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A new marine vertebrate assemblage from the Upper Cretaceous Lincoln Limestone, Comanche National Grassland, southeastern Colorado, USA, with comments on the vertebrate assemblages at or near the contact between the Graneros Shale and Greenhorn Limestone in Colorado, Kansas, and Nebraska

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The Lincoln Limestone Member of the Greenhorn Limestone is an Upper Cretaceous sedimentary rock unit formed in the North American Western Interior Seaway during the Cenomanian Stage. Here we report a new Lincoln Limestone fossil vertebrate assemblage from the Comanche National Grassland in southeastern Colorado, USA. The fossil assemblage consists of at least 22 taxa, comprising minimally 11 chondrichthyans, 10 osteichthyans, and one squamate reptile. The new fossil assemblage is compared with other chronologically similar (i.e. putatively late middle-early late Cenomanian) vertebrate assemblages in Colorado, Kansas, and Nebraska, with a revised comparative taxonomic list of those assemblages. Examining stratigraphically well-constrained fossil assemblages shows differing environments and habitat preferences across the Western Interior Seaway. Deeper water localities (Colorado) versus localities nearer to the eastern shoreline (Nebraska) exhibit variation in lithologic and taxonomic compositions due to sea level change through time and space.

Keywords: Cenomanian, depositional environment, fossil fishes, fossil vertebrates, Western Interior Seaway

INTRODUCTION

The Western Interior Seaway (Fig. 1A), an epicontinental sea of North America during the Late Cretaceous, was a dynamic system that formed due to the tectonic uplift of the Rocky Mountains creating the Western Interior Basin, coincident with increased volcanism of mid-oceanic ridges that raised eustatic sea level and resulted in

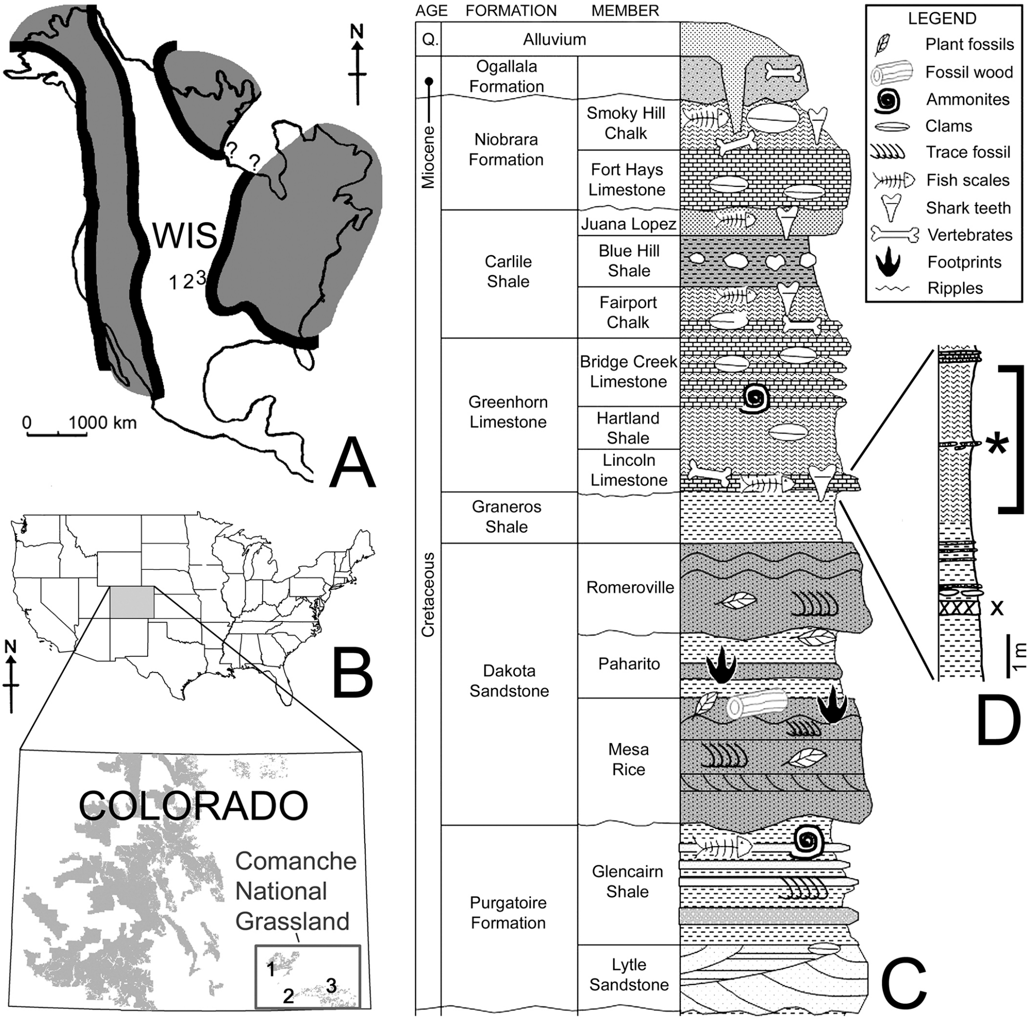

Figure 1. The geology and geographic setting of the fossil locality (Fultz Reservoir locality) examined in this study. A, mid-Cenomanian paleogeographic map of North America showing the Late Cretaceous Western Interior Seaway (WIS) and approximate position of (1) the 'Colorado assemblage' (i.e. Tobe, Table Mesa, and Fultz Reservoir localities combined: see Fig. 1B), (2) 'Kansas assemblage', and (3) 'Nebraska assemblage' discussed in this paper (mid-Cenomanian shorelines of WIS extrapolated based on late Albian and early Turonian maps of Kauffman 1984, figs. 8, 9). B, map of the United States (top) and Colorado (bottom) showing the three fossil localities within the general area of U.S. Forest Service Comanche National Grassland: 1, Fultz locality (this study); 2, Tobe locality (Shimada et al. 2006); and 3, Table Mesa locality (Gallardo, Shimada, and Schumacher 2012). C, general post-Jurassic stratigraphy in southeastern Colorado, USA. D, close-up view of near contact between Upper Cretaceous Graneros Shale and Greenhorn Limestone, showing the range of surface collected fossil samples (bracket) and calcarenite bed where rock samples were collected and treated with acid for fossil sampling (asterisk) described in this study (X mark = 'X bentonite': Hattin 1965, 1975).

transgressive and regressive pulses of ocean water covering the basin (Kauffman 1984; Kauffman and Caldwell 1993; Ogg, Hinnov, and Huang 2012; Slattery et al. 2015). The Greenhorn Limestone is a sedimentary formation of seafloor deposited beneath the Western Interior Seaway in the central United States (Hattin 1975; Kauffman and Caldwell 1993). The Lincoln Limestone Member is the basal-most stratigraphic unit of the Greenhorn Limestone and overlies the Graneros Shale. The Graneros and Lincoln Limestone represent the onset of a major seaway transgression, termed the Greenhorn Cyclothem during Cenomanian time. The Lincoln Limestone consists mainly of shaly chalk interbedded with many bentonite seams and beds and lenses of well-cemented calcarenite composed largely of inoceramid shell debris (Hattin, Siemers, and Stewart 1987). The origin of these calcarenite beds (or the so-called 'skeletal limestone' of Hattin 1975; Martin and Shimada 2008) is due to the winnowing action of marine wave and current energy (fossil lags) with the lowermost Lincoln Limestone commonly containing abundant skeletal and dental remains of sharks, bony fishes, marine reptiles, and even seabirds (e.g., Liggett et al. 2005; Shimada et al. 2006; Shimada and Martin 2008; Cumbaa, Shimada, and Cook 2010; Gallardo, Shimada, and Schumacher 2012; Bell and Everhart 2011; Shimada and Wilson 2016).

The Lincoln Limestone in southeastern Colorado contains fossiliferous lag deposits in the basal beds (e.g., Shimada et al. 2006; Gallardo, Shimada, and Schumacher 2012). Rock samples of this fossil-bearing horizon were collected from a previously undescribed locality, the 'Fultz Reservoir locality', on the Comanche National Grassland in southwestern Otero County, Colorado (Fig. 1B). In this study, we examine the taxonomic composition of fossil marine vertebrates in Fultz Reservoir rock samples and compare it to other fossil vertebrate assemblages at or near the contact between the Graneros Shale and Greenhorn Limestone in southeastern Colorado, central Kansas, and southeastern Nebraska (Fig. 1A). We present an updated taxonomic list of the assemblages and discuss broad biogeographical conclusions regarding the evolution of the Western Interior Seaway through time and space during the early phase of the Greenhorn Cyclothem.

