chalk (see Everhart, 2017, table 13.1).

The possible stratigraphic position of the bonebed can be further constrained based on the *Squalicorax* biostratigraphy. Specifically, the dominance of *Squalicorax* closely allied to *S. falcatus* in the bonebed and the absence of the two primarily Campanian–Maastrichtian species, *S. kaupi* and *S. pristodontus*, that are known to occur in the upper-most part of the Smoky Hill Chalk (see Shimada and Cicimurri, 2005), strongly suggest that the bonebed must have not come from the early Campanian portion of the Smoky Hill Chalk. Because the lowest part of the Upper Chalk is of mid-Santonian in age, and because of well-represented *S. cf. S. falcatus*, the bonebed

horizon must have lied somewhere between Hattin's (1982) MU11 and MU18 lithostratigraphically, or between the mid-Santonian (ca. 85.0 Ma) and the latest Santonian (83.6 Ma) chronostratigraphically (Fig. 1B).

The bonebed nature of the specific rock horizon could be considered as a lag deposit that often resulted from a regressive-transgressive eustatic sea-level event (e.g., Maisch et al., in press, and references therein). Specifically, fossil components in lag deposits are thought to have become condensed during a major regression, and the top-most part of such fossiliferous deposits is often marked by a sharp unconformity overlaid by a lithologically different, transgressive deposit (e.g., Becker et al., 2010; Cumbaa et al., 2006; Shimada et al., 2006; Hamm and Cicimurri, 2011; Maisch et al., 2019, in press). However, there is no such unconformity recognized within the Smoky Hill Chalk (Hattin, 1982). Nevertheless, it is still possible that the Niobrara bonebed described in this study could have formed through a regressive event, where: 1) fine sediments could have been washed away during the period to condense the vertebrate bones and teeth; and 2) the extent of the regression may not have caused the location to undergo a major lithologic change or may not have resulted in any stratigraphic hiatus. These propositions are particularly plausible given that the location where the bonebed was collected was geographically near the center (i.e., deepest part) of the Western Interior Seaway during the mid-Santonian (Fig. 1B). If so, the lack of any noticeable abrasions on fossil remains (vs. many specimens, for example, described by Shimada and Bice, 2016, and Ouroumova et al., 2016) suggest that the regressive water currents must have been strong enough to wash away the carbonate mud but not enough to tumble the skeletal and dental elements.

It is noteworthy that there were two episodes marked by the lowest sea-level through regression during the approximately 1.4-Ma time interval between the mid-Santonian and the

latest Santonian (i.e., ca. 85.0–83.6 Ma) based on Haq's (2014, fig. 2) short-term eustatic sea-level curve. The first episode is depicted with uncertainty at 85.0 Ma marking the transition from regression to transgression (note sea-level curve tenuously indicated by a broken line in Haq, 2014, fig. 2). The second episode of the lowest sea-level occurred 83.6 Ma and followed a well-defined regression (i.e., sea-level curve indicated with a solid line in Haq, 2014, fig. 2). Because that regressive event is the only major regression in the 1.4-Ma time interval, I contend that the bonebed described here possibly formed during that regressive event corresponding to KSa3 in Haq's (2014) third-order eustatic sea-level cycle. Because the regression took place from about 84.3 Ma to 83.6 Ma (Haq, 2014, fig. 2), if so, the duration of the bonebed formation must have been no more than 0.7 Ma. In fact, it is likely less than 0.7 Ma given that the water current at and near the beginning and end of that regression (i.e., the transition from and to the regressive phase) could have been weak for sediments to wash away to form the fossiliferous condensed zone. Therefore, the bonebed could be of the latest Santonian in age with an estimated age of  $84.0 \pm 0.3$  Ma.

The large number of hesperornithiform remains from the bonebed may indicate that the possible regressive event brought the shoreline or shorelines of the Western Interior Seaway slightly closer to the location even though the locality could have still been in the middle of the seaway. In this regard, the occurrence of the remains of *Lepisostidae* indet. is curious. For example, Wiley and Stewart (1977) described their lepisosteid specimen as the first marine record for the gar group, but they also proposed the possibility that the marine occurrence could have been due to transportation from a freshwater environment to the Niobrara sea by a larger fish as stomach contents. However, the occurrence of multiple lepisosteid teeth from the bonebed described here may suggest that there could have been at least one taxon of *Lepisosteidae* that

could have tolerated marine salinity. Alternatively, it is possible that the location where the bonebed formed was indeed close to either or both of the seaway shorelines. In addition, the possible regression-driven, slightly shallow-water condition brought to the locality could have made the seafloor to be well oxygenated, where the abundance of benthic guitarfish (*Rhinobatos*) teeth in the bonebed support this interpretation.

## **B. Paleoecology based on the Niobrara bonebed**

Prior studies on fossil vertebrates from the Smoky Hill Chalk of Kansas have recorded at least 18 chondrichthyan and 57 osteichthyan taxa (Shimada and Fielitz, 2006; Cicimurri et al., 2008; Shimada, 2008; Shimada and Everhart, 2009; Fielitz and Shimada, 2009, 2021) as well as at least six turtle, three pterosaur, six plesiosaur, ten mosasaur, three dinosaur, and eight avian taxa (Everhart, 2017, table 13.1), giving a minimum of 111 vertebrate taxa documented for the stratigraphic member. This present study based on a single horizon within the stratigraphic member yielded a total of at least 40,450 identifiable specimens from at least 30 taxa, including four chondrichthyans, 24 osteichthyans, and two tetrapods (Table 1). Among the reported fish taxa by Shimada and Fielitz (2006) included are the following four taxa based on materials found from FHSM VP-644: “*Squalicorax volgensis*”, “*Rhinobatos* sp.”, “*Palaeobalistum* sp.”, and “Albulidae gen. et sp. indet.” They are formally described in this paper as *Squalicorax* cf. *S. pawpawensis*, *Rhinobatos incertus*, cf. *Palaeobalistum* sp., Albulidae indet., respectively.

Whereas this study constitutes the second Niobrara record for *Nanocorax microserraton* (see Shimada, 2008), Lepisosteidae (see Wiley and Stewart, 1977), *Dixonangomius* sp. (see Taverne, 2000), and *Apateodus* (see Fielitz and Shimada, 2009), the following six tentatively identified osteichthyan taxa are new to the fossil record of the Smoky Hill Chalk: Pycnodontidae indet.,



Ichthyotringidae(?) indet., Teleostei indet. ‘Type A’, Teleostei indet. ‘Type C’, Teleostei indet. ‘Type F’, and Teleostei indet. ‘Type G’. If they indeed belong to taxa that have not been previously recognized from the Smoky Hill Chalk, it means that there are now at least 63 osteichthyan taxa and at least 117 vertebrate taxa known from the stratigraphic member.

The Smoky Hill Chalk in Kansas was deposited near the center of the Western Interior Seaway which has been described as a relatively deep sea (Hattin, 1982). The fine-grained carbonate sediments composed largely of foraminifera and coccolithophores may suggest that only weak currents primarily existed in this region representing a low-energy environment. The following small and medium-sized fishes are known to occur in a wide range of ocean environments from nearshore, shallow habitats to open-ocean habitats: *Squalicorax*, *Rhinobatos*, pycnodontids including *Palaeobalistum* sp., Lepisosteidae, *Pachyrhizodus minimus*, plethodids, Albulidae, *Apateodus*, ichthyotringids including *Stratodus*, *Enchodus*, and acanthomorphs (Applegate, 1970; Wiley and Stewart, 1977; Arratia and Chorn, 1998; Taverne, 2000; Fielitz, 2002; Hakel and Stewart, 2003; Taverne and Gayet, 2005; Shimada and Fielitz, 2006; Parris et al., 2007; Fielitz and Shimada, 2009; Bice and Shimada, 2016; and Ouroumova et al., 2016). However, the following specific vertebrate taxa from the bonebed tend to occur more commonly in deposits that represent open-ocean environments: *Nanocorax microserratodon*, *Protosphyraena*, *Dixonangomius*, ichthyodectiforms such as saurodontids and *Ichthyodectes*, *Cimolichthys*, *Platecarpus*, and curiously (but see also above) hesperornithiform birds (e.g., Cappetta and Case, 1975b; Stewart, 1988; Rees and Lindgren, 2005; Shimada and Cicimurri, 2005; Everhart, 2007; Cumbaa et al., 2010; Nagrodski et al., 2012; Nelms et al., 2014; Everhart, 2017; but see also Shimada and Hanks, 2020). Of the identified taxa, nine were likely pelagic (*Nanocorax*, *Squalicorax*, *Protosphyraena*, *Pachyrhizodus*, Saurodontidae, *Ichthyodectes*, and

*Platecarpus*), whereas some other taxa were likely predominantly demersal (pycnodontids including *Palaeobalistum*) or truly benthic (*Rhinobatos*). Whereas the most abundant chondrichthyan remains were teeth of *R. incertus* (219 specimens), remains of *Enchodus* were particularly abundant, especially *E. petrosus* (32,851 specimens), although *Pachyrhizodus minimus* was also prevalent (1,871 specimens) (Table 1).

