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Mid-Cenomanian vertebrate faunas of the Western Interior Seaway of North America and their evolutionary, paleobiogeographical, and paleoecological implications

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ABSTRACT

The Western Interior Seaway (WIS) was an epicontinental sea that extended north–south through the middle of North America during the last half of the Cretaceous, linking the Tethys Sea to the south with the boreal paleo-Arctic Ocean to the north. Aptian–Maastrichtian sedimentary deposits from the seaway crop out in the Western Interior Basin of Canada and the United States. Vertebrate remains are commonly well-preserved, and in certain stratigraphic units, abundant. The classic vertebrate fauna of the WIS, from the Upper Cretaceous Niobrara Chalk, has been studied for 150 years, but relatively little has been known of the seaway's earlier faunas until recent years. Studies of mid-Cenomanian vertebrate faunas, particularly from lag deposits (bonebeds and calcarenites) in Canada and the United States have significantly altered the previous picture of the overall biodiversity and biogeography of the WIS during the 'mid-Cretaceous.' These mid-Cenomanian faunas include diverse fish assemblages of chondrichthyans (cartilaginous fishes) and osteichthyans (bony fishes) as well as various forms of tetrapods, including marine turtles, plesiosaurs, and hesperornithiform and ichthyornithiform birds.

Our compilation of faunas indicates that at least 70 vertebrate taxa are recorded from five mid-Cenomanian WIS 'localities' situated in Alberta, Saskatchewan, the Black Hills region of South Dakota and Wyoming, Kansas, and Colorado. The faunas include 41 chondrichthyans, 21 osteichthyans, 10 non-avian tetrapods, and five avian taxa. Our study, combined with previous faunal studies, suggests that the combination of the following eight chondrichthyan species characterizes mid-Cenomanian time, which has been referred to as the 'Woodbinian Age' in the marine realm of North America: *Ptychodus decurrens*, *P. occidentalis*, *Squalicorax curvatus*, *Cretodus semiplicatus*, *Carcharias amonensis*, *C. saskatchewanensis*, *Eostriatolamia tenuiplicatus*, and *Cretomanta canadensis*. This is the geologic time when non-ptychodontid hybodonts became rare faunal components in most areas, and when a number of other fish lineages, particularly teleosts, emerged and diversified. Many of these persisted into the early Campanian, or the 'Niobrara Age' that followed the Woodbinian. Therefore, mid-Cenomanian time in the WIS can also be characterized by the genesis of the 'Niobraran fauna,' a significant radiation and diversification of fish taxa.

The five mid-Cenomanian WIS 'localities' highlighted in this study are separated by as much as 18° latitude, a north–south distance of more than 2300 km. These faunas demonstrate some clinal trends, such as more diverse faunas of benthic chondrichthyans mixed with dolichosaurid lizards to the south, and a more diverse fauna of birds to the north. However, the faunas overall show strong taxonomic homogeneity, particularly among many chondrichthyans that were cosmopolitan, indicating that passage throughout the seaway as well as to both the Boreal and Tethys oceans was utilized. These faunas also demonstrate high osteichthyan diversity in the northern waters of the WIS, which were once thought to have supported only a depauperate, cold-adapted fauna. Because of the surprisingly great diversity in vertebrate taxa, ecosystem structure and dynamics of the WIS during the mid-Cenomanian were unquestionably complex.

1. Introduction

The Western Interior Sea (WIS) was an epicontinental sea that extended generally north–south through the middle of North America during the last half of the Cretaceous (Fig. 1A). The seaway was dynamic in terms of its width and depth, changing in response to

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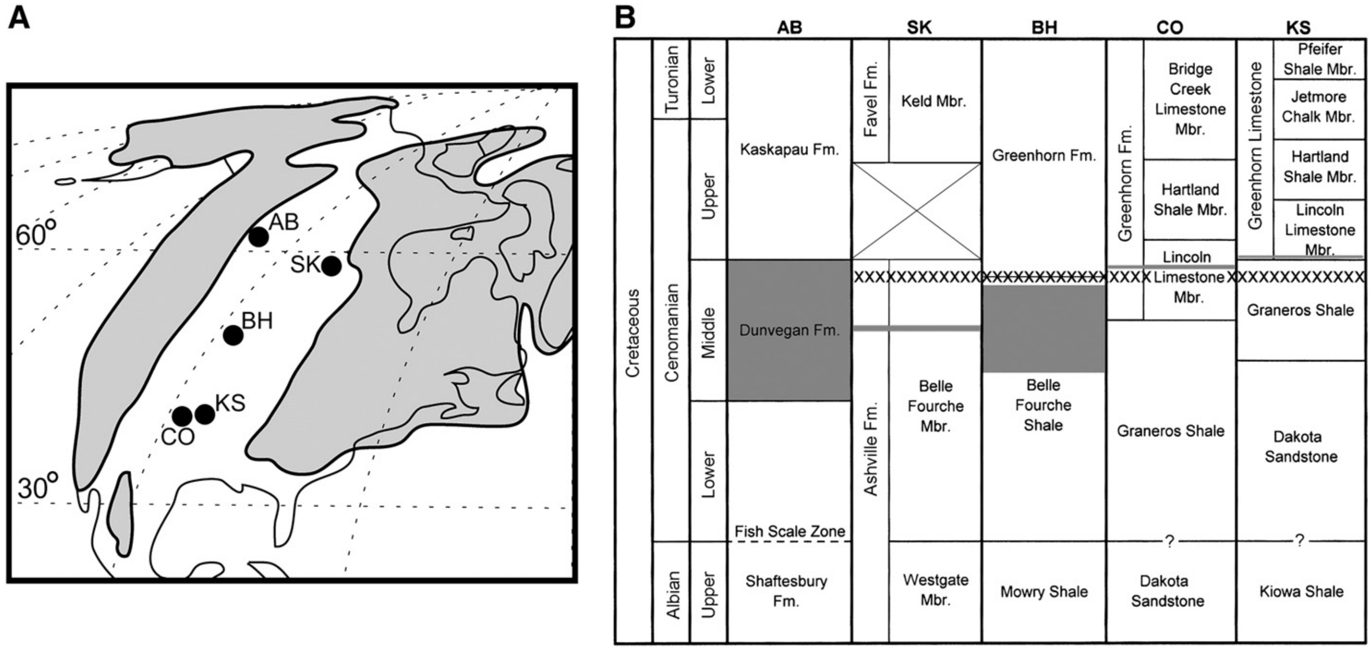


Fig. 1. Mid-Cenomanian geography and stratigraphy of North America. A) Paleogeographic map showing position of Western Interior Sea during middle Cenomanian and five mid-Cenomanian vertebrate localities discussed in this paper (locality abbreviations: AB, Alberta, Canada; SK, Saskatchewan, Canada; BH, Black Hills region, U.S.A.; CO, Colorado, U.S.A.; and KS, Kansas, U.S.A.; map based on Smith et al., 1994); B) stratigraphic correlations across five mid-Cenomanian vertebrate localities showing 'X-bentonite' horizon (repeated 'x' marks; note that X-bentonite radioactive signature cannot be traced in examined region of Alberta, Canada: see Tyagi et al., 2007) and fossil collecting interval (gray-colored zone) at each locality (data largely based on Stott, 1967, 1982; Hattin, 1975; McNeil and Caldwell, 1981; Bloch et al., 1993; Kauffman et al., 1993; Dyman et al., 1994; Cumbaa et al., 2006).

"tectonic and sedimentologic processes" (Kauffman, 1984, pp. 276). However, at its maximum coverage, the WIS extended 4800 km from the present-day Arctic Ocean to the Gulf of Mexico, and had a width of approximately 1600 km (Kauffman, 1984). Water depth in mid-sea is thought to have been on the order of 100 m (Kauffman, 1977). Its general structure consisted of a tectonically generated, deep foreland basin that was flanked by the great Cordilleran thrust belt to the west, and an extensive, stable cratonic platform to the east (Price, 1973; Jordan, 1981; Kauffman, 1984). The tectonically active western margin was the source of most of the sediment coming into the sea, with coarse clastics depositing into rapidly prograding deltaic complexes within the subsiding basin. By contrast, much of the shallow eastern margin was sediment-starved (McNeil and Caldwell, 1981; Schröder-Adams et al., 2001). It received mostly suspended fine clastics from the western basin, run-off from the low-lying hills of eastern North America, and like the rest of the WIS, volcanic ash from volcanoes on the tectonically active western margin (Kauffman, 1977). However, deltaic complexes along the eastern margin did provide the sediments of the Dakota Formation (Witzke and Ludvigson, 1994).