MATERIALS AND METHODS

One of us (BAS) conducted geologic field surveys at the Fultz Reservoir locality ('1' in Fig. 1B) and discovered several isolated fossil shark teeth as surface float in the lowermost Lincoln Limestone (Fig. 1C, D). Subsequently, BAS collected samples of a 6-cm-thick fossiliferous calcarenite bed situated approximately 3.5 m above the 'X bentonite' (sensu Hattin 1965, 1975; Fig. 1C, D). The loose fossil teeth and rock samples were transferred to DePaul University in Chicago, Illinois, for study. Some rock pieces with one or more exposed fossil elements have been conserved without modification. Approximately 2.3 lbs (ca. 1 kg) of rock pieces were submerged in a 5% acetic acid solution (household vinegar) to remove most of the rock matrix (calcium carbonate invertebrate shell debris). The acetic acid solution was exchanged once or twice a week for a newer solution until all calcareous matrix was dissolved, requiring roughly 12 gallons (ca. 45 L) of acetic acid solution. The residual fossiliferous material was then rinsed with tap water, dried, and examined with a dissecting microscope. Extracted specimens were taxonomically identified based on morphological comparisons with Late Cretaceous vertebrate fossils described from the region in published literature (e.g., Shimada et al. 2006; Allan and Shimada 2022; Juranek and Shimada 2025), and representative specimens were photographed using a Nikon 1J1 digital camera through an ocular lens of a Zeiss Stemi DV4 stereo microscope. All specimens described in this paper and their exact locality information are curated and cataloged in the vertebrate paleontology (VP) collection of Fort Hays State University's Sternberg Museum of Natural History (FHSM) in Hays, Kansas.

Results

All fossil vertebrate specimens collected from near the base of the Lincoln Limestone at the Fultz Reservoir locality (Fig. 1) are isolated anatomical elements and are listed in Appendix 1 together with relevant literature and additional taxonomic notes where needed. Shimada et al.'s (2006) study provided an extensive review of each taxon from another Lincoln Limestone locality in southeastern Colorado (Tobe locality) and is used as a primary taxonomic reference because much of the content is still current and applicable.

The fossil vertebrate assemblage of the Fultz Reservoir locality consists minimally of 22 taxa based upon modest sampling, comprising at least 11 chondrichthyan and 10 osteichthyan fishes as well as one squamate reptile (note: the counts do not include tenuously identified taxa indicated by an asterisk in Appendix 1). One or two representative specimens of each taxon are depicted in Figures 2 and 3. Remains of the two species of *Enchodus*, *E. gladiolus* (64 palatine bones and 489 teeth) and *E. shumardi* (29 palatine bones and 224 teeth), dominate the collection by number, and the next most common taxon is *Pachyrhizodus minimus* (106 teeth) (Appendix 1). All other taxa are represented by no more than 40 specimens (Appendix 1). The collection also includes phosphatic pebbles interpreted as coprolites of uncertain vertebrate(?) origins (Appendix 1), and at least one of them contains fish bone fragments as inclusions (Fig. 3N).

Discussion

Almost all the taxa recovered from the Fultz Reservoir locality (Figures 2, 3; Appendix 1) have been reported from at least one other published Lincoln Limestone locality within Comanche National Grassland: the Tobe locality (Shimada et al. 2006) and Table Mesa locality (Gallardo, Shimada, and Schumacher 2012). The only exception is Aspidorhynchidae indet., which is new to the Lincoln Limestone in Colorado, but has been reported from the basal Lincoln Limestone in central Kansas (Shimada and Martin 2008) and the upper Turonian Juana Lopez Member of the Carlile Shale in southeastern Colorado (Wood et al. 2022). Although the fossil assemblage at Fultz Reservoir is taxonomically less diverse than other similar localities, this is likely due to the smaller sample size examined in this study (ca. 1 kg or 2.3 lbs) compared to the Tobe Locality (Shimada et al. 2006: ca. 45 kg or 100 lbs) and Table Mesa Locality (Gallardo, Shimada, and Schumacher 2012; ca. 2.3 kg or 5 lbs) studies.

The examination of the Fultz Reservoir fossil vertebrate assemblage provided an opportunity to review the vertebrate fossil record of the Lincoln Limestone in Colorado (collectively 'Colorado assemblage' hereafter) with other fossil assemblages similar in geography and time, most notably the fossil record of the basal Lincoln Limestone in central Kansas (e.g., Shimada and Martin 2008; 'Kansas assemblage' hereafter) and the uppermost Graneros Shale in southeastern Nebraska (Jansen, Shimada, and Kirkland 2012; 'Nebraska assemblage' hereafter). Such a review is necessary because taxonomic names reported in many of the previous studies include inconsistent expressions, outdated taxonomy, or even misidentifications. Figure 4 shows the stratigraphic position of the Colorado assemblage (gray line; entails Tobe, Table Mesa, and Fultz Reservoir assemblages), Kansas assemblage ('1'), and Nebraska assemblage ('2'), which were reviewed in this study.

The base of the Greenhorn Limestone represented by the base of the Lincoln Limestone Member is generally placed at the horizon where rocks become sharply calcareous (e.g., Hattin 1975; MacDonald and Byers 1988; see also Cobban and Scott 1972). Using this convention, the exact boundary between the noncalcareous Graneros Shale and the calcareous Greenhorn Limestone is gradational in southeastern Colorado, and the lag-type fossiliferous horizon is situated about 2.5 m above the Graneros-Greenhorn boundary. More importantly, the fossil horizons of the three Colorado localities are positioned in a relatively narrow range about 1.5-3.5 m above the 'X bentonite'