There are no modern analogs to a trans-continental seaway, but it is possible to reconstruct the ecosystem by developing food webs based on fossil evidence. The base of the food web has been previously described in Everhart (2005) consisting of phytoplankton including coccolithophores, diatoms and other microscopic organisms that comprise primary producers that convert sunlight and nutrients into a food source. Microscopic zooplankton or protozoans make up the primary consumers which would have then been fed by small fishes or invertebrates. Alternatively, filter feeders such as the inoceramid bivalves that were also prevalent within the Seaway (Everhart, 2017) would consume the microscopic life. Extending into higher trophic levels are small and medium-sized fishes, including *Pachyrhizodus minimus*, cf. *Stratodus*(?) sp., *Enchodus gladiolus*, *E. shumardi*, acanthomorph fishes, and likely most of the indeterminate teleosts described here, as well as hesperornithiform birds (e.g., Shimada et al., 2006; Bice and Shimada, 2016; Everhart, 2017). The durophagous fishes, such as *Rhinobatos* and pycnodontids, may have fed on crustaceans and inoceramids living on the sea floor (see Shimada et al., 2006). Vertebrates in high trophic positions characterized by predators preying on smaller fishes or pelagic invertebrates (e.g., squids) include *Protosphyraena*, Saurodontidae, *Ichthyodectes*, *Cimolichthys*, and *Platecarpus* (Everhart, 2017), whereas *Nanocorax* and *Squalicorax* were likely opportunists or scavengers (see Shimada and Hanks, 2020, and references therein).

This study focused on the remains of vertebrate taxa in the Niobrara bonebed where the taxa identified from the bonebed represent only about one-quarter of the total number of taxa reported from the Smoky Hill Chalk to date (30 of at least 117 taxa: see above). Nevertheless, the bonebed is remarkable because the identified taxa encompass a very wide range of vertebrates (e.g., from benthic to pelagic taxa) and trophic positions (from lower- to higher-level consumers). The observed species richness is particularly astounding considering that the examined bonebed sample represents a very small fraction of the entire Smoky Hill Chalk that suggests the presence of a very complex ecosystem in the Western Interior Seaway during the late Santonian. Other taxa recorded from the Santonian portion of the Smoky Hill Chalk that were not recovered from the bonebed include: *Ptychodus*, *Pseudocorax*, *Squalicorax kaupi*, *Cretalamna*, *Cretoxyrhina*, *Micropycnodon*, *Bonnerichthys*, *Paraliodesmus*, *Xiphactinus*, *Gillicus*, *Prosaurodon*, *Urenchelys*, *Apsopelix*, *Pachyrhizodus leptospsis*, *Enchodus dirus*, *Niobrara*, *Zanclites*, *Caproberyx*, *Trachichthyoides*, *Megalocoelacanthus*, *Toxochelys*, *Ctenochelys*, *Protostega*, polycotylics, *Styxosaurus*, *Clidastes*, *Plesioplatecarpus*, *Selmasaurus*, *Tylosaurus*, *Ectenosaurus*, *Pteranodon*, *Nyctosaurus*, *Ichthyornis*, *Niobrarasaurus*, nodosauridae, and hadrosauridae (Everhart, 2017, table 13.1).

### **C. Biases in the Niobrara fossil record**

Several museum collections (see Materials and Methods) contain a wide assortment of vertebrate remains from the Niobrara Chalk of Kansas, including abundant pterosaur and marine reptile remains as well as complete specimens of giant fishes such as *Cretoxyrhina* and *Xiphactinus* (e.g., Russell, 1988, 1993; Shimada and Fielitz, 2006; Everhart, 2017). Table 2 shows a list of vertebrate taxa from the Niobrara Chalk of Kansas in the order of abundance in

the seven major museum collections with Niobrara vertebrate fossils (Appendix 1). The counts in the table do not include the specimens from the bonebed examined in this study, where each count can be considered as the minimum number of fossilized individuals represented in those collections for that taxon. The table shows that the top three most common genera in the museum collections are *Pteranodon*, *Platecarpus*, and *Xiphactinus*, all of which are large (reaching 4+ m) vertebrates. This is in striking contrast from the top three genera from the bonebed, which are regarded as small to medium-sized (mostly < 1 m) fishes: i.e., *Enchodus*, *Pachyrhizodus* (specifically *P. minimus*), and *Rhinobatos* (Table 1). It is also noteworthy that, whereas the dominance of fossil fishes in the Niobrara Chalk based on a small museum dataset used by Russell (1993) is consistent with the bonebed data than the museum collection data, the scarcity of *Platecarpus* (or ‘mosasaurs’) in the bonebed is markedly different from Russell’s (1993) survey (see Introduction).

Whereas Table 2 lists all the taxa registered in the seven museum collections, Table 3 lists the relative abundance of specimens by taxa from the bonebed in descending order, and compared with the relative abundance of specimens in the museum collection specifically for 17 specific taxa that are only represented in the bonebed (note: whereas some taxa were condensed to higher taxonomic categories, the following tenuously identified taxa were excluded for this purpose: Teleostei indet. ‘Type A’, ‘Type C’, ‘Type F’, and ‘Type G’ as well as ‘non-teleostean(?) Actinopterygii incertae sedis’; Appendix 2). The top three most common taxa from the bonebed are *Enchodus*, *Pachyrhizodus*, and *Rhinobatos* (see also Table 1) where *Enchodus* alone comprise 93.7% of the bonebed record, but those in the museum collections are *Platecarpus*, *Enchodus*, and *Protosphyraena* in descending order where the top two taxa (i.e., *Platecarpus* and *Enchodus*) comprise only 37.4% of the total museum record despite the

inclusion of *Enchodus* (Table 3). Therefore, also combined with the taxonomic list in Table 3, I reject my hypothesis that stated: ‘There is no difference in the composition of taxa by number of specimens between the bonebed and museum collections’ (see Introduction).

Table 3 also shows the effects of combining the bonebed data with the museum collection data, and perhaps the most significant observation is the fact that the museum collections would then become dominated by *Enchodus* and *Pachyrhizodus*. It should be noted that the minimum number of individuals for some genera listed in Table 2 may be underrepresented because specimens catalogued only at higher categories are not accounted for the counts on the table. For example, '545 individuals' of 'Squamata indet.' may include *Clidastes*, *Platecarpus*, and *Tylosaurus*, '191 individuals' of 'Beryciformes indet.' may potentially bring up the counts of holocentrid taxa like *Omosoma* and *Kansius* significantly, and '154 individuals' of 'Ichthyodectiformes indet.' may belong to genera such as *Gillicus*, *Ichthyodectes*, and *Xiphactinus* already represented by 100+ specimens or individuals. Therefore, it is entirely possible that, for example, there may be more specimens of *Platecarpus* than those of *Pteranodon* in reality, but the composition of the top three most common taxa represented in the museum collections would remain the same regardless.

Figure 7 depicts yet another way of illuminating the Niobrara vertebrate fossil record. It compares the proportions of chondrichthyan, osteichthyan, and tetrapod specimens between the bonebed data (Table 1) and museum collection data (Table 2) as well as those proportions when the two sets of data are combined. A major observation from Figure 7 is that the bonebed data significantly increase the proportion of osteichthyan fishes relative to that of chondrichthyans and tetrapods for the museum collections.

Some previous studies suggested that biases are present in the Niobrara vertebrate fossil record, including collecting and research bias towards large and well-preserved specimens (e.g., Russell, 1993; Hamm and Shimada, 2002; Shimada and Fielitz, 2006). Whereas larger vertebrate remains may preserve better in some sedimentary settings than others (Kidwell and Holland, 2002), collecting bias towards more easily accessible fossil sites or more easily identifiable specimens can also affect the understanding of ancient ecology. For example, fossil prospecting from Kansas traditionally involves walking and visually searching for remains. Identification bias dependent on collectors' preferences may increase the recovery of certain fossils over others. Furthermore, certain taxa can be readily identified to species from a partial remain (e.g., shark teeth: Welton and Farish, 1993), whereas others may be less likely to be taxonomically identified from incomplete specimens (e.g., bony fishes: Shimada and Fielitz, 2006). Although museum repositories are important, the observed differences in my comparative data (Table 3; Fig. 7) clearly demonstrate that the relative abundances by taxa in museum collections at least do not correspond to those in the bonebed.

It must be noted that: 1) each identified fossil from the bonebed was counted to represent an individual animal, 2) many fragmentary specimens were not identifiable, and 3) specimens in the smaller particle range were not collected. These factors provide infinite possibilities that my abundance data by taxa too may not necessarily accurately represent the true proportions of taxa in the ecosystem of the Western Interior Seaway during the late Santonian. For example, facts such as one vertebrate species may have more teeth in the mouth, larger teeth, more well-calcified skeletal components, or more identifiable anatomical parts than other vertebrate species would affect my faunal data. However, it is worth pointing out that the fossils in the bonebed examined here could have undergone repetitive burial and exhumation cycles from the local

sediment that mix remains of organisms that did not live contemporaneously—a process referred to as time-averaging. Time-averaged fossils blur seasonal fluctuations in species abundance that may occur from famine, intense storms, or breeding seasons and instead provides a synchronized sample within the geological record (Olszewski, 1999). Whereas biotic systems are highly dynamic and can become disrupted by isolated seasonal change, breeding seasons, or disease, time-averaged fossil beds provide a larger view that can bypass these concerns and can provide insight into the paleoecology (Kowalewski, 1996; Kidwell, 1998). Similarly, where most of the identified vertebrate remains from the bonebed are teeth, I contend that the time-averaging would have increased the preservation potential for teeth of common taxa to be more commonly represented in the bonebed for a prolonged period even if such taxa could have had fewer teeth than other contemporaneous species. In particular, the abundance of *Enchodus* remains is most certainly even greater than what I reported (Table 1), given that practically the only identifiable remains in about 1,100 mL of 1,500 mL of unexamined sediments (i.e., smaller particle size range: see Materials and Methods) are indeed teeth of *Enchodus* (Fig. 8). Therefore, my bonebed data may in fact quite possibly reflect close to the actual relative abundances of Niobrara taxa at least during the late Santonian.