The WIS was inhabited by a diverse array of species, including microscopic forms such as foraminiferans and coccolithophores, and macroscopic invertebrates such as bivalves, gastropods, cephalopods, crustaceans, and echinoderms (e.g., Hattin, 1975, 1982; Kauffman et al., 1993). Diverse forms of vertebrates were also present, including various chondrichthyans (cartilaginous fishes) and osteichthyans (bony fishes), as well as diverse forms of aquatic tetrapods, including marine turtles, mosasauroid and dolichosaurid lizards, ichthyosaurs, plesiosaurs, crocodilians, and flightless marine birds (e.g., Russell, 1993). Deposits of the WIS have also yielded remains of aerial and terrestrial vertebrates such as pterosaurs (flying reptiles) and 'shore birds' as well as dinosaurs that were washed out to sea (e.g., Eaton, 1960; Everhart, 2005). One of the best-known faunas of the WIS is that of the Smoky Hill Chalk Member of the Niobrara Formation, where over 70 fish and 40 tetrapod taxa are known (Russell, 1988; Everhart, 2005; Shimada and Fielitz, 2006). However, the taxonomic composition of the fauna of the WIS changed throughout the history of the seaway (Russell, 1988, 1993), presumably largely in response to changes in the water conditions of the sea (temperature, salinity, oxygen levels, depth, and/or turbidity) and accompanying shifts in the trophic structure.

The initial formation of the WIS began with the flooding of sea water onto the North American continent during the Aptian, but it was not until the late Aptian that the northern and southern water masses merged to form a continuous seaway (Kauffman, 1984). The vertebrate fossil record of this initial stage of the WIS is scarce, but is generally characterized by low taxonomic diversity (e.g., Everhart, 2009), represented primarily by marginal shore and shallow-water faunas that not uncommonly contain terrestrial components (e.g., Russell, 1988). This apparent low diversity of vertebrates was punctuated by an explosive radiation of taxa during the 'mid-Cenomanian,' commonly recorded in lag deposits characterized by 'bonebeds' and fossiliferous calcarenites. These lag deposits apparently reflect substantive basin-wide lowstand events in the mid–late Cenomanian, during the transgressive phase of the Greenhorn Cyclothem (Cicimurri, 2001a; Cumbaa et al., 2006). This eustatic trough appears to have been global in extent in mid-latitudes, with sedimentary records in northwestern Europe and Kazakhstan (Hancock, 2003) as well as in the United States and Canada.

The mid-Cenomanian is a critical time in the evolution of WIS ecosystems. In this paper, we review mid-Cenomanian (specifically middle Cenomanian–earliest late Cenomanian) vertebrate faunas of the WIS. Our study is based primarily on five recently published 'localities' (including clusters of localities) with vertebrate faunas (Fig. 1A): 1) northwestern Alberta, Canada (Cook et al., 2008), 2) east-central Saskatchewan, Canada (Cumbaa et al., 2006), 3) the Black Hills region of southwestern South Dakota and northeastern Wyoming, U.S.A. (VonLoh and Bell, 1998; Cicimurri, 2001a,b), 4) central Kansas, U.S.A. (Liggett et al., 2005; Shimada and Martin, 2008), and 5) southeastern Colorado, U.S.A. (Shimada et al., 2006). Our goals are to demonstrate the great diversity of vertebrates in the early WIS, and to examine possible geographic and environmental trends in the taxonomic compositions of the faunas. Our data show that the faunal composition established during this time set the stage for the remaining 35 million-year faunal history of the WIS.

2. Material and methods

2.1. Fossil collections

Our study is based on fossil specimens housed in the following North American institutions: Canadian Museum of Nature (CMN), Ottawa, Canada; Fort Hays State University, Sternberg Museum of Natural History, Vertebrate Paleontology collection (FHSM VP), Hays, Kansas, USA; University of Kansas Museum of Natural History, Vertebrate Paleontology collection (KUVP), Lawrence, Kansas, U.S.A.; Royal Saskatchewan Museum (RSM), Regina, Saskatchewan, Canada; and University of Alberta Laboratory for Vertebrate Paleontology (UALVP), Edmonton, Alberta, Canada.

2.2. Faunas and localities in space and time

Stratigraphic and chronostratigraphic correlations between the examined five faunas shown in Fig. 1A are presented in Fig. 1B. Four of the five faunas occur at localities where the basin-wide 'X-bentonite' is present. Distribution of the bonebeds within the strata ranges from 2 m or more below to 1.5 m above the X-bentonite. The measured $^{40}Ar/^{39}Ar$ ages of the X-bentonite have varied values including 94.93 ± 0.53 Ma (Obradovich, 1993), 93.3 Ma (Cadrin, 1992), and 94.96 ± 0.5 Ma (Cobban et al., 2006). It seems possible on the basis of similarity of reported argon ages that Cadrin's (1992) X-bentonite age determination is equivalent to the Bighorn River Bentonite of Tyagi et al. (2007), which lies above the X-bentonite in the Western Interior, and has an average $^{40}Ar/^{39}Ar$ age of 93.5 ± 0.2 Ma (Obradovich, 1993; Tyagi et al., 2007).

The Alberta fauna is represented by surface-collected chondrichthyan teeth recovered from a cluster of Dunvegan Formation localities situated along the Peace River in northwest Alberta (Cook et al., 2008; Fig. 2A). The Dunvegan Formation, composed of mudstones, sandstones, and conglomerates, is thought to be a deltaic complex that grades eastward into the marine shale of the Belle Fourche Formation (Stott, 1982; Bhattacharya and Walker, 1991; Bloch et al., 1993; Plint, 2000; Hay et al., 2007; Cook et al., 2008). It also correlates with the Belle Fourche Shale in the Black Hills in the United States (Cumbaa et al., 2006) and is middle Cenomanian in age (Fig. 1B) where it is assigned to the *Verneuilinoides perplexus* foraminiferal zone (Stelck et al., 1958; Caldwell et al., 1978; Stott, 1982; Singh, 1983; Bhattacharya and Walker, 1991) and the *Acanthoceras athabascense* ammonite zone (Jeletzky, 1968; Bhattacharya and Walker, 1991).

The Saskatchewan fauna is based on disarticulated fossils recovered from bonebeds at two localities, Carrot River and Bainbridge River, which are about 100 km apart in the Pasquia Hills of east-central Saskatchewan (Fig. 2B). The bonebeds occur as discontinuous layers and lenses in black shales of the upper part of the Belle Fourche Member of the Ashville Formation (Schröder-Adams et al., 2001; Fig. 2C). The bonebed lenses (Fig. 2B–D) occur approximately 2 m below what is thought to be the X-bentonite at the Bainbridge locality, and are associated with the *Ostrea beloiti* beds, a regional stratigraphic marker (Cumbaa and Bryant, 2001; McNeil and Caldwell, 1981). At the Carrot River locality, the thinner, more compact bonebed lies directly under a bentonite which has been dated to 95.17 ± 0.31 Ma (Cumbaa et al., 2006). Shales surrounding both bonebeds have produced the foraminifer *Verneuilinoides perplexus*, placing the bonebeds within the mid-Cenomanian foraminiferal *V. perplexus* Zone of Caldwell et al. (1978) (Cumbaa and Tokaryk, 1999; Schröder-Adams et al., 2001). The Belle Fourche Member is correlative to the Belle Fourche Shale of the Black Hills region, and to the upper Graneros Shale in Kansas and Colorado (McNeil and Caldwell, 1981; Fig. 1B).

The Black Hills fauna is based on fossil remains from two formations, the upper Belle Fourche Shale and the overlying Orman Lake Member of the Greenhorn Limestone, occurring in the Black Hills region of South Dakota and Wyoming (VonLoh and Bell, 1998; Cicimurri, 2001a,b). Cicimurri (2001a) reported chondrichthyan remains from the upper 14 m of the Bell Fourche Shale. The majority of the fossils were recovered from thin calcarenites and were associated with the ammonite *Acanthoceras amphibolum*, indicating a middle Cenomanian age (Cobban et al., 1994; Cicimurri, 2001a). The Belle Fourche Shale overlies the 97 Ma clay Spur Bentonite (Obradovich, 1993), and is overlain either by the X-bentonite or the Orman Lake Member of the Greenhorn Limestone (Petsch, 1949; Cobban, 1951; Cicimurri, 2001a). Chondrichthyan teeth (Cicimurri, 2001b) and marine reptiles (VonLoh and Bell, 1998) were also recovered from calcarenites in the Orman Lake Member. The ammonites associated with this recovered material included *Plesiacanthoceras wyomingense* and *Dunveganoceras pondi* which are late middle Cenomanian and early late Cenomanian (94 Ma) in age, respectively (Obradovich, 1993; VonLoh and Bell, 1998; Cicimurri, 2001b).