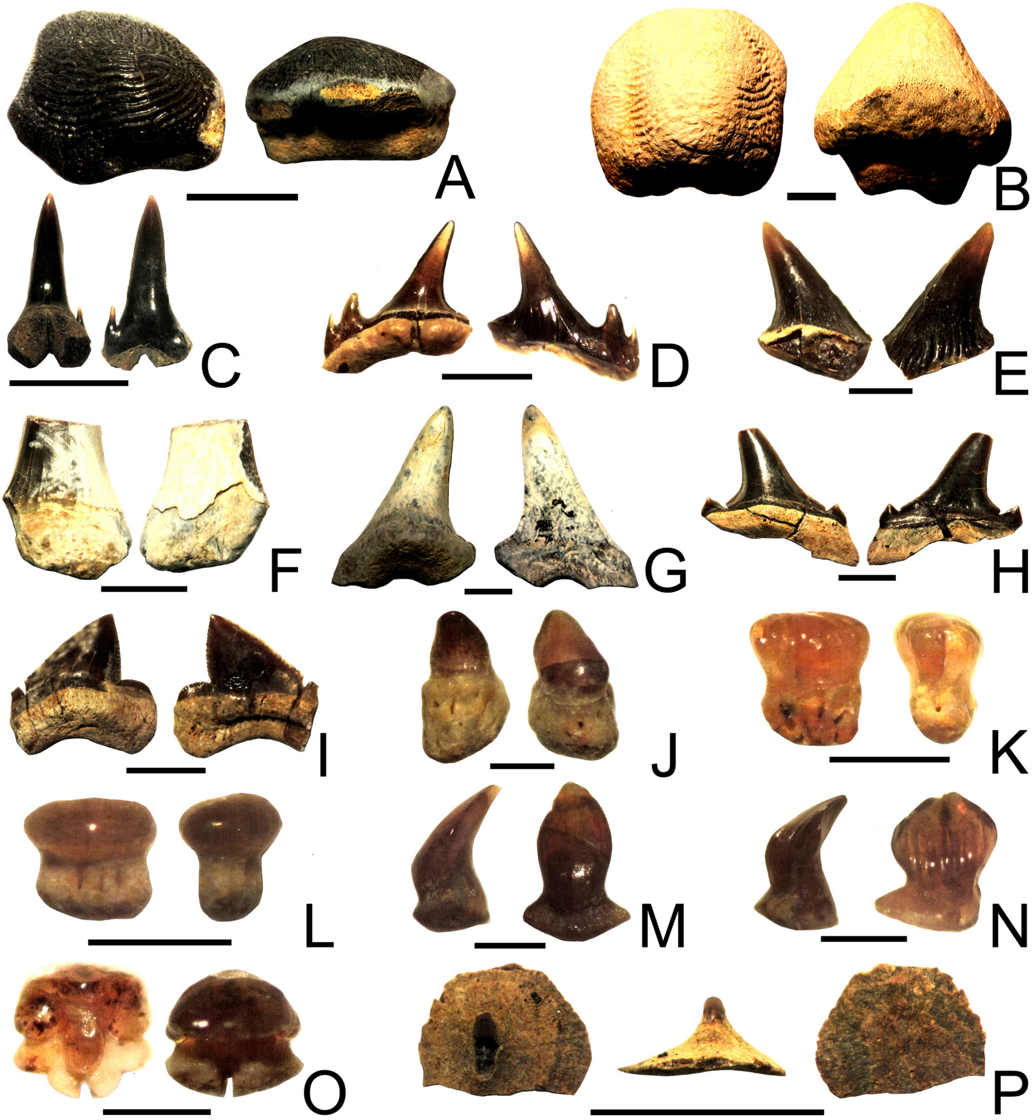

Figure 2. Chondrichthyan fossil remains from the Lincoln Limestone at Fultz reservoir locality in southeastern Colorado. A, *Ptychodus decurrens* (FHSM VP-19540, tooth); B, *Ptychodus occidentalis* (FHSM VP-19542, tooth); C, *Microcarcharias saskatchewanensis* (FHSM VP-19545, tooth); D, *Cenocarcharias tenuiplicatus* (FHSM VP-19547, tooth); E, *Cenocarcharias*(?) sp. (FHSM VP-19549, tooth); F, *Cretodus semiplicatus* (FHSM VP-19550, fragmentary tooth); G, *Cretoxyrhina mantelli* (FHSM VP-19551, tooth); H, *Archaeolamna cf. A. kopingensis* (FHSM VP-19554, tooth); I, *Squalicorax curvatus* (FHSM VP-19556, tooth); J, *Cretomanta canadensis* (FHSM VP-19559, tooth); K, Selachii indet. (Type B) (FHSM VP-19561, placoid scale); L, Selachii indet. (Type C) (FHSM VP-19562, placoid scale); M, Selachii indet (Type D) (FHSM VP-19564, placoid scale); N, Selachii indet. (Type E) (FHSM VP-19566, placoid scale); O, *Rhinobatos inertus* (FHSM VP-19558, tooth); P, Batomorphii indet. (FHSM VP-19568, dermal denticle). Orientations: A, B = occlusal and anterior views; C-J, O = lingual and labial views; K-N, profile and anterior views; P = apical, anterior, and basal views. Scale bars: A-C, F-I, P = 5 mm; D, E = 1 mm; J-O = 0.5 mm.

Figure 3. Osteichthyan, reptilian, and coprolitic remains from the Lincoln Limestone at Fultz Reservoir locality in southeastern Colorado. A, *Palaeobalistum* sp. (FHSM VP-19569, tooth); B, Aspidorhynchidae indet. (FHSM VP-19571, tooth); C, Plethodidae indet. (FHSM VP-19573, tooth); D, *Pachyrhizodus minimus* (FHSM VP-19575, tooth); E, *Enchodus gladiolus* (FHSM VP-19577, left palatine bone); F, *Enchodus gladiolus* (FHSM VP-19579, tooth); G, *Enchodus* cf. *E. shumardi* (FHSM VP-19581, left palatine bone); H, *Enchodus* cf. *E. shumardi* (FHSM VP-19583, tooth); I, Albulidae indet. (FHSM VP-19585, tooth plate); J, Osteichthyes indet. (Type A) (FHSM VP-19586, tooth); K, Osteichthyes indet. (Type B) (FHSM VP-19588, tooth); L, Osteichthyes indet. (Type C) (FHSM VP-19590, tooth); M, Dolichosauridae indet. (FHSM VP-19593, tooth); N, Vertebrata (?) indet. (FHSM VP-19596, coprolite with osteichthyan bones). Orientations: A = occlusal, basal, and lateral views; B, F, H, J-M = labial, profile, and lingual views; C, D = anterior and profile views; E, G, left lateral view; I = profile and occlusal views; N = freshly broken surface. All scale bars = 1 mm.

(sensu Hattin 1965, 1975), a basin-wide, chronological time stratigraphic marker (volcanic ash) that has been dated to 95.11 ± 0.16 Ma (Shimada et al. 2006) at the type section of the Greenhorn Limestone in Pueblo County, Colorado (see Cobban and Scott 1972), and 95.53 ± 0.15 Ma in Russell County, Kansas, based on 40Ar/39Ar dating (note: 95.87 ±0.10 Ma based on U/Pb dating by Barker et al. (2011); 95.53 ±0.25 for Ar/Ar dating referenced by Schmitz (2020) for Soap Creek Bentonite, which is equivalent to X bentonite per Cobban and Scott (1972)). Whereas the X bentonite occurs within the upper part of the Graneros Shale in central Kansas-southeastern Nebraska (Fig. 4), it is situated within the lowermost Lincoln Limestone at the Tobe and Table Mesa localities in southeastern Colorado (Shimada et al. 2006; Gallardo, Shimada, and Schumacher 2012) and within the uppermost Graneros Shale at the Fultz Reservoir locality (BAS field notes and measured sections; see also Fig. 1D).

The fossiliferous lag calcarenites at the Tobe, Table Mesa, and Fultz Reservoir localities are somewhat variable in lithology and precise position, but geochronological differences (if any) are considered negligible. They are all situated slightly above the X bentonite within the seemingly continuously bedded Lincoln Limestone without any marked disconformity that would indicate the presence of hiatus, other than the lag deposits themselves which include intermittent lenses and thin layers of coquinoidal limestone (see Fig. 4; Shimada et al. 2006). Based upon their stratigraphic position in relation to the X bentonite and comparisons with the invertebrate biostratigraphic index fossils for this interval across the Western Interior Basin (Kauffman et al. 1993), the three Colorado assemblages are collectively regarded to have formed during the late (or latest) part of the middle Cenomanian. In contrast, fossil vertebrates are sporadically present throughout the Lincoln Limestone in central Kansas (e.g., Shimada and Schumacher 2003), but the lag-type fossil concentrated beds occur in the basal-most portion of the Greenhorn Limestone, again just slightly above the X bentonite (Liggett et al. 2005; Shimada and Martin 2008; Bell and Everhart 2011; Shimada and Wilson 2016). The Graneros-Greenhorn contact in Kansas is represented by a sharp disconformity, indicating a considerable hiatus (Hattin 1965, 1975). Calcarenite beds of the Lincoln Limestone in central Kansas are 25–67 cm thick and directly overlie the erosional contact with the underlying Graneros Shale, and the X bentonite occurs 0.5-1 m below this disconformity (Hattin 1975; Martin and Shimada 2008). Fossils near the Graneros-Greenhorn contact in central Kansas have been interpreted as middle Cenomanian in age (e.g., Liggett et al. 2005) based upon stratigraphic position in relation to the X bentonite and most recent biostratigraphic information for this interval across the Western Interior basin (Kauffman et al. 1993). Uncertainty remains if upper Cenomanian beds may have eroded away and/or become partially disseminated within surviving basal beds during a period of non-deposition. Whereas fossils from the basal Lincoln Limestone beds in central Kansas have been interpreted as middle Cenomanian (e.g., Liggett et al. 2005) and the early part of the late Cenomanian (Shimada and Martin 2008), the prominent disconformity indicates that the 'basal Lincoln Limestone fossil assemblage' in central Kansas is likely a time-averaged, diachronous assemblage, to a higher degree than the Colorado localities.