In a broad sense, the Niobrara fossil record represented in museum collections may also be collectively viewed as a ‘time-averaged’ assemblage containing fossils collected from different horizons within the formation from western Kansas, albeit artificially. However, if the natural assemblage represented by the bonebed examined here is taken at face value, museum collections are interpreted to be heavily biased towards large vertebrate remains. My study strongly suggests that a more accurate reconstruction of the paleoecology of the Western Interior Seaway requires more research on smaller vertebrate taxa.

## V. CONCLUSIONS

Ecological research can extend back in geologic time for prehistoric ecosystems and involves consideration of both the abiotic and biotic factors within them. During the Late Cretaceous, the North American continent experienced intense geologic activity, including the emergence and disappearance of the Western Interior Seaway and sediment deposition and accumulation along its seafloor through eustatic transgressions and regressions (Kauffman and Caldwell, 1993; Ogg et al., 2012). One of the eustatic fluctuations in the seaway, the so-called ‘Niobrara cycle’, produced a relatively large increase in the sea-level rise from 90.25 Ma to 81.5 Ma, that resulted in the formation of a stratigraphic formation called the Niobrara Chalk now most prominently observed in western Kansas (Hattin, 1982; Fig. 1).

In this study, I examined a unique fossiliferous bonebed collected from an uncertain horizon within the Smoky Hill Chalk Member of the Niobrara Chalk in southwestern Gove County, Kansas (Figs. 1, 2). I examine the taxonomic composition of its vertebrate fauna, determine its stratigraphic horizon, age, and depositional environment based on collected fossils along with available geographic and geologic data, and made inferences about the paleoecology of the Western Interior Seaway of Kansas when the bonebed formed. Furthermore, I examined and discussed potential biases in the Niobrara fossil record by comparing the faunal data from the bonebed with Niobrara vertebrate inventory data in seven major museum collections.

The bonebed pieces were submerged under acetic acid solution to dissolve calcium carbonate components where undissolved disaggregated materials consisting primarily of vertebrate remains were collected, rinsed with tap water, dried, screened, and analyzed. More than 40,450 taxonomically identifiable specimens were collected, consisting of at least four



chondrichthyans, 24 osteichthyans, and two tetrapods (Table 1; Figs. 2–6). They are: *Nanocorax microserraton*, *Squalicorax* cf. *S. pawpawensis*, *S.* cf. *S. falcatus*, *Rhinobatos incertus*, cf. *Palaeobalistum* sp., Pycnodontidae indet., Lepisosteidae indet., *Protosphyraena* sp., non-teleostean(?) Actinopterygii incertae sedis, *Pachyrhizodus caninus*, *P. minimus*, Saurodontidae indet., *Ichthyodectes ctenodon*, *Dixonangomius* sp., Plethodidae indet., Albulidae indet., *Apateodus* sp., Ichthyotringidae(?) indet., cf. *Stratodus* sp., *Cimolichthys nepaholica*, *Enchodus gladiolus*, *E. petrosus*, *E. shumardi*, Acanthomorpha indet., Teleostei indet. (Types ‘A’, ‘C’, ‘F’, and ‘G’), *Platecarpus tympaniticus*(?), and Hesperornithiformes indet. The collected specimens also included numerous small coprolites possibly of vertebrates in origin.

The general area where the bonebed was collected exposes the so-called ‘Upper Chalk’ of the Smoky Hill Chalk, ranging from the mid-Santonian through the lower Campanian. The abundance of hesperornithiform teeth, the occurrence of the likely *Platecarpus tympaniticus*, and well-represented *Squalicorax* closely allied to *S. falcatus* in the bonebed suggests that the bonebed horizon must have lied somewhere between Hattin’s (1982) MU11 and MU18, or between the mid-Santonian (ca. 85.0 Ma) and the latest Santonian (83.6 Ma) (Fig. 1B). The bonebed possibly formed through a regressive event near the deepest center of the Western Interior Seaway where fine sediments could have been washed away during the period to condense the vertebrate bones and teeth. Between the mid-Santonian and the latest Santonian, there was only one major regression (Haq, 2014), the bonebed described here is interpreted to have formed during that regressive event, that corresponds to Haq’s (2014) ‘KSa3’ third-order eustatic sea-level cycle. Hence, the age of the bonebed is further constrained to the latest Santonian in age with an estimated age of  $84.0 \pm 0.3$  Ma. Although still quite far from the shoreline(s), the possible regression-driven slight shallowing of water could have brought the

seafloor to a well-oxygenated condition supported by the abundance of benthic *Rhinobatos* teeth in the bonebed.

This present study based on a single horizon within the stratigraphic member yielded at least 30 vertebrate taxa. These include *Nanocorax microserratodon*, Lepisosteidae, *Dixonangomius* sp., and *Apateodus* as the second documentations for these taxa from the Smoky Hill Chalk, and Pycnodontidae indet., Ichthyotringidae(?) indet., Teleostei indet. ‘Type A’, Teleostei indet. ‘Type C’, Teleostei indet. ‘Type F’, and Teleostei indet. ‘Type G’, as the first record for these taxa from the stratigraphic member. Thus, there are now at least 18 chondrichthyan, 63 osteichthyan, and 36 tetrapod (turtles, pterosaurs, plesiosaurs, mosasaurs, non-avian dinosaurs, and birds) taxa, making a total of at least 117 vertebrate taxa known from the Smoky Hill Chalk (Shimada and Fielitz, 2006; Cicimurri et al., 2008; Shimada, 2008; Shimada and Everhart, 2009; Fielitz and Shimada, 2009, 2021; Everhart, 2017, table 13.1; this study). This study focused on the remains of vertebrate taxa in the Niobrara bonebed where the taxa identified from the bonebed represent only about one-quarter of the total number of taxa reported from the Smoky Hill Chalk to date. Nevertheless, the species richness from the bonebed sample is particularly astounding considering that the examined sample represents a very small fraction of the entire Smoky Hill Chalk, and yet suggests the presence of a very complex ecosystem in the Western Interior Seaway during the late Santonian.

I examined the abundance of Niobrara vertebrate specimens by taxa in seven major museum collections (Appendix 1). The top three most common genera in the museum collections in descending order are *Pteranodon*, *Platecarpus*, and *Xiphactinus* (Table 2), all of which are known to reach 4+ m (e.g., see Everhart, 2017). That is strikingly different from the top three common genera from the bonebed that are characterized as small to medium-sized fishes (mostly

<1 m): i.e., *Enchodus*, *Pachyrhizodus* (specifically *P. minimus*), and *Rhinobatos* (Table 1). When only taxa represented in the bonebed were compared (Table 3), the top three most common taxa in the museum collections in descending order are *Platecarpus*, *Enchodus*, and *Protosphyraena*. Thus, I refute my hypothesis: ‘There is no difference in the composition of taxa by number of specimens between the bonebed and museum collections.’ My study is significant because it suggests that the Niobrara fossil record based on museum collections is clearly biased towards large vertebrates, particularly reptilian remains. However, my faunal data do also have some limitations. For example, in my study, 1) each identified fossil from the bonebed was counted to represent an individual animal, 2) many fragmentary specimens were not identifiable, and 3) specimens in the smaller particle range were not collected. These factors provide infinite possibilities that my abundance data by taxa too may not necessarily accurately represent the true ecological condition of the Western Interior Seaway during the late Santonian. However, because the fossils in the bonebed likely represents a time-averaged assemblage, the time-averaging would have made anatomical elements of common taxa to be more commonly preserved in the bonebed for a prolonged period, where my bonebed data possibly reflect close to the actual relative abundances of Niobrara taxa at least during the late Santonian, particularly dominated by *Enchodus* spp. (Figs. 7, 8). Thus, despite the limitations, this study demonstrates the importance of examining smaller vertebrate taxa for better paleoecological reconstruction.

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**Table 1.** List of identified taxa from the examined Niobrara bonebed. This table excludes numerous jaw fragments of *Enchodus* spp. (FHSM VP-19703), eight jaw fragments and numerous vertebrae of Teleostei indet. (FHSM VP-19713–VP-19715), two fragmentary bones of Vertebrata indet. (FHSM VP-19644), and numerous coprolites of Vertebrata incertae sedis (FHSM VP-19722 and VP-19723), as well as fossil elements still represented in rock pieces or sediments (FHSM VP-644, VP-19642, VP-19643, and VP-19645–VP-19647).

Taxa	Fossil elements
<b>Chondrichthyes</b>	
<i>Nanocorax microserratodon</i>	10 teeth
<i>Squalicorax</i> cf. <i>S. pawpawensis</i>	1 tooth
<i>Squalicorax</i> cf. <i>S. falcatus</i>	23 teeth
<i>Rhinobatos incertus</i>	219 teeth
<b>Osteichthyes</b>	
cf. <i>Palaeobalistum</i> sp.	26 molariform teeth; 3 incisiform teeth
Pycnodontidae indet.	3 molariform teeth
Lepisosteidae indet.	16 teeth
<i>Protosphyraena</i> sp.	2 teeth
Non-teleostean(?) Actinopterygii incertae sedis	1 tooth
<i>Pachyrhizodus caninus</i>	3 teeth
<i>Pachyrhizodus minimus</i>	1,871 teeth
Saurodontidae indet.	40 teeth
<i>Ichthyodectes ctenodon</i>	2 teeth
<i>Dixonangomius</i> sp.	1 jaw fragment
Plethodidae indet.	14 jaw fragments; 2 teeth
Albulidae indet.	1 tooth plate
<i>Apateodus</i> sp.	3 teeth
Ichthyotringidae(?) indet.	1 tooth
cf. <i>Stratodus</i> (?) sp.	20 teeth
<i>Cimolichthys nepaholica</i>	13 teeth
<i>Enchodus gladiolus</i>	10 palatine bones; ca. 3,101 teeth
<i>Enchodus petrosus</i>	ca. 1,826 palatine bone; ca. 32,851 teeth
<i>Enchodus shumardi</i>	31 palatine bone; 53 teeth
Acanthomorpha indet.	186 fin spines
Teleostei indet. ‘Type A’	13 teeth
Teleostei indet. ‘Type C’	5 teeth
Teleostei indet. ‘Type F’	4 teeth
Teleostei indet. ‘Type G’	1 tooth
<b>Tetrapoda</b>	
<i>Platecarpus tympaniticus</i> (?)	5 teeth
Hesperornithiformes indet.	89 teeth
Total = ca. 40,450 fossil elements	

**Table 2.** Minimum number of individuals for each genus from the Niobrara Chalk of Kansas represented by  $\geq 30$  individuals in museum collections organized in the order of abundance (based on Appendix 1). It should be noted that the following taxonomic categories also had a count of  $\geq 30$  (minimum number of individuals in parentheses): Chondrichthyes indet. (68), Ichthyodectiformes indet. (154), Beryciformes indet. (191), Plethodidae indet. (29), Aulopiformes indet. (47), Actinopterygii indet. (54), Testudines indet. (87), Plesiosauria indet. (49), and Squamata indet. (545) (Appendix 1).