The Kansas fauna is based on disarticulated fossils recovered from surface collecting and from fossiliferous calcarenites in the basal Lincoln Limestone Member of the Greenhorn Limestone, in Russell County, Kansas (Liggett et al., 2005; Shimada and Martin, 2008; Fig. 2G). The fossiliferous unit (Fig. 2H) that reflects the 'calcarenite wedging' is situated about 0.5 m above the X-bentonite, which occurs in the upper part of the non-calcareous Graneros Shale (Martin and Shimada, 2008). The age of the X-bentonite based on $^{40}Ar/^{39}Ar$ analysis in central Kansas yielded a reliable plateau age of 95.53 ± 0.15 Ma (Shimada et al., 2006). The Graneros–Greenhorn contact is interpreted to be a disconformity with a minor hiatus. Macroinvertebrates suggest that the fossiliferous calcarenite is early late Cenomanian in age (Hattin, 1975; Hattin et al., 1987).

The Colorado fauna is based on disarticulated vertebrate fossils recovered from calcarenite beds at the base of the Lincoln Limestone Member of the Greenhorn Limestone at a locality in Comanche National Grassland in southeastern Colorado (Shimada et al., 2006; Fig. 2E). The calcarenite (Fig. 2F) contains abundant inoceramid shell fragments and prisms. This unit occurs about 1.5 m above the X-bentonite within the calcareous Greenhorn Limestone, and is likely due to an early arrival of oceanic waters, which allowed the earlier formation of calcareous beds, compared with those of the Greenhorn Limestone in Kansas. Based on bivalve and ammonite taxa from adjacent stratigraphic horizons and the close stratigraphic proximity to the X-bentonite, the age of the fossiliferous calcarenite is determined as mid-Cenomanian, between approximately 95 Ma and 94.7 Ma (Fig. 1B).

It should be noted that Case et al. (1990) reported a bonebed fauna from a locality on the Carrot River, Saskatchewan that is within 2 km of one of our Saskatchewan localities. It is of interest as it contains a number of the same chondrichthyan taxa reported here in Table 1. Originally reported as coming from Niobrara exposures, a re-evaluation of the geology and the circumstances of the bonebed collection indicate that it came from unidentified strata within a lower Turonian exposure (Cumbaa and Tokaryk, 1999). Fieldwork in 2006 at the locality by one of us (SLC) identified the probable source as an inoceramid bed near the exposed base of the Favel Formation. The underlying Belle Fourche Member of the Ashville Formation, source of the middle Cenomanian bonebeds from which our Saskatchewan fauna is derived, is not exposed at Case et al.'s (1990) locality. Foraminiferal studies are forthcoming, but we expect these strata to match upper Cenomanian–lower Turonian zones reported in the Manitoba Escarpment by McNeil and Caldwell (1981). Because the oldest probable age for the deposit is latest Cenomanian, we have not included Case et al.'s (1990) data in our study.

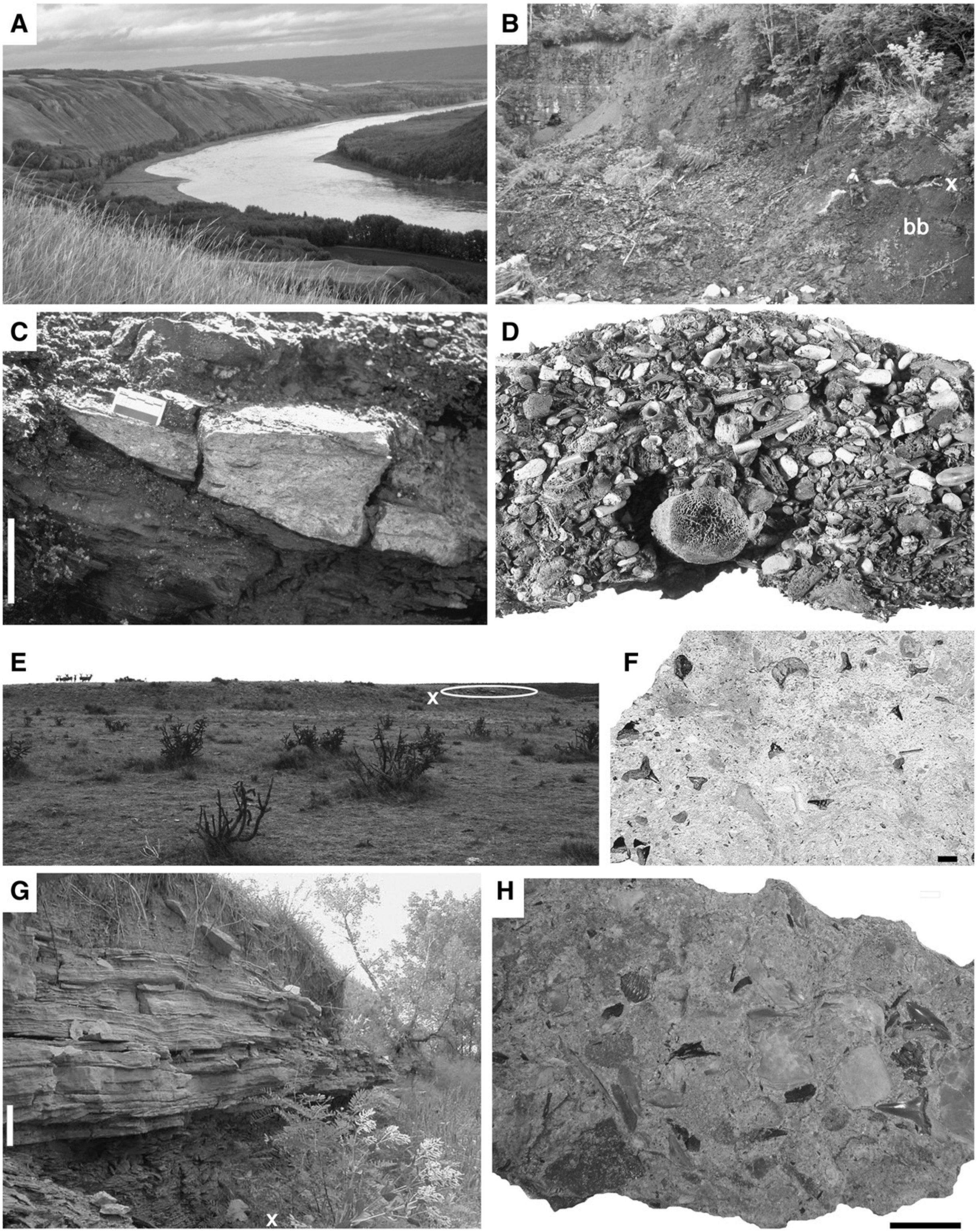


Fig. 2. Examples of mid-Cenomanian localities and vertebrate-bearing rocks of North American Western Interior Sea. A) Dunvegan Formation exposed along northern bank of Peace River in northwestern Alberta, Canada; B) uppermost part of Belle Fourche Member of Ashville Formation (bottom half of photo; use 1.8-m-tall man for scale) in east-central Saskatchewan, Canada, with 'X-bentonite' (light-colored layer marked 'x') and bonebed lens (partially exposed immediately right to label 'bb'); C) bonebed lens in situ in uppermost part of Belle Fourche Member in east-central Saskatchewan, Canada (cf. Fig. 2B; vertical scale = 10 cm); D) close-up view of bonebed (partially prepared in 5% acetic acid) from uppermost part of Belle Fourche Member in east-central Saskatchewan, Canada (cf. Fig. 2C), showing numerous bioclastics including bones and teeth of various vertebrates (e.g., large columnar bone at bottom center = probable plesiosaurian rib) as well as phosphatic pebbles presumably representing coprolites of uncertain origins (light-colored, rounded elements); E) vertebrate-bearing horizon (marked by oval) of Lincoln Limestone Member of Greenhorn Limestone in southeastern Colorado, U.S.A. (use mule deer 90 cm in shoulder height for scale; 'x' indicates approximate horizon of 'X-bentonite' in Lincoln Limestone Member); F) close-up view of calcarenite (partially prepared in 5% acetic acid) from Lincoln Limestone Member in southeastern Colorado, U.S.A. (cf. Fig. 2E; scale = 1 cm), showing scattered bones and teeth of various vertebrates (predominantly chondrichthyan teeth); G) basal Lincoln Limestone Member of Greenhorn Limestone in central Kansas, U.S.A., showing sharp discomformable contact with underlying unindurated Graneros Shale that contains 'X-bentonite' (approximate bentonite horizon marked 'x'; vertical scale = 10 cm); H) close-up view of calcarenite from Lincoln Limestone Member in central Kansas, U.S.A. (cf. Fig. 2G; scale = 1 cm), showing scattered bones and teeth of various vertebrates (predominantly chondrichthyan teeth).

Table 1
Vertebrate taxa reported from five mid-Cenomanian localities in North America: Alberta [AB], Canada (Dunvegan fauna: Cook et al., 2008); Saskatchewan [SK], Canada (data from Bainbridge River fauna and Carrot River fauna combined: Cumbaa et al., 2006; Underwood and Cumbaa, 2010); Black Hills region [BH], U.S.A. (data from localities in South Dakota and Wyoming: VonLoh and Bell, 1998; Cicimurri, 2001a,b); Kansas [KS], U.S.A. (Liggett et al.; 2005; Shimada and Martin, 2008; Everhart and Bell, 2009); and Colorado [CO], U.S.A. (Shimada et al., 2006). Occurrence data ("X" marks) in bold are those that have been reported from at least three of five localities. Taxonomic names in bold are taxa that have been reported from Woodbine Group of Texas (based on Russell, 1988; Welton and Farish, 1993; Cappetta and Case, 1999; asterisk (*) indicates genera known from Woodbine Group of Texas but may not be conspecific to those listed).