Jansen, Shimada, and Kirkland's (2012) fossil fish assemblage in southeastern Nebraska is a fossiliferous lag horizon below the Graneros-Greenhorn contact, within the Graneros Shale about 0.5 m above the X bentonite. The Graneros Shale in central Kansas through southeastern Nebraska is generally considered middle or upper Cenomanian in age (Juranek and Shimada 2025, and references therein), and the stratigraphic position of the Nebraska assemblage is interpreted to be the upper (or upper-most) part of the middle Cenomanian. These geochronological interpretations, including those made for the central Kansas locality (see above), need further corroboration with invertebrate biostratigraphy and thus should be regarded as tentative. Nevertheless, the Nebraska assemblage is posited to be

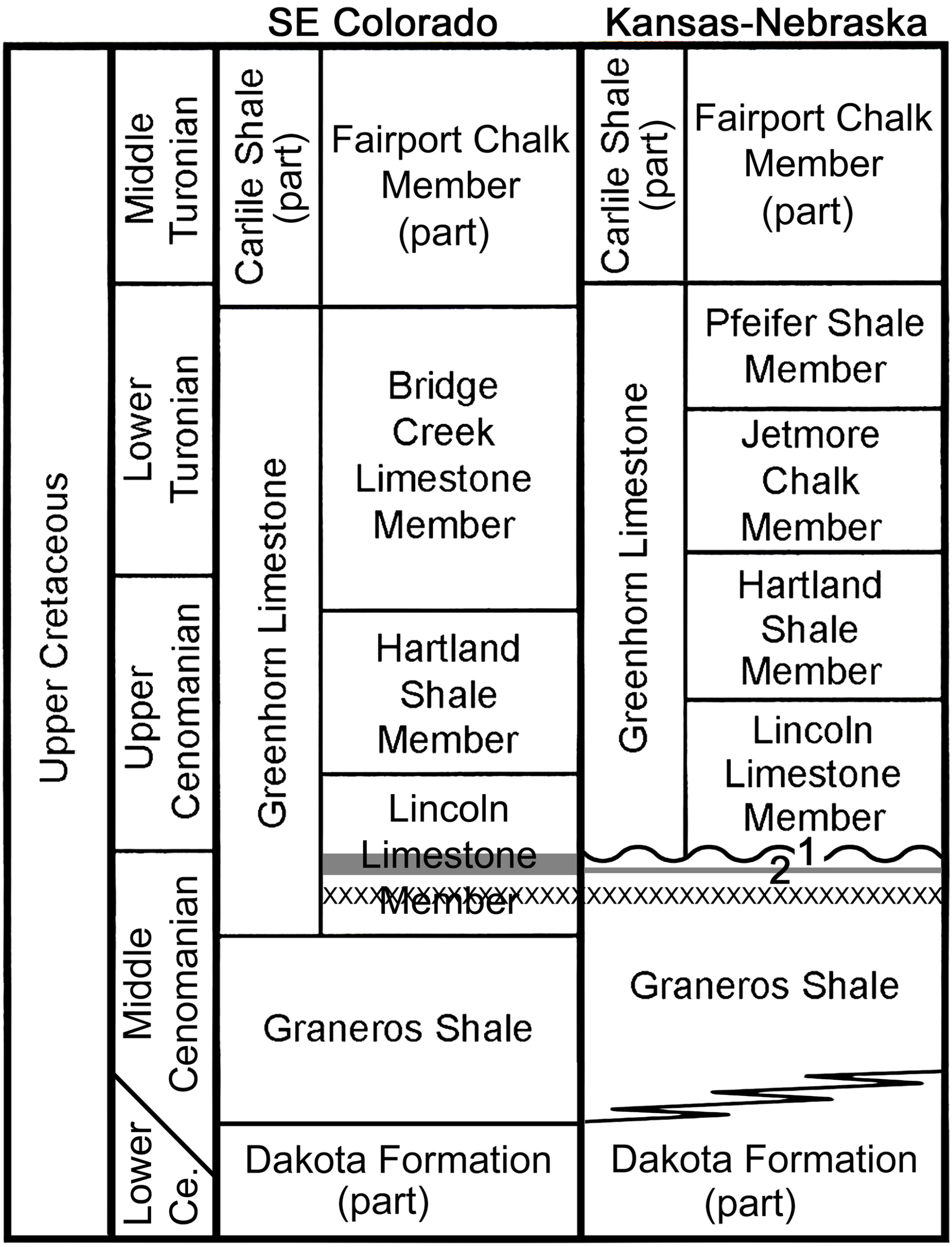

Figure 4. Partial Upper Cretaceous stratigraphy of southeastern Colorado as well as central Kansas through southeastern Nebraska. Series of X-symbols denotes Hattin's (1965, 1975) 'X bentonite', a time-correlative unit across the region (stratigraphic information based primarily on Hattin, Siemers, and Stewart 1987; Shimada et al. 2006; Nagrodski, Shimada, and Schumacher 2012; Juranek and Shimada 2025). Notes: Gray line within the Lincoln Limestone in southeastern Colorado denotes stratigraphic position of the three Lincoln Limestone localities (i.e.Tobe, Table Mesa, and Fultz

Figure 4. (continued)
Reservoir: see Fig. 1B); the wavy line denotes disconformity (‘1’) between the Lincoln Limestone and Graneros Shale in central Kansas, where the fossiliferous horizon has been studied in numerous locations by Liggett et al. (2005), Shimada and Martin (2008), Bell and Everhart (2011), and Shimada and Wilson (2016); the gray line (‘2’) within the Graneros Shale represents a fossiliferous horizon in southeastern Nebraska studied by Jansen, Shimada, and Kirkland (2012).

slightly older than the Kansas assemblage, and chronologically equivalent to the Colorado assemblage, even though the Colorado and Nebraska assemblages are from different lithologies at the Graneros-Greenhorn contact (i.e. Graneros Shale in Nebraska; Lincoln Limestone in Colorado).

Table 1 provides a summary of reported vertebrate taxa from the three Lincoln limestone localities in southeastern Colorado (Tobe [‘CO1’], Table Mesa [‘CO2’], and Fultz Reservoir [‘CO3’] localities) as well as the Colorado assemblage (i.e. composite data of the three Colorado localities [‘CO*]: upper middle Cenomanian) compared with the Kansas assemblage (‘KS’: lower upper Cenomanian) and Nebraska assemblage (‘NE’: upper middle Cenomanian). The Tobe, Table Mesa, and Fultz Reservoir localities have produced a minimum of 43, 28, and 22 vertebrate taxa, respectively. However, it is noted that the most intensively surveyed locality, the Tobe locality (Shimada et al. 2006), has the greatest number of taxa, and the least sampled locality, the Fultz Reservoir locality (this study) has the least diversity. Compilation of the three localities reveals that the Colorado assemblage (i.e. ‘CO*’) consists of minimally 49 vertebrate taxa, comprising 25 chondrichthyan, 19 osteichthyan, and five tetrapod taxa. The Kansas assemblage comprises at least 40 taxa consisting of 19 chondrichthyan, 14 osteichthyan, and seven tetrapod taxa, and the Nebraska assemblage at least 23 taxa consisting of 14 chondrichthyan and nine osteichthyan taxa. The Nebraska assemblage consists of fewer taxa than the Colorado and Kansas assemblages and does not include ‘large taxa’ or tetrapod taxa. The scope of the Nebraska study (Jansen, Shimada, and Kirkland 2012) was limited to fossil fishes with only small sediment samples examined under a microscope, relative to the more robust sampling for the Colorado and Kansas assemblages, which also include direct surface-collected fossil specimens and all fossil vertebrates found (e.g., Liggett et al. 2005; Shimada et al. 2006; Shimada and Martin 2008).

Two broad observations of faunal comparison gleaned from Table 1 are noteworthy. The overall taxonomic composition of fish taxa (chondrichthyans and osteichthyans) between the Colorado and Kansas assemblages is similar and substantially different from the Nebraska assemblage. The major difference is that the Nebraska assemblage includes several chondrichthyans that are not present in the Colorado or Kansas assemblages (e.g., *Meristodonoides* sp., *Chiloscyllium greeni, Scapanorhynchus raphiodon, Pseudohypolophus mcnultyi, Ptychotrygon triangularis*, and *Ischyrhiza texana*), although they that are common in other Upper Cretaceous shoreface deposits in North America (e.g., Cappetta 1973; Cicimurri 2004; Bice and Shimada 2016; Ouroumova, Shimada, and Kirkland 2016; Maisch, Becker, and Shimada 2021; Juranek and Shimada 2025). Also of note, the Kansas assemblage includes several aerial (‘flying’) vertebrates (e.g., pterosaur and avian taxa), while none have been recognized within the Colorado assemblage.