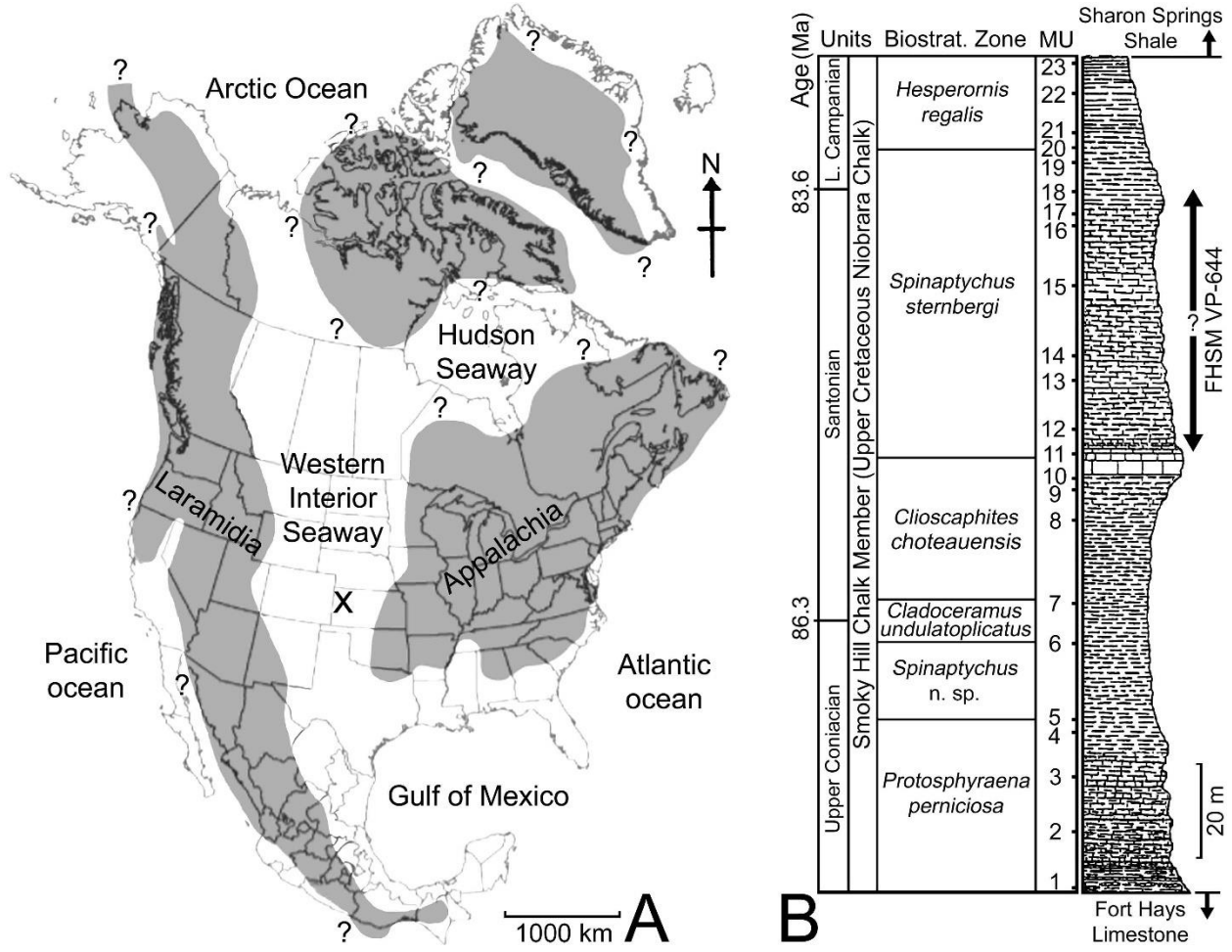
Genera	Higher category	Individuals
<i>Pteranodon</i>	Reptilia	844
<i>Platecarpus</i>	Reptilia	731
<i>Xiphactinus</i>	Osteichthyes	463
<i>Enchodus</i>	Osteichthyes	398
<i>Protosphyraena</i>	Osteichthyes	354
<i>Tylosaurus</i>	Reptilia	349
<i>Cimolichthys</i>	Osteichthyes	304
<i>Clidastes</i>	Reptilia	251
<i>Squalicorax</i>	Chondrichthyes	248
<i>Pachyrhizodus</i>	Osteichthyes	220
<i>Cretoxyrhina</i>	Chondrichthyes	200
<i>Ichthyodectes</i>	Osteichthyes	181
<i>Toxochelys</i>	Reptilia	138
<i>Ptychodus</i>	Chondrichthyes	128
<i>Gillicus</i>	Osteichthyes	111
<i>Omosoma</i>	Osteichthyes	101
<i>Hesperornis</i>	Aves	99
<i>Ichthyornis</i>	Aves	93
<i>Saurodon</i>	Osteichthyes	80
<i>Bananogmius</i>	Osteichthyes	70
<i>Martinichthys</i>	Osteichthyes	61
<i>Ctenochelys</i>	Reptilia	48
<i>Saurocephalus</i>	Osteichthyes	41
<i>Cretalamna</i>	Chondrichthyes	39

Note: Taxa represented by <30 individuals: Holocephali (*Eumylodus*), *Scapanorhynchus*, *Johnlongia*, *Pseudocorax*, *Rhinobatos*, *Anomoeodus*, *Micropycnodon*, Pycnodontiformes indet., *Paraliodesmus*, Lepisosteidae (*Lepisosteus*), *Bonnerichthys*, Pachycormiformes indet., *Apsopelix*, *Prosaurodon*, *Luxilites*, *Pentanogmius*, *Niobrara*, *Thryptodus*, *Zanclites*, *Palelops*, Albulidae indet., *Urenchelys*, *Anguillavus*, *Apateodus*, *Letpecodon*, *Stratodus*, *Kansius*, *Ferrifrons*, *Laminospondylus*, *Aethocephalichthys*, *Megalocoelacanthus*, Actinistia indet., *Archelon*, *Calcarichelys*, *Chelosphargis*, *Chedighaii*, *Lophochelys*, *Prionochelys*, *Protostega*, *Dolichorhynchops*, *Elasmosaurus*, *Polycotylus*, *Styxosaurus*, *Ectenosaurus*, *Halisaurus*, *Lestosaurus*, *Liodon*, *Mosasaurus*, *Plesioplatecarpus*, *Prognathodon*, *Nyctosaurus*, Pterosauria indet., *Cionodon*, *Hadrosaurus*, *Hierosaurus*, *Niobrarasaurus*, Ornithischia indet., *Baptornis*, *Graculavus*, *Paraesperornis*, and Reptilia indet.

**Table 3.** List of identified taxa from the examined Niobrara bonebed organized from the most abundant to the least abundant by number of specimens collected, compared with those taxa represented in seven major museum collections as well as effects of combining the bonebed data with the museum data. Taxa with the same percentage values due to rounding are listed in the sequence of actual individual counts in descending order based on Table 1 and Appendix 2.