Class							
Species	Higher categories	AB	SK	BH	KS	CO	Fig.
Chondrichthyes							
Edaphodon sp.	Edaphodontidae; Chimaeriformes	–	X	–	–	–	3A
Chimaeroidea indet.	Chimaeroidea indet.; Chimaeriformes	–	X	–	–	–	3B
Meristodonoides rajkovichi[a]	Hybodontidae; Hybodontiformes	**X**	**X**	**X**	–	–	3C
***Hybodus* sp.**	Hybodontidae; Hybodontiformes	–	X	–	–	–	3D, E
Ptychodus anonymus[b]	Ptychodontidae; ?Hybodontiformes	–	**X**	**X**	**X**	**X**	3F
Ptychodus decurrens[c]	Ptychodontidae; ?Hybodontiformes	–	**X**	–	**X**	**X**	3G
Ptychodus occidentalis[d]	Ptychodontidae; ?Hybodontiformes	–	**X**	**X**	**X**	**X**	3H
Ptychodus rhombodus	Ptychodontidae; ?Hybodontiformes	–	X	–	–	–	3I
cf. *Pararhincodon* sp.[*,e]	Parascylliidae; Orectolobiformes	–	–	–	–	X	3J
Cretorectolobus robustus	*incertae familiae*; Orectolobiformes	–	X	–	–	–	3K
Orectoloboides angulatus	*incertae familiae*; Orectolobiformes	–	X	–	–	–	3L
Cardabiodon venator[f]	Cardabiodontidae; Lamniformes	–	–	–	X	X	3M
Cardabiodon sp.	Cardabiodontidae; Lamniformes	–	–	–	X	–	3N
Cretoxyrhina denticulata[g]	Cretoxyrhinidae; Lamniformes	X	X	–	–	–	3O
Cretoxyrhina mantelli	Cretoxyrhinidae; Lamniformes	–	**X**	**X**	**X**	**X**	3P
Cretodus semiplicatus	Cretoxyrhinidae; Lamniformes	**X**	**X**	**X**	**X**	**X**	3Q
Protolamna carteri	Cretoxyrhinidae; Lamniformes	X	–	–	–	–	3R
Archaeolamna kopingensis[h]	Archaeolamnidae; Lamniformes	**X**	**X**	–	**X**	**X**	3S
Telodontaspis agassizensis[g]	?Archaeolamnidae; Lamniformes	–	X	–	–	X	3T
Cretalamna appendiculata[i]	Otodontidae; Lamniformes	–	**X**	**X**	**X**	–	3U
Carcharias amonensis	Odontaspididae; Lamniformes	–	–	**X**	**X**	**X**	4A
Carcharias saskatchewanensis	Odontaspididae; Lamniformes	–	–	**X**	**X**	**X**	4B
Eostriatolamia tenuiplicatus[j]	Odontaspididae; Lamniformes	–	–	–	X	X	4C
Eostriatolamia paucicorrugata[k]	Odontaspidae; Lamniformes	–	X	?	–	–	4D
Johnlongia parvidens[l]	Odontaspididae; Lamniformes	X	–	–	–	X	4E
Roulletia canadensis[m]	Odontaspididae; Lamniformes	–	X	–	–	X	4F
Megachasma comanchensis[n]	Megachasmidae; Lamniformes	–	–	–	–	X	4G
Microcorax crassus	Anacoracidae: ?Lamniformes	–	–	–	–	X	4H
Squalicorax curvatus[o]	Anacoracidae: ?Lamniformes	**X**	**X**	**X**	**X**	**X**	4I
Squalicorax falcatus[p]	Anacoracidae: ?Lamniformes	–	–	–	X	X	4J
Squalicorax sp.	Anacoracidae: ?Lamniformes	–	–	–	X	X	4K
Paleoanacorax aff. *P. pawpawensis*[q]	Anacoracidae: ?Lamniformes	–	**X**	**X**	**X**	–	4L
Carcharhiniformes indet.	Carcharhiniformes *incertae sedis*	–	–	–	–	X	4M
Squatina sp.	Squatiniformes; Squatinidae	–	–	X	–	–	4N
Pseudohypolophus mcnultyi	Rhinobatidae; Rajiformes	X	–	–	–	–	4O
Rhinobatos* cf. *R. incertus[r]	Rhinobatidae; Rajiformes	–	**X**	**X**	**X**	**X**	4P
Rajidae *incertae sedis*	Rajidae; Rajiformes	–	–	–	X	–	4Q
***Ptychotrygon* sp.**[*]	Sclerorhynchidae; Sclerorhynchiformes	–	–	–	–	X	4R
Onchopristis dunklei	Sclerorhynchidae; Sclerorhynchiformes	–	–	–	X	–	4S, T
Sclerorhynchidae indet.[s]	Sclerorhynchidae; Sclerorhynchiformes	–	X	–	–	X	4U
Cretomanta canadensis[t]	?Batomorphii *incertae sedis*	–	**X**	**X**	**X**	**X**	4V
Osteichthyes (non-tetrapod taxa)							
Hadrodus(?) sp.	Pycnodontidae; Pycnodontiformes	–	–	–	X	–	5A, B
Micropycnodon kansasensis[u]	Pycnodontidae; Pycnodontiformes	–	**X**	–	**X**	**X**	5C, D
cf. *Palaeobalistum* sp.[v]	Pycnodontidae; Pycnodontiformes	–	X	–	–	X	5E, F
Caturidae indet.	Caturidae; Amiiformes	–	X	–	X	–	5G
Belonostomus sp.[w]	Aspidorhynchidae; Aspidorhynchiformes	–	X	–	X	–	5H
Actinopterygii indet.[x]	Actinopterygii *incertae sedis*	–	–	–	X	X	5I
Protosphyraena sp.	Pachycormidae; Pachycormiformes	–	**X**	–	**X**	**X**	5J
Plethodidae indet.[y]	Plethodidae; Tselfatiiformes	–	**X**	–	**X**	**X**	5K
Ichthyodectes cf. *I. ctenodon*[z]	Ichthyodectidae; Ichthyodectiformes	–	X	–	?	–	5L
Xiphactinus audax	Ichthyodectidae; Ichthyodectiformes	–	**X**	–	**X**	**X**	5M
Elopopsis sp.	Pachyrhizodontidae; Elopiformes	–	X	–	–	–	5N
Pachyrhizodus minimus	Pachyrhizodontidae; Elopiformes	–	**X**	–	**X**	**X**	5O, P
cf. *Pachyrhizodus* sp.	Pachyrhizodontidae; Elopiformes	–	–	–	X	X	5Q
cf. Albulidae	Albulidae; Albuliformes	–	–	–	X	X	5R
Salmoniformes indet.[aa]	Salmoniformes indet.	–	X	–	–	–	5S
Enchodus* cf. *E. gladiolus[*]	Enchodontidae; Aulopiformes	–	**X**	–	**X**	**X**	5T, U
Enchodus* cf. *E. shumardi[*]	Enchodontidae; Aulopiformes	–	**X**	–	**X**	**X**	5V, W
Acanthomorpha indet.	Acanthomorpha indet.	–	X	–	–	–	5X
Teleostei indet. (Teleost A)	Teleostei *incertae sedis*	–	–	–	X	X	5Y
Teleostei indet. (Teleost B)	Teleostei *incertae sedis*	–	–	–	X	X	5Z
Teleostei indet. (Teleost C)	Teleostei *incertae sedis*	–	–	–	X	X	AA, AB
Reptilia (non-avian taxa)							
Protostegidae indet.	Protostegidae; Testudines	–	X	–	–	–	6A
Testudines indet.	Testudines *incertae sedis*	–	X	–	–	–	6B
Coniasaurus crassidens[ab]	Dolichosauridae; Squamata; Lepidosauria	–	–	**X**	**X**	**X**	6C, D
Squamata(?) indet.[ac]	Squamata *incertae sedis*; Lepidosauria	–	X	X	–	?	6E

(continued on next page)

Table 1 (*continued*)

Class							
Species	Higher categories	AB	SK	BH	KS	CO	Fig.
Reptilia (non-avian taxa)							
Brachauchenius lucasi[ad]	Pliosauridae; Plesiosauria	–	?	–	X	X	6F
Elasmosauridae indet.[ae]	Elasmosauridae; Plesiosauria	–	X	–	?	?	6G
Polycotylidae indet.	Polycotylidae; Plesiosauria	–	**X**	–	**X**	**X**	6H
Pterodactyloidea indet.	Pterodactyloidea; Pterosauria	–	–	–	X	–	6I
Ornithischia indet.	Ornithischia; Dinosauria	–	X	–	–	–	6J
Aves							
Pasquiaornis hardiei	Baptornithidae; Hesperornithiformes	–	X	–	–	–	6K
Pasquiaornis tankei	Baptornithidae; Hesperornithiformes	–	X	–	–	–	6L
Hesperornithiformes indet.	Hesperornithiformes *incertae sedis*	–	X	–	X	–	6M
Ichthyornis sp.[af]	Ichthyornithidae; Ichthyornithiformes	–	X	–	–	–	6N
Enantiornithine? indet.	?Enantiornithine; ?Enantiornithiformes	–	X	–	–	–	6O

Cicimurri (2001a, pp. 189) reported "plesiosauroids and pliosauroids, chelonioids, pterosaurs, *Protosphyraena, Enchodus*, ichthyodectiform and pycnodont fish, and coelacanth scales" from the Bell Fourche Shale. No specific descriptions or figures of these taxa were provided; as such, we have not included this information in the table.