These two broad observations reflect facies variation and different ecosystems during the middle-late Cenomanian time of the Western Interior Seaway. Although the Colorado and Nebraska assemblages are contemporaneous (see above), the Colorado assemblage accumulated in the deepest part of the seaway while the Nebraska assemblage was deposited near the eastern shoreline (Fig. 1A). As the transgressive phase of the Greenhorn Cyclothem deepened and widened the seaway (i.e. including eastward migration of the eastern shoreline), open marine conditions responsible for the deposition of the Lincoln Limestone proper persisted across the basin in the late Cenomanian. Because Colorado localities are believed to be

Table 1. Revised list of marine vertebrate taxa reported from the basal part of the Lincoln Limestone from three localities in Comanche National Grassland in southeastern Colorado (Shimada et al. 2006, ‘Tobe’ locality [CO1]; Gallardo, Shimada, and Schumacher 2012, ‘Table Mesa’ locality [CO2]; this present study, ‘Fultz Reservoir’ locality [CO3]: see Fig. 1B), and the composite southeastern Colorado data [CO*] compared with the data of the basal Lincoln Limestone in central Kansas (KS: Liggett et al. 2005; Everhart 2007; Shimada and Martin 2008; Everhart and Bell 2009; Bell and Everhart 2011; Shimada and Wilson 2016) and the uppermost Graneros Shale in southeastern Nebraska (NE: Jansen, Shimada, and Kirkland 2012) (see Fig. 4). ‘X’ denotes ‘reported’, whereas ‘-’ denotes ‘unreported’. Taxa with a number in superscript are those with clarifications or additional notes given in Appendix 2.

Taxon	CO1	CO2	CO3	CO*	KS	NE
CHONDRICHTHYES						
Meristodonoides sp.	-	-	-	-	-	X
Chiloscyllium greeni	-	-	-	-	-	X
Cretorectolobus sp.	-	-	-	-	-	X
cf. *Pararhincodon* sp.	X	-	-	X	-	-
Scapanorhynchus raphiodon^{1}	-	-	-	-	-	X
Ptychodus anonymus^{2}	X	-	-	X	X	-
Ptychodus decurrens	X	-	X	X	X	-
Ptychodus occidentalis^{3}	X	X	X	X	X	-
Haimirichia amonensis^{4}	X	-	-	X	X	X
Microcarcharias saskatchewanensis^{5}	X	X	X	X	X	X
Cenocarcharias tenuiplicatus^{6}	X	X	X	X	X	X
Cenocarcharias sp.^{7}	-	-	X	X	-	-
Johnlongia cf. *J. parvidens*	X	-	-	X	-	-
Pseudomegachasma comanchensis^{8}	X	X	-	X	-	-
Cretodus semiplicatus	X	X	X	X	X	-
*Cardabiodon venator/*sp.^{9}	X	-	-	X	X	-
Cretoxyrhina mantelli	X	X	X	X	X	-
Archaeolamna cf. A. kopingensis^{10}	X	X	X	X	X	-
Teleodontaspis agassizensis^{11}	X	X	-	X	X	-
Cretalamna ‘appendiculata’^{12}	X	X	-	X	X	X
Microcorax crassus	X	-	-	X	-	-
Squalicorax curvatus^{13}	X	X	X	X	X	X
Squalicorax sp. (1)^{14}	X	-	-	X	X	-
Squalicorax sp. (2)^{14}	-	-	-	-	X	-
Cretomanta canadensis^{15}	X	X	X	X	X	X
Carcharhiniformes incertae sedis	X	-	-	X	-	-
Rhinobatos incertus^{16}	X	X	X	X	X	-
Rajidae incertae sedis (1)^{17}	-	X	-	X	-	-
Rajidae incertae sedis (2)^{17}	-	-	-	-	X	-

Pseudohypolophus mcnultyi	-	-	-	-	-	X
Onchopristis dunklei	-	-	-	-	X	X
Ischyrhiza texana[18]	-	-	-	-	-	X
Sclerorhinchidae(?) incertae sedis	X	-	-	X	-	-
Ptychotrygon triangularis	-	-	-	-	-	X
Ptychotrygon sp.	X	-	-	X	-	-
OSTEICHTHYES						
Micropycnodon kansasensis[19]	X	X	-	X	X	-
cf. "*Nursallia*" sp.	X	-	-	X	-	-
cf. *Palaeobalistum* sp.	X	-	X	X	-	-
Pycnodontidae indet.	-	X	-	X	-	-
Caturidae(?) indet.[20]	-	X	-	X	-	X
Aspidorhynchidae indet.[21]	-	-	X	X	X	X
Protosphyraena sp.	X	X	-	X	X	-
Nonteleostean(?) Actinopterygii (1)[22]	X	X	-	X	-	-
Nonteleostean(?) Actinopterygii (2)[22]	-	-	-	-	X	-
Plethodidae indet.[23]	X	X	X	X	X	X
Xiphactinus audax	X	-	-	X	X	-
Pachyrhizodus minimus[24]	X	X	X	X	X	X
cf. *Pachyrhizodus* sp.	X	-	-	X	X	-
Elopopsis sp.[25]	-	-	-	-	-	X
Albulidae incertae sedis[26]	X	X	X	X	X	-
cf. *Stratodus* sp.[27]	X	-	-	X	-	-
Enchodus gladiolus[28]	X	X	X	X	X	X
Enchodus shumardi[29]	X	X	X	X	X	X
Osteichthyes indet. (Type A)[30,31]	X	X	X	X	X	-
Osteichthyes indet. (Type B)[30,32]	X	X	X	X	X	X
Osteichthyes indet. (Type C)[30,33]	X	X	X	X	X	-
Osteichthyes indet. (Type E)[30,34]	-	-	-	-	-	X
TETRAPODA						
Dolichosauridae indet.[35]	X	X	X	X	X	-
Scincomorpha indet. (Contogeniidae?)[36]	-	X	-	X	-	-
Brachauchenius lucasi[37]	X	-	-	X	X	-
Polycotylidae indet.[38]	X	-	-	X	-	-
Plesiosauria indet.[39]	X	-	-	X	X	-
Pterosauria ('pteranodontoid') indet.	-	-	-	-	X	-
Baptornithidae indet.	-	-	-	-	X	-
cf. *Ichthyornis* sp.[40]	-	-	-	-	X	-
Aves ('ornithurine') indet.[41]	-	-	-	-	X	-

located within the deepest part of the basin, minor regressive pulses at the onset of the Greenhorn Cyclothem transgressive event did not result in any major disconformities such as the sharply demarcated Graneros-Greenhorn contact in Kansas and Nebraska. Nevertheless, regressive pulses did result in minor reworking and winnowing of the seafloor in southeastern Colorado, forming the fossiliferous lag horizon(s?), including the fact that the concentrated preserved fossils show different degrees of surface abrasion most likely due to their hydraulically induced tumbling and transportation (Shimada et al. 2006; Gallardo, Shimada, and Schumacher 2012; this study). Thus, the depositional surface immediately below each lag-type fossiliferous bed may be regarded as a small-scale disconformity in southeastern Colorado, even though bedding within the Lincoln Limestone generally appears continuous without any perceived lithologic anomalies. Other small-scale disconformities are signified by the common presence of thin layers, lenses, and elongate gutter casts of coquinoidal limestone formed of concentrated, unbroken oyster valves (*Ostrea beloiti*: e.g., see Shimada et al. 2006, fig. 4) and interpreted as winnowed scour features from wave action impinging on the seafloor. However, it should be clarified that regressive-transgressive pulses during deeper water phases of the Greenhorn Limestone did not result in intensive winnowing or disconformity of seafloor substrate, as exemplified by the conformably alternating calcareous shale and limestone beds of the Bridge Creek Limestone in Colorado and the Jetmore Chalk in Kansas (e.g., Hattin 1975; Elder and Kirkland 1985). Conversely, the central Kansas-southeastern Nebraska localities were situated near the eastern edge of the Western Interior Basin (Fig. 1A), and shallow conditions during middle-late Cenomanian regressive events resulted in more extensive reworking and winnowing of seafloor substrate. The fossils from these localities also show a wide range of surface abrasion likely from their hydraulically induced tumbling and transportation (Shimada and Martin 2008; Jansen, Shimada, and Kirkland 2012), although it is possible that the area could have even experienced episodes of aerial exposure. The presence of an evident erosional surface at the Graneros-Greenhorn contact in central Kansas-southeastern Nebraska, marked by a sharp disconformity (vs. the more continuous deposition of sediments in Colorado), likely formed through one or more such regressive episodes, followed by a major transgression that resulted in the deposition of the basal Lincoln Limestone. Similar depositional processes have also been reported for the upper Turonian Juana Lopez Member of the Carlile Shale, representing a distinct fossiliferous lag, that is immediately overlain by the massive limestone bed of the basal Niobrara Chalk at the onset of the Niobrara Cyclothem transgression (Hattin 1975; Schumacher and Everhart, 2022; Wood et al. 2022).