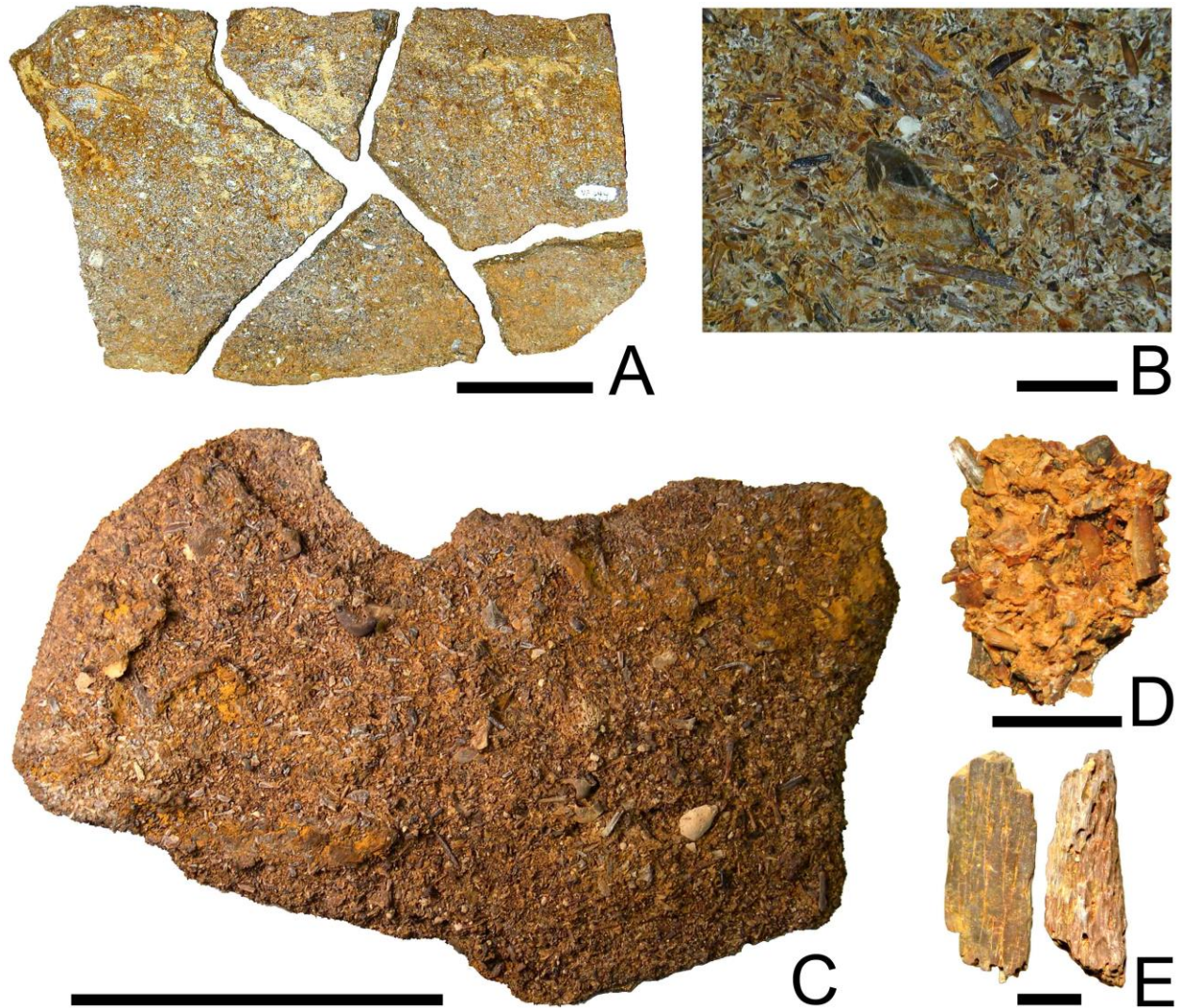
Bonebed	Museum collections	Combined
<i>Enchodus</i> (93.7%)	<i>Platecarpus</i> (24.2 %)	<i>Enchodus</i> (88.1%)
<i>Pachyrhizodus</i> (4.6%)	<i>Enchodus</i> (13.2%)	<i>Pachyrhizodus</i> (4.8%)
<i>Rhinobatos</i> (0.5%)	<i>Protosphyraena</i> (11.7%)	<i>Platecarpus</i> (1.7%)
Acanthomorpha <sup>1</sup> (0.5%)	Acanthomorpha <sup>1</sup> (10.6%)	Acanthomorpha <sup>1</sup> (1.2%)
Hesperornithiformes (0.2%)	<i>Cimolichthys</i> (10.1%)	<i>Protosphyraena</i> (0.8%)
Saurodontidae (<0.1%)	Anacoracidae <sup>2</sup> (8.2%)	<i>Cimolichthys</i> (0.7%)
Anacoracidae <sup>2</sup> (<0.1%)	<i>Pachyrhizodus</i> (7.3%)	Anacoracidae <sup>2</sup> (0.6%)
Pycnodontidae (<0.1%)	<i>Ichthyodectes</i> (6.0%)	<i>Rhinobatos</i> (0.5%)
<i>Stratodus</i> (<0.1%)	Hesperornithiformes (3.3%)	Hesperornithiformes (0.4%)
Plethodidae <sup>4</sup> (<0.1%)	Saurodontidae (2.6%)	<i>Ichthyodectes</i> (0.4%)
Lepisosteidae (<0.1%)	Plethodidae <sup>4</sup> (1.0%)	Saurodontidae (0.3%)
<i>Cimolichthys</i> (<0.1%)	<i>Stratodus</i> (0.7%)	Plethodidae <sup>4</sup> (0.1%)
<i>Platecarpus</i> (<0.1%)	<i>Rhinobatos</i> (0.4%)	Pycnodontidae (0.1%)
<i>Apateodus</i> <sup>3</sup> (<0.1%)	Pycnodontidae (0.4%)	<i>Stratodus</i> (<0.1%)
<i>Protosphyraena</i> (<0.1%)	<i>Apateodus</i> <sup>3</sup> (0.2%)	Lepisosteidae (<0.1%)
<i>Ichthyodectes</i> (<0.1%)	Albulidae (0.1%)	<i>Apateodus</i> <sup>3</sup> (<0.1%)
Albulidae (<0.1%)	Lepisosteidae (<0.1%)	Albulidae (<0.1%)

<sup>1</sup>Includes Beryciformes indet., *Kansius*, *Omosoma*, and *Ferrifrons*; <sup>2</sup>includes *Nanocorax* and *Squalicorax*; <sup>3</sup>includes Ichthyotringidae(?); <sup>4</sup>includes *Dixonangomius*.

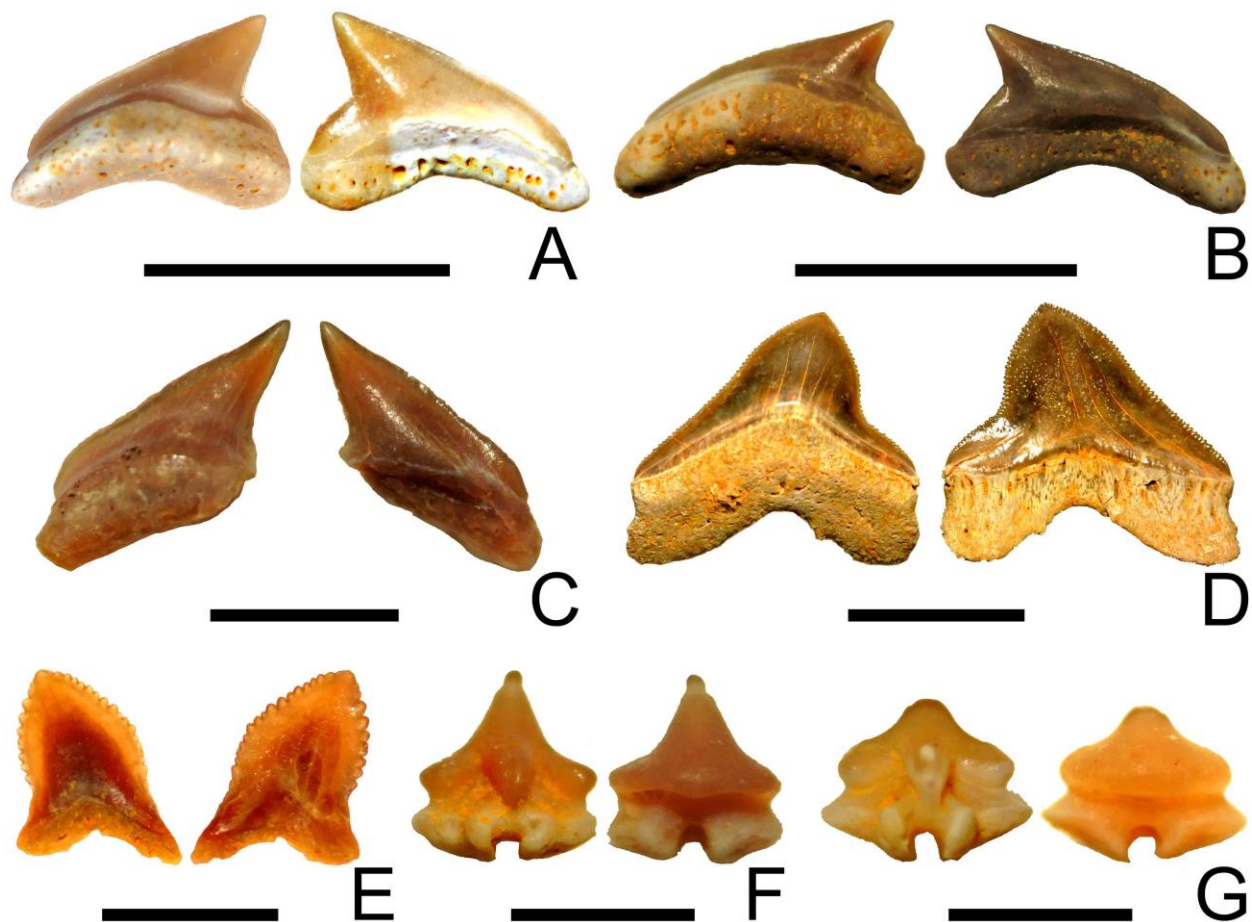


**Figure 1.** Geographic and stratigraphic settings. **A**, paleogeographic map showing possible extent of Western Interior Seaway during mid-Santonian (modified from Slattery et al., 2015, figs. 13, 14), showing approximate location of where FHSM VP-644 was collected (X mark); **B**, generalized stratigraphic column of Smoky Hill Chalk Member of Niobrara Chalk in western Kansas (modified from Everhart, 2011, fig. 3), showing the range of possible horizon where FHSM VP-644 was collected (MU = Marker Units of Hattin, 1982).