Cumbaa et al. (2006) reported specimens referred to *Ptychodus* sp, *Carcharias* sp. and *Enchodus* sp.; however, they may belong to the reported species of the respective genera and thus these taxa are not listed in this table. Other taxa known from the Woodbine Group (including Pepper Formation) of Texas based on Russell (1988), Welton and Farish (1993) and Cappetta and Case (1999): *Hybodus butleri*, *Lissodus breve*, *Lissodus* spp., cf. *Odontaspis striatula*, "*O. gracilis*," cf. *O. subulata*, *Scapanorhynchus* aff. *S. praeraphiodon*, *S. rhaphiodon*, *Squalicorax baharijensis*, *S. kaupi* (based on misidentification by Bilelo, 1969), *Leptostyrax macrorhiza*, "*Lamna planidens*," *Protolamna* aff. *P. sokolovi*, *Protolamna* sp., *Paraisurus compressus*, cf. *Squatirhina aegyptiaca*, ?*Squatirhina* sp., *Chiloscyllium greeni*, *Cantioscyllium decipiens*, *Cantioscyllium* sp., Scyliorhinidae gen. indet., *Ptychotrygon hooveri*, *P. slaughteri*, *P. texana*, *P. triangularis*, *Enantiobatis tarrantensis*, *Dasyatis* spp., ?Dasyatidae, Hypolophidae gen. indet., *Apocopodon* sp., *Ceratodus* sp., *Microdon* sp., *Anomoeodus* sp., *Lepidotus mantelli*, Chelonia gen. indet., Mesosuchia gen. indet., Taeniolabidoidea gen. indet., and Theria gen. indet.

[a] Cicimurri (2001a) and Cook et al. (2008) reported it as *Hybodus* sp.; Cumbaa et al. (2006) as *Hybodus butleri.* Here we follow Underwood and Cumbaa (2010).

[b] Shimada et al. (2006) and Shimada and Martin (2008) reported material as *Ptychodus* cf. *P. anonymus*.

[c] Cicimurri (2001a) also reported material as *Ptychodus* cf. *P. occidentalis*.

[d] Underwood and Cumbaa (2010) reported the material from SK and CO as *Ptychodus* ex. gr. *decurrens*.

[e] Taxon that may consist of multiple species.

[f] Shimada and Martin (2008) reported it as *Cardabiodon venator*; the taxon may be referable to *C. ricki* (Siverson, personal communication to K. Shimada, 2007).

[g] Includes material referred to as *Cretoxyrhina mantelli*, here we follow Underwood and Cumbaa (2010).

[h] Cumbaa et al. (2006) and Cook et al. (2008) reported it as *Archaeolamna* sp.; Shimada et al. (2006) and Shimada and Martin (2008) reported material as *Archaeolamna* cf. *A. kopingensis*; a tooth reported as *Dallasiella willistoni* by Cook et al. (2008) is likely *Archaeolamna kopingensis* (Underwood and Cumbaa, 2010).

[i] Includes rare teeth from localities in SK that are referred to *Cretalamna* sp. by Underwood and Cumbaa, 2010.

[j] Cumbaa et al. (2006) reported *Carcharias* cf. *C. amonensis* and *Dallasiella willistoni* from SK; these specimens are now identified as *Roulletia canadensis*. *Roulletia canadensis* co-occurs in CO with *C. amonensis* (Underwood and Cumbaa, 2010).

[k] Shimada et al. (2006) and Shimada and Martin (2008) reported it as *Carcharias tenuiplicatus*; for taxonomic discussion, see Underwood and Cumbaa (2010), Cumbaa et al. (2006) reported it as *Cenocarcharias tenuiplicatus*; may also include *Carcharias tenuiplicatus* of Cicimurri (2001b).

[l] Shimada et al. (2006) reported it as *Johnlongia* cf. *J. parvidens.*

[m] Includes specimens identified as *Carcharias amonensis* (Cumbaa et al., 2006; Shimada et al., 2006) and as *Dallasiella willistoni* (Cumbaa et al., 2006); here we follow Underwood and Cumbaa, 2010.

[n] Shimada et al. (2006) reported it as cf. *Johnlongia* sp. (see Shimada, 2007).

[o] Cook et al. (2008) reported it as *Squalicorax* sp. (see Underwood and Cumbaa, 2010)

[p] Material referred to as *Squalicorax falcatus* in North America may belong to different *Squalicorax* species according to Siverson et al. (2007).

[q] Includes material referred to as *Squalicorax volgensis*; here we follow Underwood and Cumbaa (2010).

[r] Includes *Rhinobatos* sp. of Shimada et al. (2006) and Shimada and Martin (2008) and may include *Rhinobatis incertus* of Cicimurri (2001b) (see Underwood and Cumbaa, 2010)

[s] Oral teeth from the Bainbridge River locality, SK, reported by Cumbaa et al. (2006) may not be conspecific with rostral teeth from CO reported by Shimada et al. (2006).

[t] It has been suggested that material referred to this taxon may represent dermal scales of a pycnodont, *Micropycnodon kansasensis* (Shimada and Martin, 2008); however, there is a pulp cavity and we follow the use in Underwood and Cumbaa, 2010.

[u] Shimada et al. (2006) reported it as *Micropycnodon* cf. *M. kansasensis*, and Cumbaa et al. (2006) reported it as *Micropycnodon* sp.; a tooth of cf. "*Nursallia*" sp. reported by Shimada et al. (2006) is re-identified as a tooth of *M. kansasensis* (see Shimada and Martin, 2008).

[v] Includes "*Gyrodus cretaceus*" of Cumbaa et al. (2006) and "unidentified Pycnodontidae" (see Shimada and Martin, 2008).

[w] Includes material referred to Aspidorhynchidae incertae sedis by Shimada and Martin (2008).

[x] May include multiple taxa.

[y] Cumbaa et al.'s (2006) material may not be conspecific with material reported by Shimada et al. (2006), Shimada and Martin (2008) and Shimada and Schumacher (2003) reported a rostral bone of *Thryptodus* cf. *T. zitelli* in central Kansas from a slightly higher horizon than materials described by Liggett et al. (2005) and Shimada and Martin (2008).

[z] The possible occurrence in KS is noted by Shimada and Martin (2008).

[aa] Shimada et al. (2006) and Shimada and Martin (2008) reported numerous unidentified osteichthyan vertebrae, which may include this taxon.

[ab] Liggett et al. (2005) reported it as *Coniasaurus* cf. *C. crassidens*; Cumbaa et al. (2006) reported ?*Coniasaurus crassidens* from Bainbridge River locality, SK, but the material is subsequently identified as Squamata indet. (see Shimada and Ystesund, 2007); Shimada et al. (2006) reported teeth of Mosasauroidea incertae sedis, but they are subsequently re-identified as teeth of *Coniasaurus crassidens* (see Polcyn et al., 2008).

[ac] VonLoh and Bell (1998) and Shimada et al. (2006) reported teeth of Squamata(?) incertae sedis but also noted that they may be teleostean in origin; even if they are in fact from a squamate, they likely represent teeth of a squamate that is different from a squamate (originally assigned to ?*Coniasaurus crassidens*) reported by Cumbaa et al. (2006).

[ad] Shimada et al. (2006) assigned their material to cf. *Brachauchenius* sp.; Cumbaa et al. (2006) reported Pliosauridae indet. from SK but some teeth are tentatively assigned to *Brachauchenius lucasi* here.

[ae] The questionable occurrences in CO and KS are based on material identified Plesiosauria indet. by Liggett et al. (2005) and Shimada et al. (2006).

[af] Tokaryk et al. (1997) reported three species of *Ichthyornis* sp. (referred as species A, B, and C) but they may be conspecific and are treated as such here. *Ichthyornis* is also reported from the Bainbridge River locality, SK (Cumbaa et al., 2006).