The occurrence of aerial vertebrates (e.g., pterosaur and avian taxa), that require terrestrial habitat, in central Kansas and their absence (at least so far) in the Colorado assemblages reflect that the Kansas assemblage was situated close to the eastern shoreline. However, the Kansas assemblage lacks taxa commonly found in other Upper Cretaceous nearshore deposits (see above), suggesting that central Kansas was a fully marine (offshore) environment during the deposition of the Lincoln Limestone, albeit shallower in water depth compared to southeastern Colorado. Hattin (1975) interpreted the presence of calcarenite in the basal Lincoln Limestone in Kansas to be evidence for “a relatively wide, high-energy, offshore zone of wave impingement” (p. 91) on the bottom of the seaway during the transgressive phase of the Greenhorn Cyclothem. Depositional conditions of the Colorado assemblage were similar but took place in a deeper marine environment (Shimada et al. 2006). Yet, it is noteworthy that Gallardo et al. (2012) reported a terrestrial scincomorph lizard (dentary) from the Table Mesa locality. This aberrant occurrence could represent the long-distance floating of a lizard carcass from a shoreline (e.g., the so-called “bloat-and-float carrion”) or a potential food item dropped, regurgitated, or excreted by an aerial or aquatic predator.

CONCLUSIONS

The Western Interior Seaway of North America was a dynamic system (see Introduction). The term Greenhorn Cyclothem represents a singular large-scale transgressive and regressive event over millions of years, but episodes of short-term sea level drop due to regressions are known (Haq 2014). Sea level fluctuations in the initial phase of the Greenhorn Cyclothem transgression had broad and predictable effects on paleoenvironments across the Western Interior Basin. Current and wave energy in shallow-watered shoreline environments is effective at winnowing and concentrating bioclastic content and is accentuated by the lack of detrital input within this system, resulting in the highly informative fossil assemblages discussed herein. Alone, the newly described Fultz Reservoir fossil assemblage consisting of 22 vertebrate taxa does not reveal the dynamic nature of the Western Interior Seaway. However, comparison with other isochronous fossil assemblages across the ocean basin (e.g., Russell 1998, 1993; VonLoh and Bell 1998) will increasingly provide insight into time-correlative differences in environment and the preferred habitat of various marine vertebrate taxa. This study offers insight into how sea level change and proximity to the shoreline alter the taxonomic composition of a marine community. These are critical questions in the context of the current global climate change resulting in the rise of sea level, among other effects, where marine ecosystems and biodiversity are currently under scrutiny (e.g., Hoegh-Guldberg and Bruno 2010; Doney et al. 2012; Lauchlan and Nagelkerken 2020; Colombano et al. 2021).

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APPENDIX

Appendix 1. List of vertebrate taxa from the basal Lincoln Limestone at Fultz Reservoir locality in southeastern Colorado, along with FHSM catalog numbers, sample sizes, and select relevant literature and additional notes (if any) in brackets. Taxa with an asterisk (*) denote those that are not included in the taxonomic counts of the fossil assemblage because they are thought to belong to multiple taxa or may represent anatomical parts of other taxa already listed in the same appendix that are taxonomically identified decisively.

CHONDRICHTHYES (ELASMOBRANCHII)

Ptychodus decurrens Agassiz (Selachii: Lamniformes: Ptychodontidae): FHSM VP-19540, 1 tooth; FHSM VP-19541, 1 tooth [Shimada et al. 2006; see additional information on this taxon by Hamm (2020)]

Ptychodus occidentalis Leidy (Selachii: Lamniformes: Ptychodontidae): FHSM VP-19542, 1 tooth; FHSM VP-19543, 22 teeth; FHSM VP-19544, 1 tooth [Shimada et al. 2006; see additional information of this taxon by Hamm (2020)]

Microcarcharias saskatchewanensis (Case, Tokaryk, and Baird) (Selachii: Lamniformes: Odontaspididae): FHSM VP-19545, 1 tooth; FHSM VP-19546, 39 teeth [Shimada et al. 2006, as "*Carcharias saskatchewanensis*"; the generic assignment is according to Guinot and Carillo-Briceño 2018]

Cenocarcharias tenuiplicatus (Cappetta and Case) (Selachii: Lamniformes: Odontaspididae): FHSM VP-19547, 1 tooth; FHSM VP-19548, 1 tooth [Shimada et al. 2006, as "*Carcharias tenuiplicatus*"; the generic assignment is according to Cappetta and Case 1999]

Cenocarcharias(?) sp. (Selachii: Lamniformes: Odontaspididae?): FHSM VP-19549, 1 tooth [This specimen is represented by an incomplete crown that somewhat resembles the crown of *C. tenuiplicatus* by exhibiting several longitudinal ridges extending apically from the crown base on the labial face, but it is considerably larger than the teeth of *C. tenuiplicatus*; thus, although it represents a distinct odontaspidid-type taxon, its taxonomic identification is highly tentative. Other odontaspidid specimens from the Upper Cretaceous of North America, but likely not conspecific with the material reported here, include teeth of *Eostriatolamia paucicorrugata* Underwood and Cumbaa 2010, and "*Eostriatolamia*(?) sp." (Jansen, Shimada, and Kirkland 2012; Ouroumova, Shimada, and Kirkland 2016)]

Cretodus semiplicatus (Münster in Agassiz) (Selachii: Lamniformes: Pseudoscapanorhynchidae): FHSM VP-19550, 1 tooth [Shimada et al. 2006; see additional information of this taxon by Armagno and Shimada 2024]

Cretoxyrhina mantelli (Agassiz) (Selachii: Lamniformes: Cretoxyrhinidae): FHSM VP-19551, 1 tooth; FHSM VP-19552, 7 teeth; FHSM VP-19553, 2 teeth [Shimada et al. 2006; at least one tooth of "*C. agassizensis*" from the Lincoln Limestone in Russell County, Kansas, illustrated by Meyerkort et al. (2024, fig. 3C-E) is considered to fall within the variation range of *C. mantelli*]

Archaeolamna cf. *A. kopingensis* Siverson (Selachii: Lamniformes: Archaeolamnidae): FHSM VP-19554, 1 tooth; FHSM VP-19555, 1 tooth [Shimada et al. 2006; these specimens are interpreted to be comparable with some teeth of "*C. agassizensis*" from the Lincoln Limestone in Russell County, Kansas, illustrated by Meyerkort et al. (2024, fig. 3E-G), but they are here considered as a form of *Archaeolamna* as in Shimada et al.'s (2006) study]

Squalicorax curvatus (Williston) (Selachii: Lamniformes: Anacoracidae): FHSM VP-19556, 1 tooth; FHSM VP-19557, 9 teeth [Shimada et al. 2006: note that all teeth of *S. falcatus* described in Shimada et al.'s (2006) study are now interpreted to belong to *S. curvatus* (see Underwood and Cumbaa 2010)]

Cretomanta canadensis Case, Tokaryk, and Baird (Selachii: Lamniformes?: Aquilolamnidae?; see Vullo et al. 2021): FHSM VP-19559, 1 tooth; FHSM VP-19560, 6 teeth [Shimada et al. 2006]