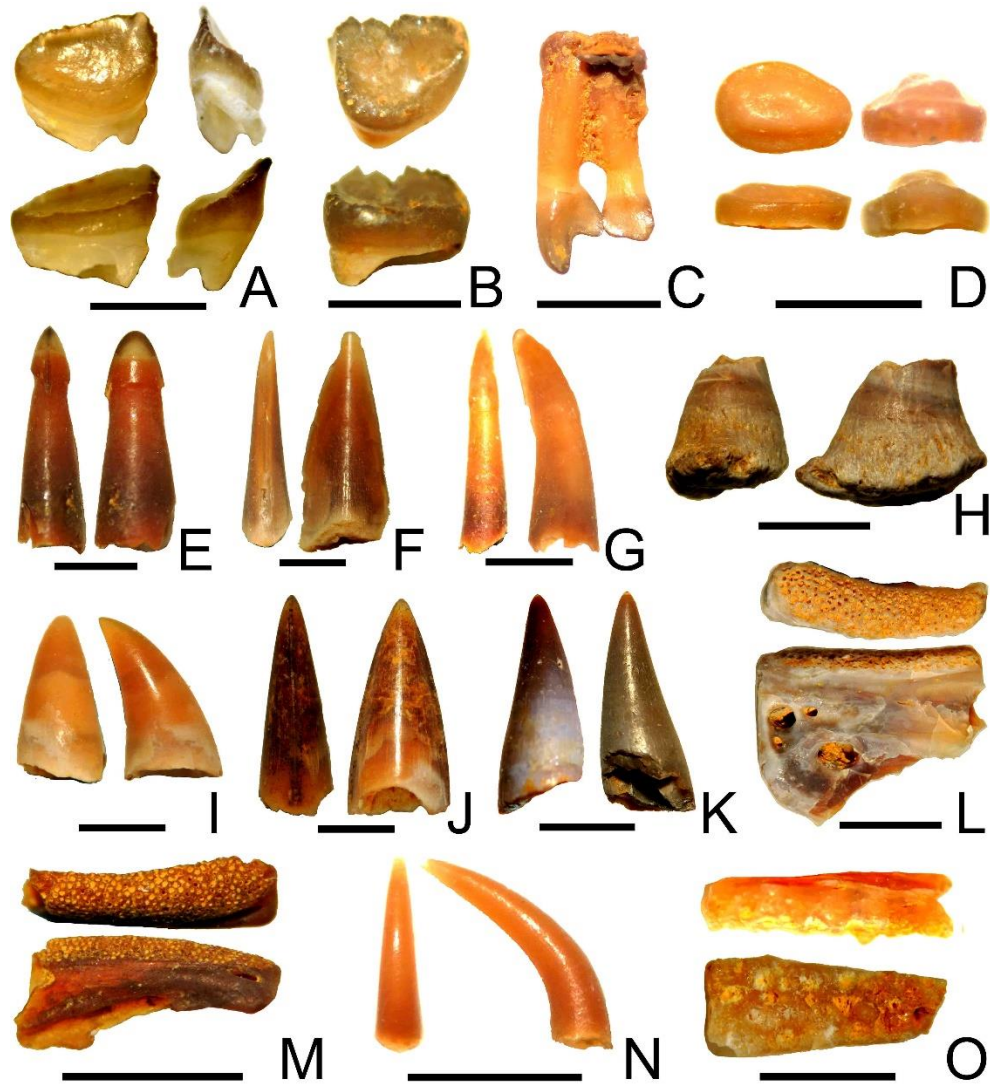




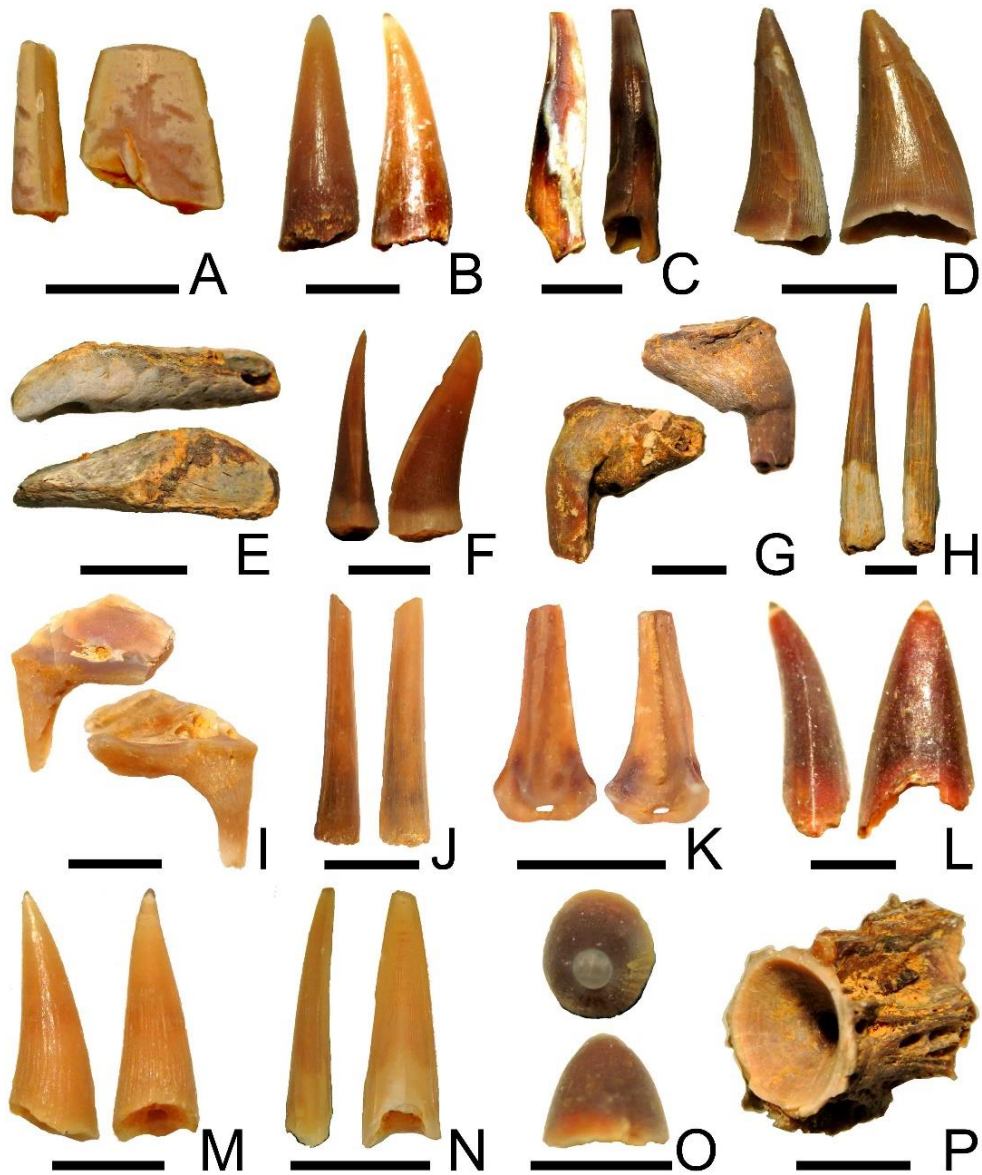
**Figure 2.** Examined bonebed sample from Niobrara Chalk of western Kansas (FHSM VP-644 and its derivatives). **A**, original condition of FHSM VP-644 broken into five segments (top right slab, that is now FHSM VP-644 sensu stricto, is preserved as is); **B**, close-up view of one section of original sample (center = *Squalicorax* tooth; many elongate pieces = *Enchodus* teeth); **C**, fossiliferous matrix partially treated with acetic acid (FHSM VP-19642 that is same as left-most slab in Fig. 1A); **D**, close-up view of partially acid-treated bonebed piece (FHSM VP-19643), showing numerous small bone and tooth fragments; **E**, two isolated fragmentary bones of Vertebrata indet. (FHSM VP-19644), representing the largest fossil elements from the bonebed sample. Scale bars: A, C = 10 cm; B = 1 cm; D, E = 5 mm.



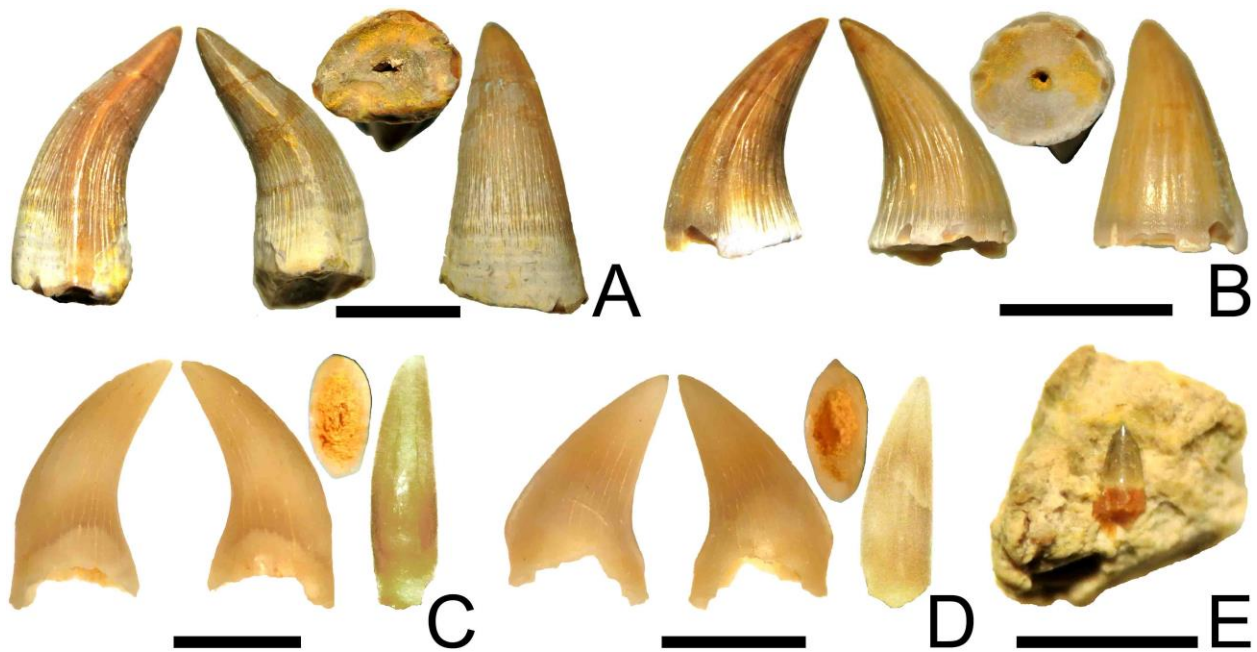
**Figure 3.** Representative chondrichthyan teeth from examined bonebed. **A**, tooth of *Nanocorax microserratodon* (FHSM VP-19648); **B**, tooth of *N. microserratodon* (FHSM VP-19649); **C**, tooth of *Squalicorax* cf. *S. pawpawensis* (FHSM VP-19651); **D**, tooth of *Squalicorax* cf. *S. falcatus* (FHSM VP-19652); **E**, tooth of *S.* cf. *S. falcatus* (FHSM VP-19653); **F**, male tooth of *Rhinobatos incertus* FHSM VP-19655); **G**, female tooth of *R. incertus* (FHSM VP-19656). Orientations: A–G = lingual (left) and labial (right) views. Scale bar = A, B, D = 5 mm; C, E–G = 1 mm.