There are a few other studies on Cenomanian marine vertebrates from North America that are not included here because of the need to refine their geographic and/or chronostratigraphic ranges, re-examine taxonomic assignments, and/or analyze associated faunal components in order to conduct adequate comparisons. Examples include studies of chondrichthyan faunas by Kirkland (1989), Williamson et al. (1993), and Case (2001), and a primarily osteichthyan fauna by Wilson and Chalifa (1989; see also Fox, 1984; originally described as Turonian, but re-interpreted as late Cenomanian in age by Varban and Plint, 2005; Rylaarsdam et al., 2006). A few mid-Cenomanian vertebrate specimens have been reported separately that are not included in our Table 1 or discussion, but which may help characterize the WIS vertebrate fauna of the time. These include a paraclupeid fish, *Tycheroichthys dunveganensis* from the Dunvegan Formation of northwestern Alberta (Hay et al., 2007), a plethodid fish, *Thryptodus* cf. *T. zitteli* from the basal Greenhorn Limestone of Kansas (Shimada and Schumacher, 2003), and a small goniopholidid crocodile, *Coelosuchus reedi*, from the Graneros Shale of Wyoming (Williston, 1906). VonLoh and Bell (1998) reported *Polyptychodon interruptus* from the Orman Lake Member of the Greenhorn Limestone in South Dakota; however, that taxon is best referred to Pliosauridae indet., and needs further examination (see Schumacher, 2008). That record is also not included in Table 1.

Besides North America, Cenomanian vertebrate localities are sporadically distributed nearly worldwide, including Asia, Russia, Europe, the Middle East, Africa, Australia, and South America (e.g., Glickman and Shvazhaite, 1971; Cappetta, 1980a, 1980b, 1987; Werner, 1990; Siverson, 1996, 1999; Underwood and Mitchell, 1999; Sato and Storrs, 2000; Antunes and Cappetta, 2002; Smith and Batten, 2002; Forey et al., 2003; Caldwell, 2000; Caldwell and Lee, 1997; Vullo et al., 2003, 2005, 2009; Pereira and Medeiros, 2008). However, the comparisons of our data with those studies are beyond the scope of this study, primarily because holistic studies examining all vertebrate components together from a stratigraphically well-constrained unit (e.g., Cumbaa et al., 2006; Shimada et al., 2006) are scarce.

3. Results

3.1. Taxonomic compositions and faunal comparisons

The five mid-Cenomanian faunas examined here are rich in vertebrate taxa (Table 1). Cook et al. (2008) reported at least eight taxa of chondrichthyans in the Alberta fauna. Cumbaa et al. (2006) reported a total of at least 22 cartilaginous fishes, 14 bony fishes, and 12 tetrapod taxa in the Saskatchewan fauna. Cicimurri (2001a,b) reported 14 taxa of cartilaginous fishes from the Black Hills region. Liggett et al. (2005) reported four reptilian taxa in the Kansas fauna, followed by Shimada and Martin's (2008) study that added at least 19 cartilaginous fishes and 16 bony fishes to the fauna. In addition, Everhart and Bell (2009) added a hesperornithiform bird to the Kansas fauna. Shimada et al.'s (2006) study on the Colorado fauna showed at least 26 cartilaginous fishes, 15 bony fishes, and at least three reptilian taxa. Together, these faunas constitute the largest sample available to date for characterizing middle to early late Cenomanian marine vertebrate assemblages from North America.

3.2. Faunal commonalities and distinctiveness

The discussion below is based on Table 1, which summarizes the taxonomic composition of each fauna and reflects our attempt to standardize taxonomic names and interpretations from each of the original papers. Table 1 shows that there are at least 70 vertebrate taxa recorded from the five mid-Cenomanian localities combined. These vertebrate taxa include at least 41 chondrichthyans, 21 osteichthyans, nine non-avian tetrapods, and five avian taxa. However, it must be noted that not all of the studies reported on chondrichthyan, osteichthyan, and tetrapod remains from each locality, even if they were present. For example, osteichthyan, and reptilian remains were not described by Cicimurri (2001a, b). He did note, without any specific descriptions or figures, the co-occurrence of “plesiosauroids and pliosauroids, chelonioids, pterosaurs, *Protosphyraena*, *Enchodus*, ichthyodectiform and pycnodont fish, and coelacanth scales” (Cicimurri, 2001a). However, VonLoh and Bell (1998) did examine the marine reptiles of the Black Hills region. As well, Cook et al. (2008) only documented the elasmobranch taxa that were recovered from the Dunvegan Formation localities of Alberta.

3.2.1. Chondrichthyan taxa

Cartilaginous fishes (Figs. 3 and 4) that are common to all five of these geographically widespread faunas include the following two shark taxa (Table 1): *Cretodus semiplicatus* (Fig. 3Q) and *Squalicorax curvatus* (Fig. 4I). In addition to these two species, six taxa are common to four of the five localities. They include: *Ptychodus anonymus* (Fig. 3F), *P. occidentalis* (Fig. 3H), *Cretoxyrhina mantelli* (Fig. 3P), *Archaeolamna kopingensis* (Fig. 3S), *Rhinobatos* cf. *R. incertus* (Fig. 4P), and *Cretomanta canadensis* (Fig. 4V). Common to three of the five localities, in addition to the preceding taxa, are *Meristodonoides rajkovichi* (Fig. 3C), *Ptychodus decurrens* (Fig. 3G), *Carcharias amonensis* (Fig. 4A), *C. saskatchewanensis* (Fig. 4B), and *Paleoanacorax* aff. *P. pawpawensis* (Fig. 4L). Thus, 13 of the 35 chondrichthyan taxa are shared by at least three of our five localities.

3.2.2. Osteichthyan taxa

Bony fishes (Fig. 5) were present and described from only three of our five regional ‘localities’: Saskatchewan, Kansas, and Colorado. However, seven taxa are common to all three localities (Table 1): *Micropycnodon kansasensis* (Fig. 5C, D), *Protosphyraena* sp. (Fig. 5J), Plethodidae indet. (Fig. 5K), *Xiphactinus audax* (Fig. 5M), *Pachyrhizodus minimus* (Fig. 5O, P), *Enchodus* cf. *E. gladiolus* (Fig. 5T, U), and *Enchodus* cf. *E. shumardi* (Fig. 5V, W). Bony fish taxa found in two of the three faunas, in addition to the above, include: cf. *Palaeobalistum* sp. (Fig. 5E, F) in Colorado and Saskatchewan; Caturidae indet. (Fig. 5G) and *Belonostomus* sp. (Fig. 5H) in Kansas and Saskatchewan; and Actinopterygii indet. (Fig. 5I), cf. *Pachyrhizodus* sp. (Fig. 5Q), cf. Albulidae (Fig. 5R), Teleostei indet. A (Fig. 5Y), Teleostei indet. B (Fig. 5Z), and Teleostei indet. C (Fig. AA, AB) in Kansas and Colorado.

3.2.3. Tetrapod taxa

Remains of tetrapod taxa (Fig. 6) are far less common than fish remains at the localities situated in Saskatchewan, the Black Hills, Kansas, and Colorado (and presumably also in Alberta). However, they are represented by diverse sizes and forms (Table 1). For example, both long- and short-necked plesiosaurs (Fig. 6F–H) are common to three of the geographically widespread faunas. The aquatic lizard *Coniasaurus* (Fig. 6C, D) is common to the Black Hills, Kansas and Colorado faunas, although it has not been recorded in the Saskatchewan fauna.

3.2.4. Unique faunal records

Whereas the Saskatchewan fauna includes unique (found only in one of the five faunas described herein) land-dwelling taxa (e.g., terrestrial lizard and dinosaur: Fig. 6E, J), there are a few marine taxa that are unique to each of the five faunas treated here (Table 1). In the Dunvegan fauna of Alberta, there are two chondrichthyan taxa unique to our grouping: *Protolamna carteri* (Fig. 3R) and *Pseudohypolophus mcnultyi* (Fig. 4O). The unique elements of the Saskatchewan fauna include the following taxa: chondrichthyans such as *Edaphodon* sp. (Fig. 3A), Chimaeroidea indet. (Fig. 3B), *Hybodus* sp. (Fig. 3D, E), *Ptychodus rhombodus* (Fig. 3I), *Eostriatolamia paucicorrugata* (Fig. 4D), *Cretorectolobus robustus* (Fig. 3K), and *Orectoloboides angulatus* (Fig. 3L); and *Cretoxyrhina denticulata* (Fig. 3O); osteichthyan taxa such as *Elopopsis* sp. (Fig. 5N), and Acanthomorpha indet. (Fig. 5X); and tetrapods such as turtles (a protostegid and at least one undetermined taxon: Fig. 6A, B), and birds such as *Pasquiaornis hardiei* (Fig. 6K), *P. tankei* (Fig. 6L), and at least one species of *Ichthyornis* (Fig. 6N). The chondrichthyan unique to the Black Hills fauna is *Squatina* sp. (Fig. 4N). Unique aspects of the Kansas fauna include chondrichthyan taxa such as Rajidae *incertae sedis* (Fig. 4Q) and *Onchopristis dunklei* (Fig. 4S, T); an osteichthyan, *Hadrodus*(?) sp. (Fig. 5A, B); and a pterosaur (Fig. 6I). Unique taxonomic components of the Colorado fauna include the following chondrichthyans: cf. *Pararhincodon* sp. (Fig. 3J), *Megachasma comanchensis* (Fig. 4G), *Microcorax crassus* (Fig. 4H), Carcharhiniformes indet. (Fig. 4M), and *Ptychotrygon* sp. (Fig. 4R).