*Selachii indet. (likely multiple taxa): FHSM VP-19561, 1 placoid scale (Type B); FHSM VP-19562, 1 placoid scale (Type C); FHSM VP-19563, 1 placoid scale (Type C); FHSM VP-19564, 1 placoid scale (Type D); FHSM VP-19565, 1 placoid scale (Type D); FHSM VP-19566, 1 placoid scale (Type E); FHSM VP-19567, 1 placoid scale (Type E) [These specimens may belong to one or more of the selachian taxa listed above, but their exact taxonomic identification is uncertain; therefore, this category is not included in the taxonomic counts of the fossil assemblage described here; scale types are based on Nelms, McIntosh, and Shimada 2014]

Rhinobatos inertus Cappetta (Batomorphii: Rajiformes: Rhinobatidae): FHSM VP-19558, 1 tooth [Shimada et al. 2006]

*Batomorphii indet. (Order and family incertae sedis): FHSM VP-19568, 1 dermal denticle [Its exact taxonomic identification is uncertain; therefore, this category is not included in the taxonomic counts of the fossil assemblage described here]

OSTEICHTHYES (ACTINOPTERYGII)

Palaeobalistum sp. (Holostei: Pycnodontiformes: Pycnodontidae): FHSM VP-19569, 1 tooth; FHSM VP-19570, 7 teeth [Shimada et al. 2006]

Aspidorhynchidae indet.: FHSM VP-19571, 1 tooth; FHSM VP-19572, 2 teeth [Maisch, Becker, and Shimada 2021, and references therein]

Plethodidae indet.: FHSM VP-19573, 1 tooth; FHSM VP-19574, 4 teeth [Shimada et al. 2006]

Pachyrhizodus minimus Stewart (Teleostei: Elopiformes: Pachyrhizodontidae): FHSM VP-19575, 1 tooth; FHSM VP-19576, 105 teeth [Shimada et al. 2006]

Enchodus gladiolus (Cope) (Teleostei: Aulopiformes: Enchodontidae): FHSM VP-19577, 1 palatine bone; FHSM VP-19578, 63 palatine bones; FHSM VP-19579, 1 tooth; FHSM VP-19580, 488 teeth [Shimada et al. 2006, as "*E.* cf. *E. gladiolus*"]

Enchodus shumardi Leidy (Teleostei: Aulopiformes: Enchodontidae): FHSM VP-19581, 1 palatine bone; FHSM VP-19582, 18 palatine bones; FHSM VP-19583, 1 tooth; FHSM VP-19584, 223 teeth

[Shimada et al. 2006, as "*E*. cf. *E. shumardi*"]

Albulidae indet.: FHSM VP-19585, 1 tooth plate [Shimada et al. 2006]

Osteichthyes indet. (Type A): FHSM VP-19586, 1 tooth; FHSM VP-19587, 3 teeth [The notion of 'Type A' bony fish here is the same as 'Type A' of Allen and Shimada (2022, fig. 5L) that possess well-marked cutting edges and not that of Shimada et al. (2006, specifically tooth illustrated in Fig. 14.11, which is re-identified as cf. *Stratodus* sp.), Jansen, Shimada, and Kirkland (2012, fig. 3J), Gorman, Shimada, and Witzke (2014, fig. 3N), and Ouroumova, Shimada, and Kirkland (2016, fig. 3Q) that appear to have mistaken Type B for Type A (see Juranek and Shimada 2025)]

Osteichthyes indet. (Type B): FHSM VP-19588, 1 tooth; FHSM VP-19589, 6 teeth [The notion of 'Type B' used here is consistent with that of Shimada et al. (2006, fig. 14.13, 14.14) and Nagrodski, Shimada, and Schumacher (2012, fig. 4Q), where it is characterized by a single blunt cutting edge present on only one side of the tooth, if at all, and Type B teeth are rounder in cross-section relative to Type A teeth (see Juranek and Shimada 2025)]

Osteichthyes indet. (Type C): FHSM VP-19590, 2 teeth; FHSM VP-19591, 10 teeth [Shimada et al. 2006]

*Osteichthyes indet. (multiple taxa): FHSM VP-19592, numerous isolated vertebrae [These specimens most certainly belong to multiple taxa, but their exact taxonomic identification is uncertain; therefore, this category is not included in the taxonomic counts of the fossil assemblage described here]

TETRAPODA

Dolichosauridae indet. (Reptilia: Lepidosauria: Squamata): FHSM VP-19593, 1 tooth; FHSM VP-19594, 2 teeth [All squamate specimens previously reported to belong to the genus *Coniasaurus* from North America (e.g., Liggett et al. 2005; Shimada et al. 2006; Gallardo, Shimada, and Schumacher 2012) need review (Augusta 2019); thus, we refer our materials conservatively to 'Dolichosauridae indet.']

MISCELLANEOUS

*Vertebrata indet. (multiple taxa): FHSM VP-19595, Numerous bone and tooth fragments [These specimens most certainly belong to multiple taxa, but their exact taxonomic identification is uncertain; therefore, this category is not included in the taxonomic counts of the fossil assemblage described here]

*Vertebrata(?) indet.: FHSM VP-19596, 1 coprolite with osterichthyan bones; FHSM VP-19597, numerous coprolites [These specimens may belong to, or come from, one or more of the vertebrate taxa listed above, but their exact taxonomic identification or origin is uncertain; therefore, this category is not included in the taxonomic counts of the fossil assemblage described here]

Appendix 2. Clarifications and additional notes (where needed) of each taxonomic category listed in Table 1.

1. Originally described as "*Eostriatolamia* sp." by Jansen, Shimada, and Kirkland (2012).
2. Originally described as "*Ptychodus* cf. *P. anonymus*" by Shimada et al. (2006) and Shimada and Martin (2008) (see Hamm 2020); also note that the genus *Ptychodus* is now considered to belong to Lamniformes (Vullo et al. 2024).
3. Teeth of "*Ptychodus rhombodus*" reported by Gallardo, Shimada, and Schumacher (2012) is here interpreted to belong to *P. occidentalis* (see additional information on *P. rhombodus* in Hamm 2020).
4. Originally described as "*Carcharias amonensis*" by Shimada et al. (2006), Shimada and Martin (2008), and Jansen, Shimada, and Kirkland (2012) (see Vullo, Guinot, and Barbe 2016).
5. Originally described as "*Carcharias saskatchewanensis*" by Shimada et al. (2006), Shimada and Martin (2008), Gallardo, Shimada, and Schumacher (2012), and Jansen, Shimada, and Kirkland (2012).
6. Originally described as "*Carcharias tenuiplicatus*" by Shimada et al. (2006) and Shimada and Martin (2008); some papers placed the species under the genus *Cenocarcharias* erroneously (e.g., Maisch, Becker, and Shimada 2021; Ortiz and Shimada 2024).
7. Material referred to as "*Eostriatolamia* sp." Jansen, Shimada, and Kirkland (2012) is re-interpreted to

belong to tooth of *Scapanorhynchus raphiodon* (see '1' above).