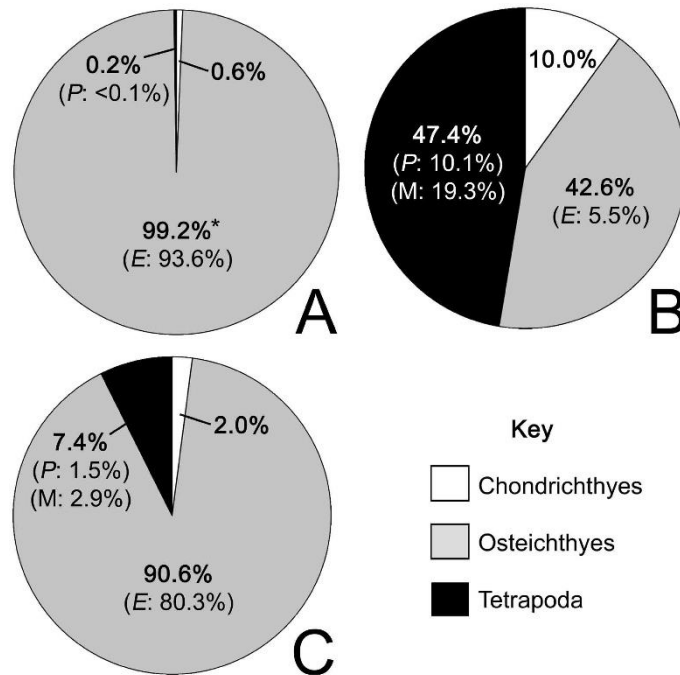
**Figure 4.** Representative osteichthyan teeth from examined bonebed (see also Fig. 5). **A**, molariform tooth of cf. *Palaeobalistum* sp. (FHSM VP-19660); **B**, molariform tooth of cf. *Palaeobalistum* sp. (FHSM VP-19661); **C**, pair of premaxillary incisoriform teeth of cf. *Palaeobalistum*(?) sp. (FHSM VP-19663); **D**, molariform tooth of Pycnodontidae indet. (FHSM VP-19665); **E**, tooth of Lepisosteidae indet. (FHSM VP-19658); **F**, tooth of *Protosphyraena* sp. (FHSM VP-19668); **G**, tooth of non-teleostean(?) Actinopterygii incertae sedis (FHSM VP-19667); **H**, tooth of *Pachyrhizodus caninus* (FHSM VP-19670); **I**, tooth of *Pachyrhizodus minimus* (FHSM VP-19672); **J**, tooth of Saurodontidae indet. (FHSM VP-19674); **K**, tooth of *Ichthyodectes ctenodon* (FHSM VP-19676); **L**, left dentary of *Dixonangomius* sp. (FHSM VP-19678); **M**, right dentary of Plethodidae indet. (FHSM VP-19679); **N**, tooth of Plethodidae indet. (FHSM VP-19681); **O**, vomerine tooth plate of Albulidae indet. (FHSM VP-19683). Orientations: A, D (clockwise from top left) = occlusal, anterior, posterior, and medial views; B, occlusal (top) and view (bottom) views; C = lingual view; E–K, N = anterior/labial (left) and profile (right); L (anterior to the left) = occlusal (top) and left lateral (bottom) views; M, O (anterior to the right) = occlusal (top) and right lateral (bottom) views. Scale bar: A–E, I, N, O = 1 mm; F, G, J, L, M = 2 mm; H, K = 4 mm.



**Figure 5.** Representative osteichthyan teeth from examined bonebed (see also Fig. 4). **A**, tooth of *Apateodus* sp. (FHSM VP-19684); **B**, tooth of Ichthyotringidae(?) indet. (FHSM VP-19686); **C**, tooth of *Stratodus*(?) sp. (FHSM VP-19687); **D**, tooth of *Cimolichthys nepaholica* (FHSM VP-19689); **E**, palatine bone of *Enchodus gladiolus* (FHSM VP-19691); **F**, tooth of *E. gladiolus* (FHSM VP-19693); **G**, palatine bone of *E. petrosus* (FHSM VP-19695); **H**, tooth of *E. petrosus* (FHSM VP-19697); **I**, palatine bone of *E. shumardi* (FHSM VP-19699); **J**, tooth of *E. shumardi* (FHSM VP-19701); **K**, fin spine of Acanthomorpha indet. (FHSM VP-19704); **L**, tooth of Teleostei indet. ‘Type A’ (FHSM VP-19706); **M**, tooth of Teleostei indet. ‘Type C’ (FHSM VP-19708); **N**, tooth of Teleostei indet. ‘Type F’ (FHSM VP-19710); **O**, tooth of Teleostei indet. ‘Type G’ (FHSM VP-19712); **P**, vertebra of Teleostei indet. (FHSM VP-19713). Orientations: A–D, F, H, J, L, M, N = anterior (left) and profile (right) views; E, G, I = lateral (top) and medial (bottom) views; K = anterior (left) and posterior (right) views; O = occlusal (top) and profile (bottom) views; P = anterodorsal oblique view. Scale bars: A, C, F, G, K = 2 mm; B, L, M, O = 1 mm; D, E, P = 5 mm; H–J, N = 3 mm.



**Figure 6.** Representative tetrapod teeth and coprolite from examined bonebed. **A**, tooth of *Platecarpus tympaniticus*(?) (FHSM VP-19716); **B**, tooth of *P. tympaniticus*(?) (FHSM VP-19717); **C**, tooth of Hesperornithiformes indet. (FHSM VP-19719); **D**, tooth of Hesperornithiformes indet. (FHSM VP-19720); **E**, coprolite of Vertebrata(?) incertae sedis, containing crown tip of possible *Enchodus* tooth (FHSM VP-19722). Orientations: A, B (from left to right) = mesial, distal, basal, and anterior views; C, D (from left to right) = lingual, labial, basal, and anterior views. Scale bar = A, B = 5 mm; C–E = 1 mm.



**Figure 7.** Pie charts showing relative abundances of chondrichthyan, osteichthyan, and tetrapod taxa, as well as *Enchodus* (E), *Platecarpus* (P), and all mosasaur individuals combined (M). **A**, bonebed examined in this study (n=40,450; based on Table 1; asterisk [\*] = rounding 99.14%); **B**, compilation of museum collection data (n=7,212; based on Appendix 1); **C**, museum collection data (B) combined with bonebed data (A) (n=47,662).



**Figure 8.** Sample close-up view of unsorted bonebed sediment sample (FHSM VP-19647) demonstrating numerous *Enchodus* teeth (arrows) that were not included in Table 1 or comparative analyses (Table 3; Fig. 7). Note that the vast majority of other particles in the photograph are unidentifiable fragmentary teleost bones. Scale bar = 2 mm.

**Appendix 1.** Minimum number of individuals for each vertebrate taxon from the Niobrara Chalk of Kansas represented in museum collections (see Materials and Methods for institutional abbreviations; the list contains a small number of fossils from the Fort Hays Limestone, including those described by Shimada, 1996, and Shimada and Everhart, 2003). Each count represents each catalog lot, where the presumption that different skeletal or dental elements from one animal are typically not cataloged separately, except for the following specific catalog lots that were interpreted to have come from multiple individuals or required taxonomic adjustments: *Ptychodus* = two teeth cataloged under a total of one catalog lot counted separately (FMNH UF 914); *Cretoxyrhina* = a total of 42 teeth cataloged under seven catalog lots counted separately (KUVP 40337, 40346, 49521, 55291; YPM 042105, 060154, 030235), and a total of nine questionable teeth from two catalog lots counted as Lamniformes indet. (KUVP 68982, 82933); *Cretalamna* = two teeth cataloged under one catalog lot counted separately (KUVP 40339); a total of nine teeth cataloged under KUVP 64541–64549 considered as *Cretoxyrhina* (see Shimada and Fielitz, 2006); *Squalicorax* = a total of 43 teeth cataloged under nine catalog lots counted separately (KUVP 40338, 40347, 49522, 55346; YPM 059678, 059116, 056409, 060038, 059110), and two teeth from two catalog lots counted as Lamniformes indet. (KUVP 84877, 84878); *Paraliodesmus* = a total of nine individuals preserved on inoceramid bivalve shells cataloged under two catalog lots counted separately (FMNH PF 14383; KUVP 66123); *Protosphyraena* = three teeth cataloged under one catalog lot counted separately (KUVP 40340); *Kansanus* = five individuals preserved on an inoceramid shell cataloged under one catalog lot counted separately (NMNH 18259); *Enchodus* = 19 palatine bones cataloged under KUVP 835 and eight mandibles under KUVP 67880 counted separately; *Omosoma* = a total of 94 individuals preserved on an inoceramid shell cataloged under three catalog lots counted separately (FMNH PF 3040; KUVP 32398, 65738); Holocentridae (Beryciformes) = a total of six individuals preserved on inoceramid bivalve shells cataloged under three catalog lots counted separately (KUVP 345, 36248, 60602); ‘*Inocentrus*’ (Beryciformes) = a total of 125 individuals preserved on inoceramid shells under seven catalog lots counted separately (KUVP 57261, 60601, 65699, 65700, 65701, 66122, 80813).