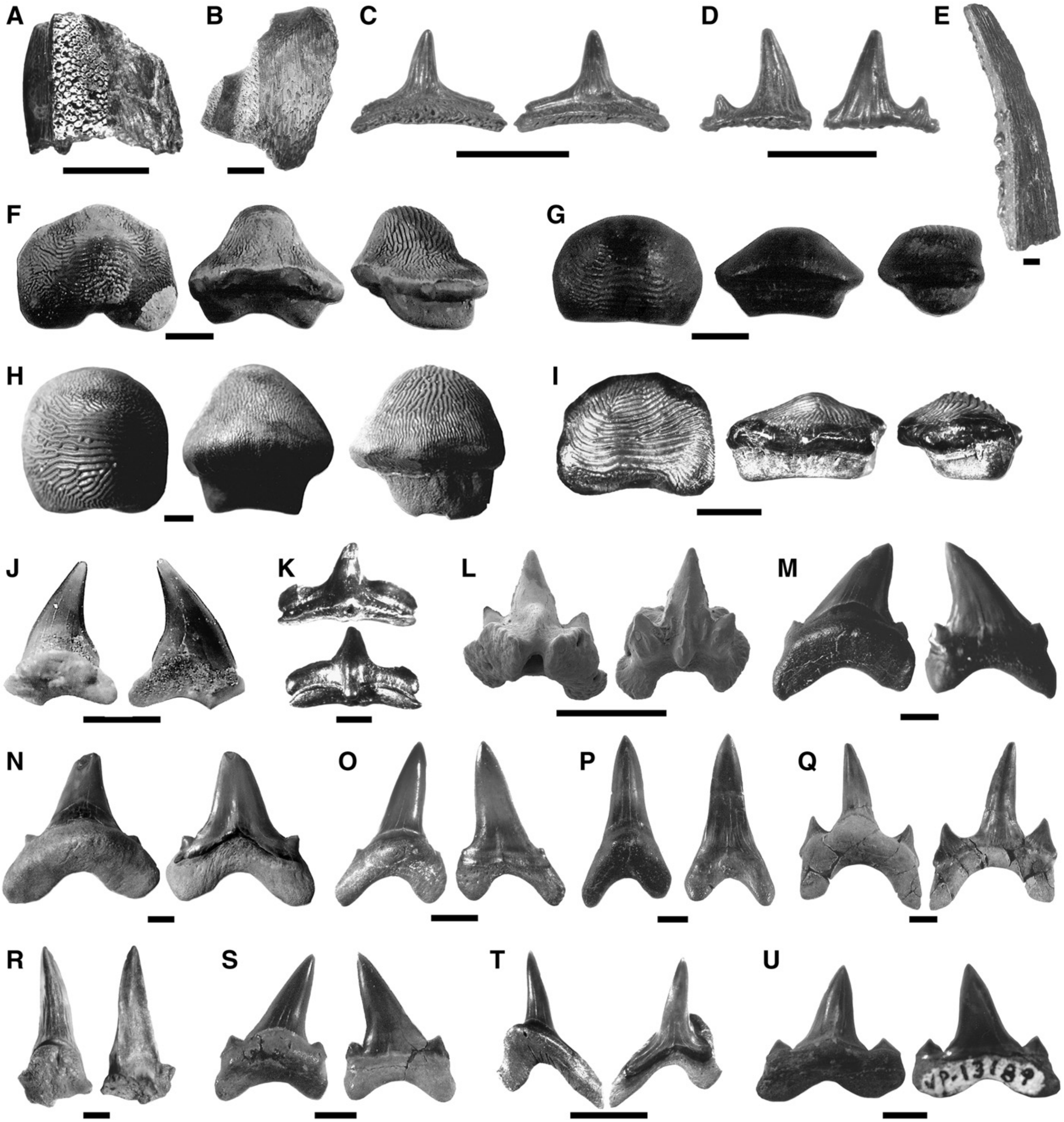


Fig. 3. Representative specimens of mid-Cenomanian chondrichthyan fishes of North American Western Interior Sea (continue to Fig. 4). A) *Edaphodon* sp. (RSM P2989.43; partial palatine plate from Saskatchewan, Canada); B) Chimaeroidea indet. (RSM P2626.21, mandible from Saskatchewan, Canada); C) *Meristodonoides rajkovichi* Underwood and Cumbaa (RSM P2626.22, tooth from Saskatchewan, Canada); D) *Hybodus* sp. (RSM P2995.10, tooth from Saskatchewan, Canada); E) *Hybodus* sp. (RSM P2077.82, dorsal fin spine from Saskatchewan, Canada); F) *Ptychodus anonymus* Williston (FHSM VP-15071, tooth from Colorado, U.S.A.); G) *Ptychodus decurrens* Agassiz (FHSM VP-15073, tooth from Colorado, U.S.A.); H) *Ptychodus occidentalis* Leidy (one of three teeth in FHSM VP-16712 from Kansas, U.S.A.); I) *Ptychodus rhombodus* Underwood and Cumbaa (RSM P2989.52, tooth from Saskatchewan, Canada); J) cf. *Pararhincodon* sp. (FHSM VP-15098, tooth from Colorado, U.S.A.); K) *Cretorectolobus robustus* Underwood and Cumbaa (RSM P2989.188, tooth from Saskatchewan, Canada); L) *Orectoloboides angulatus* Underwood and Cumbaa (RSM P2989.176, tooth from Saskatchewan, Canada); M) *Cardabiodon venator* Siverson (one of 25 teeth in FHSM VP-16701, from Kansas, U.S.A.); N) Cardabiodon sp. (FHSM VP-16718, tooth from Kansas, U.S.A.); O) *Cretoxyrhina denticulata* Glickman (RSM P2989.67, tooth from Saskatchewan, Canada); M) *Cardabiodon venator* Siverson (one of 25 teeth in FHSM VP-16701, from Kansas, U.S.A.); N) *Cardabiodon* sp. (FHSM VP-16718, tooth from Kansas, U.S.A.); O) *Cretoxyrhina denticulata* Glickman (RSM P2989.67, anterior tooth from Saskatchewan, Canada); P) *Cretoxyrhina mantelli* (Agassiz) (FHSM VP-15093, tooth from Colorado, U.S.A.); Q) *Cretodus semiplicatus* (Munster) (FHSM VP-15089, tooth from Colorado, U.S.A.); R) *Protolamna carteri* Cappetta and Case (UALVP 49419, tooth from Alberta, Canada); S) *Archaeolamna kopingensis* (Davis) (FHSM VP-15087, tooth from Colorado, U.S.A.); T) *Telodontaspis* agassizensis Underwood and Cumbaa (P2989.144, tooth from Saskatchewan, Canada); U) *Cretalamna appendiculata* (Agassiz) (FHSM VP-13189, tooth from Kansas, U.S.A.). Orientations: A, B, occlusal view; C, D, J–U, left (or top) = lingual view, right (or below) = labial view; E, right lateral view; F–I, from left to right = occlusal, anterior, profile views. Scale: A–I, M–Q, S–U = 5 mm; J–L, R = 1 mm.