8. Originally described as "cf. *Johnlongia* sp." by Shimada et al. (2006) and "*Megachasma comanchensis*" by Gallardo, Shimada, and Schumacher (2012) (see Shimada et al. 2015).
9. Shimada and Martin (2008) reported both "*Cardabiodon venator*" and "*Cardabiodon* sp.", but they are conservatively lumped together here.
10. The taxon referred here to as "*Archaeolamna* cf. *A. kopingensis*" is the same notion as Shimada et al.'s (2006) "*Archaeolamna* cf. *A. kopingensis*", which is interpreted to be comparable with some teeth of "*C. agassizensis*" illustrated by Meyerkort et al. (2024, fig. 3E-G), but not likely with those of Underwood and Cumbaa's (2010) "*Archaeolamna* ex. gr. *kopingensis*") or Juranek and Shimada's (2025) "*Archaeolamna* sp."
11. Originally referred questionably to as 'small' teeth of "*Cretoxyrhina mantelli*" by Shimada et al. (2006) and Shimada and Martin (2008) (see Underwood and Cumbaa 2010); Meyerkort et al. (2024) considered this taxon to be a species of *Cretoxyrhinia* (*C. agassizensis*), but it is here considered a distinct taxon of the original generic assignment as intended by Underwood and Cumbaa (2010); it should be noted that only one tooth of "*C. agassizensis*" from the Lincoln Limestone in Russell County, Kansas, illustrated by Meyerkort et al. (2024, fig. 3D) is considered to belong to this species, whereas their other teeth (Meyerkort et al. 2024, fig. 3C, E-G) are consider to belong to either *C. mantelli* or *Archaeolamna* cf. *A. kopingensis* here (see Appendix 1).
12. Originally described as "*Cretalamna appendiculta*" or "*C. appendiculta*(?)" by Shimada et al. (2006), Shimada and Martin (2008), Gallardo, Shimada, and Schumacher (2012), and Jansen, Shimada, and Kirkland (2012), but its species-level identification remains questionable (see Siversson et al. 2015).
13. Specimens originally described as *Squalicorax falcatus* by Shimada et al. (2006) and Shimada and Martin (2008) are now considered to belong to *S. curvatus* (see Underwood and Cumbaa 2010).
14. *Squalicorax* sp. (1) here refers to the form described as "*Squalicorax* sp." by Shimada et al. (2006) and Shimada and Martin (2008), whereas *Squalicorax* sp. (2) refers to the form referred to as "*Squalcorax volgensis*" by Shimada and Martin (2008), the latter of which may be conspecific to the form previously reported as '*Squalicorax* sp. B' (Cook et al. 2013) or '*Squalicorax* cf. *S. pawpawensis*' (e.g., Bice and Shimada 2016; McIntosh, Shimada, and Everhart 2016; Arroyo and Shimada 2023).
15. This taxon is now considered to questionably belong to Lamniformes (see Vullo et al. 2021).
16. Originally described as "*Rhinobatos* sp." or "*R.* cf. *R. incertus*" by Shimada et al. (2006), Shimada and Martin (2008), and Gallardo, Shimada, and Schumacher (2012) (see also Everhart 2007).
17. Specimens referred to as "Rajidae incertae sedis" were described by Shimada and Martin (2008) and Gallardo, Shimada, and Schumacher (2012), but those two materials are considered not conspecific here.
18. Originally described as "*Ischyrhiza* cf. *I. texana*" by Jansen, Shimada, and Kirkland (2012).
19. Originally described as "*Micropycnodon* cf. *M. kansasensis*" by Shimada et al. (2006).
20. Tooth illustrated as "Caturidae incertae sedis" by Shimada and Martin (2008, fig. 8E) is here interpreted to belong to Nonteleostean(?) Actinopterygii (2).
21. Tooth illustrated as "Caturidae incertae sedis" by Shimada and Martin (2008, fig. 8F) is here interpreted to belong to Aspidorhynchidae indet.
22. Nonteleostean(?) Actinopterygii (1) here refers to teeth described by Shimada et al. (2006), Gallardo, Shimada, and Schumacher (2012), whereas Nonteleostean(?) Actinopterygii (2) refers to the tooth illustrated as form referred to as "Caturidae incertae sedis" by Shimada and Martin (2008, fig. 8E) (see '19' above).
23. Originally described as "cf. Plethodidae(?) incertae sedis" by Shimada et al. (2006) and Shimada and Martin (2008).
24. Originally described as "*Pachyrhizodus minimus*" by Shimada et al. (2006) and Shimada and Martin (2008).
25. *Elopopsis* sp. reported by Gallardo, Shimada, and Schumacher (2012) is not included here because the material may represent dense fragmentary teleost bones.
26. Originally described as "Albulidae incertae sedis" by Shimada et al. (2006) and Shimada and Martin (2008), and as "cf. Albulidae" by Gallardo, Shimada, and Schumacher (2012).

27. The tooth illustrated as "Teleostei incertae sedis (Teleost A)" in Figure 14.12 by Shimada et al. (2006) is re-interpreted to belong to cf. *Stratodus* sp. (see "Teleostei indet. (Type A)" in Appendix 1).
28. Originally described as "*Enchodus* cf. *E. gladiolus*" by Shimada et al. (2006), Shimada and Martin (2008), Gallardo, Shimada, and Schumacher (2012), and Jansen, Shimada, and Kirkland (2012).
29. Originally described as "*Enchodus* cf. *E. shumardi*" by Shimada et al. (2006), Shimada and Martin (2008), Gallardo, Shimada, and Schumacher (2012), and Jansen, Shimada, and Kirkland (2012).
30. This set of taxa based on tooth-based morphotypes needs future reviews because, as more samples have been added, possibilities began to emerge for a morphotype to be represented by more than one taxon (e.g., see Allen and Shimada 2022; Juranek and Shimada 2025). Including the fact that the tooth apex of some specimens among these morphotypes is found, or appears, to be composed of an acrodin cap (e.g., Fig. 3L), these morphotypes may include, or be mixed with, non-teleostean bony fish taxa. Therefore, all these tooth-based bony fish morphotypes are here conservatively relabeled as "Osteichthyes indet."
31. Originally described as "Teleostei incertae sedis (Teleost A)" or "Teleost indet. (species A)" by Shimada et al. (2006), Shimada and Martin (2008), Gallardo, Shimada, and Schumacher (2012), and Jansen, Shimada, and Kirkland (2012); the notion of 'Type A' bony fish here is the same as 'Type A' teleost of Allen and Shimada (2022, fig. 5L) that possess well-marked cutting edges and not that of the specific tooth illustrated in Figure 14.11 by Shimada et al. (2006; re-identified as "cf. *Stratodus* sp."; see '26' above) and in Figure 3J by Jansen, Shimada, and Kirkland (2012; re-identified as "Osteichthyes indet. (Type B)") (see also "Osteichthyes indet. (Type A)" in Appendix 1).
32. Originally described as "Teleostei incertae sedis (Teleost B)" or "Teleost indet. (species B)" by Shimada et al. (2006), Shimada and Martin (2008), and Gallardo, Shimada, and Schumacher (2012); the notion of 'Type B' bony fish here is consistent with 'Type B' teleost of Shimada et al. (2006, specifically fig. 14.13, 14.14) and Nagrodski, Shimada, and Schumacher (2012, fig. 4Q) that possess a single blunt cutting edge present on only one side of the tooth, if at all, and teeth of Type B are rounder in cross-section relative to teeth of Type A (see also "Osteichthyes indet. (Type B)" in Appendix 1); "Teleostei incertae sedis (species A)" reported by Jansen, Shimada, and Kirkland (2012) is re-identified as "Osteichthyes indet. (Type B)" (see '29' above).
33. Originally described as "Teleostei incertae sedis (Teleost C)" or "Teleost indet. (species C)" by Shimada et al. (2006), Shimada and Martin (2008), and Gallardo, Shimada, and Schumacher (2012).
34. Originally described as "Teleostei incertae sedis (species E)" by Jansen, Shimada, and Kirkland (2012).
35. Originally described as "*Coniasaurus crassidens*" by Liggett et al. (2005), Shimada et al. (2006), and Gallardo, Shimada, and Schumacher (2012); Shimada et al.'s (2006) "Squamata(?) incertae sedis" and "Mosasauroidea incertae sedis" are also included in this taxonomic category (see also "Dolichosauridae indet." in Appendix 1; Polcyn et al. 2008).
36. Gallardo, Shimada, and Schumacher (2012) reported a jaw fragment of "Scincomorpha indet. (Contogeniidae?)", a terrestrial lizard, interpreted to have washed into the sea.
37. "cf. *Brachauchenius* sp." reported by Shimada et al. (2006) is tentatively included in this taxonomic category.
38. Originally described as "Polycotylidae incertae sedis" by Shimada et al. (2006), this is considered a distinct taxon not conspecific with *Brachauchenius lucasi* or Plesiosauria indet. listed.
39. This category includes a questionable taxon referred to as "Plesiosauria(?) incertae sedis", where all reported materials in this category may not be conspecific; nevertheless, they are listed together to denote that at least one indeterminate plesiosaur taxon was most likely present besides the other plesiosaur taxa already listed.
40. The possible record of "*Ichthyornis*" reported by Bell and Everhart (2011) is included in this category used by Shimada and Wilson (2016).
41. This category denotes that the assemblage likely includes at least one more avian taxon (i.e. other than Baptornithidae indet. and cf. *Ichthyornis* sp.) represented in the vertebrate assemblage (see Everhart and Bell 2009; Bell and Everhart 2011).