Taxon	Total	AMNH	FHSM	FMNH	KUVP	LACM	NMNH	YPM
Holocephali ( <i>Eumylodus</i> )	1		1					
<i>Ptychodus</i>	128	13	70	2	23	2	9	9
<i>Scapanorhynchus</i>	15		10		3			2
<i>Johnlongia</i>	3		2					1
<i>Cretoxyrhina</i> <sup>1</sup>	200	5	55		83	13	2	42
<i>Cretalamna</i>	39	4	17		8	5		5
<i>Pseudocorax</i>	6		4		2			
<i>Squalicorax</i> <sup>2</sup>	248	6	66	2	122	16	2	34
<i>Rhinobatos</i>	12		7		4	1		
Chondrichthyes indet. <sup>3</sup>	67	7	8	1	26	25		
<i>Anomoeodus</i>	1		1					
<i>Micropycnodon</i>	11		5		5			1
Pycnodontiformes indet. <sup>4</sup>	11		1				1	9
<i>Paraliodesmus</i>	22		3	3	11	4	1	
Lepisosteidae ( <i>Lepisosteus</i> )	1				1			



<i>Bonnerichthys</i> <sup>5</sup>	19		18		1			
<i>Protosphyraena</i> <sup>6</sup>	354	48	44	5	180	14	8	55
Pachycormiformes indet.	3		2					1
<i>Apsopelix</i>	29	4	6	1	12	5	1	
<i>Pachyrhizodus</i> <sup>7</sup>	220	43	20	5	93	17	9	33
<i>Gillicus</i>	111	22	3	9	59	5	1	12
<i>Prosaurodon</i>	2					2		
<i>Saurocephalus</i>	41	21	5	1	12			2
<i>Saurodon</i>	80	2	14	4	34	9	1	16
<i>Ichthyodectes</i>	181	60	13	3	48	5	3	49
<i>Xiphactinus</i>	463	150	29	8	95	9	13	159
Ichthyodectiformes indet.	154		13		14		2	125
<i>Bananogmius</i> <sup>8</sup>	70	27		4	35	3	1	
<i>Luxilites</i>	1				1			
<i>Martinichthys</i>	61	1	36		14	10		
<i>Niobrara</i>	3				3			
<i>Pentanogmius</i>	26		4		17			5
<i>Thryptodus</i>	6	1	4		1			
<i>Zanclites</i>	1				1			
Plethodidae indet. <sup>9</sup>	29	2	5		13	9		
<i>Palelops</i>	1			1				
Albulidae indet.	4			1	3			
<i>Urenchelys</i>	3		1		2			
<i>Anguillavus</i>	1				1			
<i>Apateodus</i>	7	1			2	1		3
<i>Letpecodon</i>	2		1		1			
<i>Stratodus</i>	22	2		1	11	1	1	6
Aulopiformes indet. <sup>10</sup>	47	6	1					40
<i>Cimolichthys</i>	304	107	17	2	76	11	12	79
<i>Enchodus</i> <sup>11</sup>	398	32	35	5	272	21	4	29
<i>Omosoma</i>	101	1	1	25	73	1		
<i>Kansius</i>	28	1	4		23			
Beryciformes indet. <sup>12</sup>	191		2		172	10	6	1
<i>Ferrifrons</i>	1				1			
<i>Laminospondylus</i>	1				1			
<i>Aethocephalichthys</i>	3		3					
Actinopterygii indet. <sup>13</sup>	54	11		4	34	4	1	
<i>Megalocoelacanthus</i> <sup>14</sup>	1	1						
Actinistia indet. <sup>15</sup>	4				2	2		
<i>Archelon</i>	3			1				2
<i>Calcarichelys</i>	1			1				
<i>Chelosphargis</i>	14	1		6	5			2
<i>Chedighaii</i>	1							1
<i>Ctenochelys</i>	48	37		2	3	3	3	
<i>Lophochelys</i>	6			5				1
<i>Prionochelys</i>	1			1				

<i>Protostega</i>	28	5	6	3	9	2	3	
<i>Toxochelys</i>	138	18	15	13	32	10	13	37
Testudines indet.	87	1	18		10			58
<i>Dolichorhynchops</i>	3		1		1		1	
<i>Elasmosaurus</i>	4				2			2
<i>Polycotylus</i>	25	3	1	1	7		1	12
<i>Styxosaurus</i>	2				1			1
Plesiosauroidea indet. <sup>16</sup>	49	4	12	6	1	2	2	22
<i>Clidastes</i>	251	45	25	5	9	2	18	147
<i>Ectenosaurus</i>	3		2			1		
<i>Halisaurus</i>	1						1	
<i>Lestosaurus</i>	2						2	
<i>Liodon</i>	1							1
<i>Mosasaurus</i>	18		3		6			9
<i>Platecarpus</i>	731	86	26	17	26	4	49	523
<i>Plesioplatecarpus</i>	16		6					10
<i>Prognathodon</i>	1	1						
<i>Tylosaurus</i>	349	56	37	4	20	8	35	189
Squamata indet. <sup>17</sup>	545		61	2	11	3		468
<i>Nyctosaurus</i>	16	3		1	5	1		6
<i>Pteranodon</i> <sup>18</sup>	844	60	52	6	179	19	19	509
Pterosauria indet.	5							5
<i>Cionodon</i>	1	1						
<i>Hadrosaurus</i>	3		1					2
<i>Hierosaurus</i>	1							1
<i>Niobrarasaurus</i>	5		5					
Ornithischia indet. <sup>19</sup>	3	1		1				1
<i>Baptornis</i>	5	1		1			3	
<i>Graculavus</i>	2							2
<i>Hesperornis</i>	99	28			7	5	15	44
<i>Ichthyornis</i>	93	1			19			73
<i>Parahesperornis</i>	2						1	1
Reptilia indet.	13				4	2	7	

<sup>1</sup>Includes '*Isurus*'; <sup>2</sup>includes '*Galeocerdo*' or '*Carcharhinus*'; <sup>3</sup>includes '*Odontaspis*', '*Paranomotodon*' described by Shimada (1996); 'Lamniformes indet.', '*Galeorhinus*', 'Selachimorpha indet.' or '*Aetobatus*'; <sup>4</sup>includes '*Mesodon*'; <sup>5</sup>includes '*Ichthyriapus*'; <sup>6</sup>includes '*Erisichthe*' and '*Pelecopterus*'; <sup>7</sup>includes '*Eurychir*', '*Kansanus*', and '*Oricardinus*'; <sup>8</sup>includes '*Anogmius*'; <sup>9</sup>includes 'Tselfatiiformes indet.'; <sup>10</sup>includes '*Benthesikyme*' and '*Ichthyotringa*'; <sup>11</sup>includes '*Tetheodus*'; <sup>12</sup>includes '*Caproberyx*', '*Inocentrus*', '*Trachichthyoides*', and 'Holocentridae indet.'; <sup>13</sup>includes '*Belonostomus*', '*Cionichthys*', '*Leptichthyes*', '*Sardinius*', '*Spaniodon*', 'Clupeiformes indet.', 'Crossognathiformes indet.', 'Myctophiformes indet.' and 'Teleostei indet.'; <sup>14</sup>based on Dutel et al., (2012) that was not included in analyzed database; <sup>15</sup>includes '*Macropoma*'; <sup>16</sup>includes '*Thalassiosaurus*'; <sup>17</sup>includes '*Coniasaurus*'; <sup>18</sup>includes '*Pterodactylus*'; <sup>19</sup>includes '*Polygonax*'.

**Appendix 2.** Minimum number of individuals by taxa that are only represented in the bonebed fauna (Table 1) compared to the museum collection data (Appendix 1).

Taxa	Bonebed	Museum collections
Chondrichthyes		
Anacoracidae ( <i>Nanocorax</i> and <i>Squalicorax</i> )	34	248
<i>Rhinobatos</i>	219	12
Osteichthyes		
Pycnodontidae	32	11
Lepisosteidae	16	1
<i>Protosphyraena</i>	2	354
<i>Pachyrhizodus</i>	1,874	220
Saurodontidae	40	80
<i>Ichthyodectes</i>	2	181
Plethodidae <sup>1</sup>	17	29
Albulidae	1	4
<i>Apateodus</i> <sup>2</sup>	4	7
<i>Stratodus</i> or cf. <i>Stratodus</i>	20	22
<i>Cimolichthys</i>	13	304
<i>Enchodus</i>	ca. 37,872	398
Acanthomorpha <sup>3</sup>	186	321
Tetrapoda		
<i>Platecarpus</i>	5	731
Hesperornithiformes	89	99
	Total = ca. 40,426	3,022

<sup>1</sup>Includes *Dixonangomius*; <sup>2</sup>includes Ichthyotringidae(?); <sup>3</sup>includes *Ferrifrons*, *Kansius*, *Omosoma*, and Beryciformes indet.