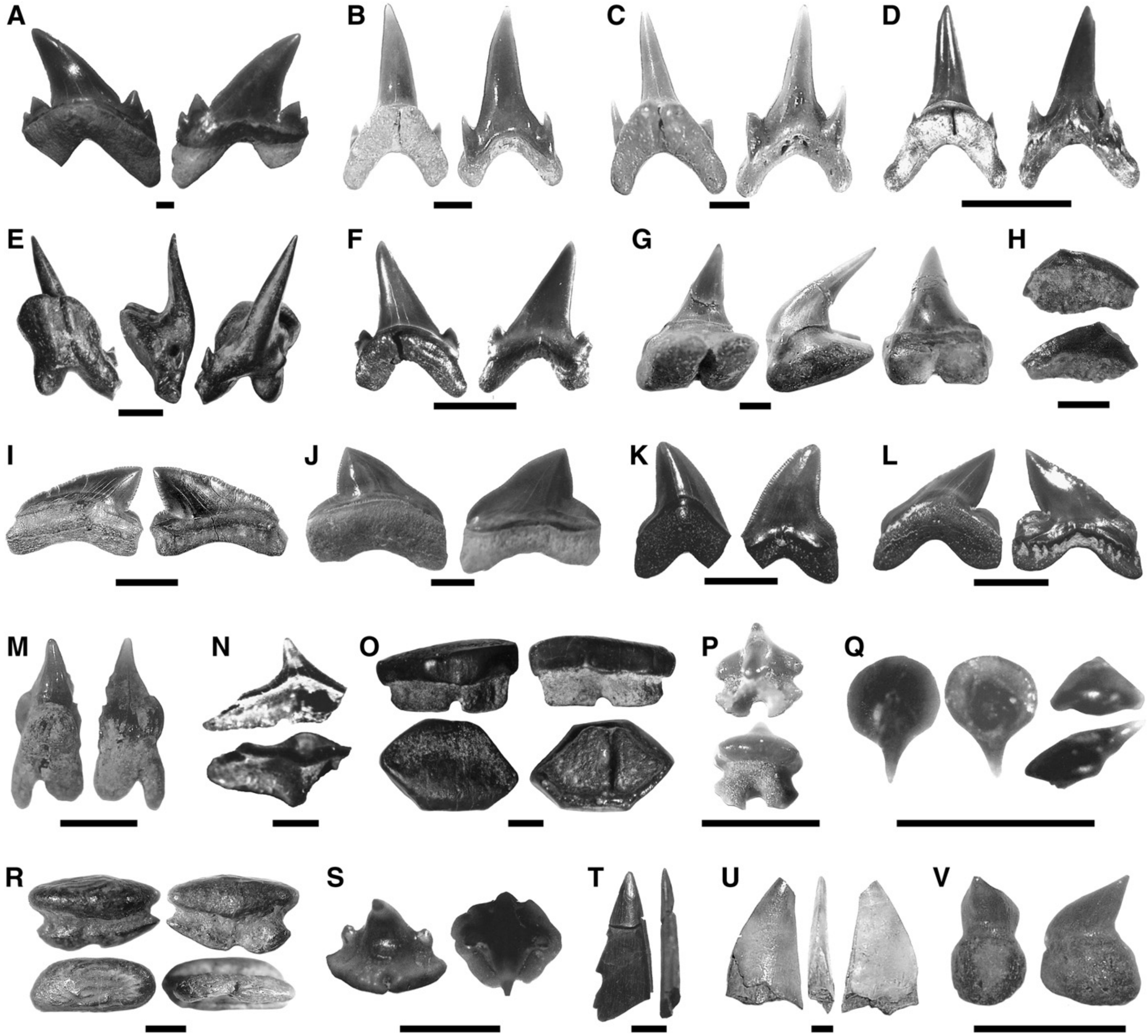
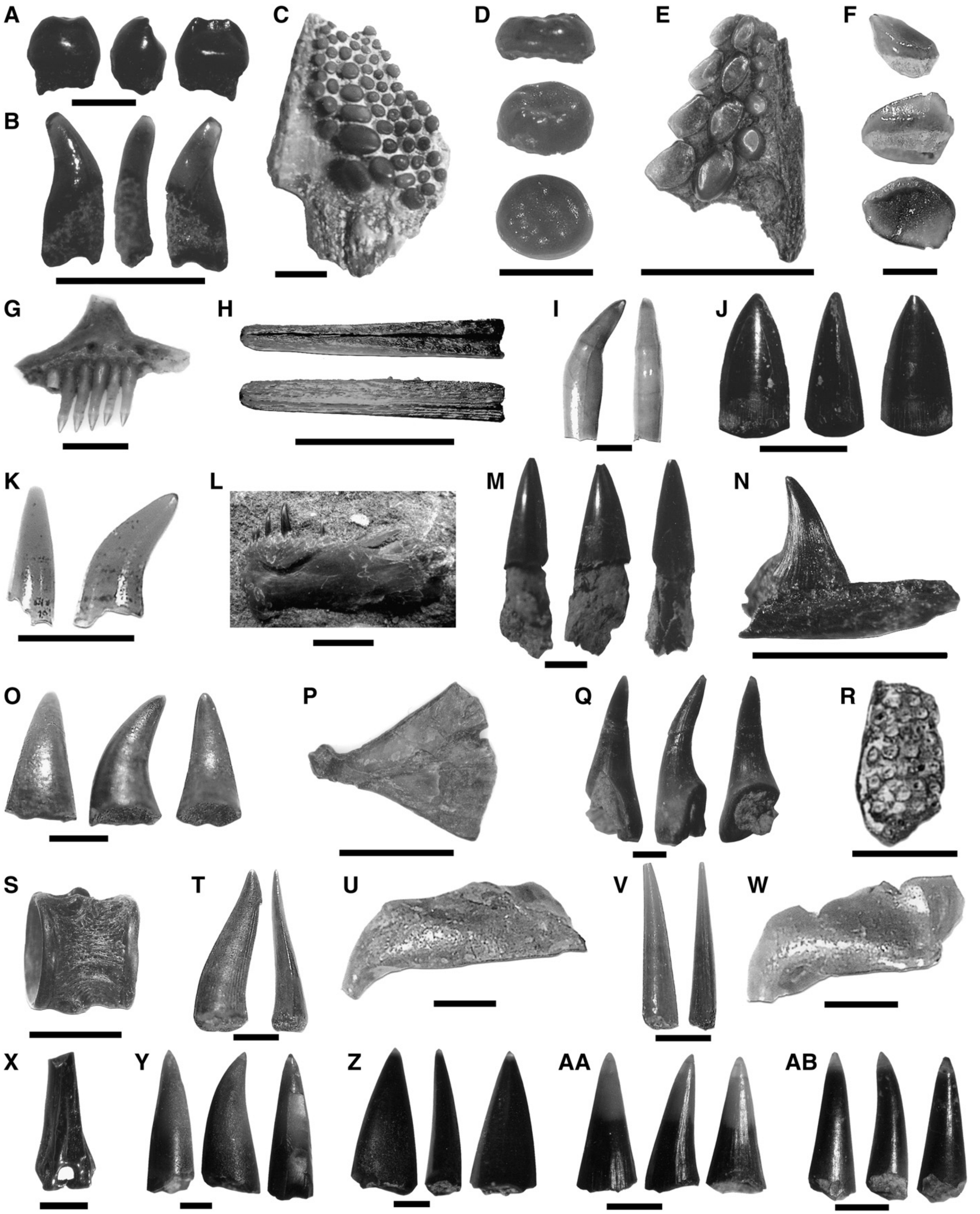


Fig. 4. Representative specimens of mid-Cenomanian chondrichthyan fishes of North American Western Interior Sea (continued from Fig. 3). A) *Carcharias amonensis* (Cappetta and Case) (one of 14 teeth in FHSM VP-13209 from Kansas, U.S.A.); B) *Carcharias saskatchewanensis* (Case, Tokaryk, and Baird) (FHSM VP-15085, tooth from Colorado, U.S.A.); C) *Eostriatolamia tenuiplicatus* (Cappetta and Case) (FHSM VP-15086, tooth from Colorado, U.S.A.); D) *Eostriatolamia paucicorrugata* Underwood and Cumbaa (RSM P2989.85, tooth from Saskatchewan, Canada); E) *Johnlongia parvidens* (Cappetta) (UALVP 49421, tooth from Alberta, Canada); F) *Roulletia canadensis* Underwood and Cumbaa (RSM P2989.95, tooth from Saskatchewan, Canada); G) *Megachasma comanchensis* Shimada (FHSM VP-15095, tooth from Colorado, U.S.A.); H) *Microcorax crassus* Cappetta and Case (FHSM VP-15079, tooth from Kansas, U.S.A.); I) *Squalicorax curvatus* Williston (FHSM VP-15080, tooth from Colorado, U.S.A.); J) *Squalicorax falcatus* (Agassiz) FHSM VP-15082, tooth from Kansas, U.S.A.); K) *Squalicorax* sp. (one of six teeth in FHSM VP-16706 from Kansas, U.S.A.); L) *Palaeoanacorax* aff. *P. pawpawensis* Siverson (one of six teeth in FHSM VP-14770 from Kansas, U.S.A.); M) Carcharhiniformes indet. (FHSM VP-15096, tooth from Colorado, U.S.A.); N) *Squatina* sp. (one of two teeth in SDSM 34912 from Black Hills region, U.S.A.); O) *Pseudohypolophus mcnultyi* (Thurmond) (UALVP 49428, tooth from Alberta, Canada); P) *Rhinobatos* sp. (FHSM VP-15197, tooth from Colorado, U.S.A.); Q) Rajidae incertae sedis (FHSM VP-16713, tooth from Kansas, U.S.A.); R) *Ptychotrygon* sp. (FHSM VP-15199, tooth from Colorado, U.S.A.); S) *Onchopristis dunklei* McNulty and Slaughter (KUVP 120053, oral tooth from Kansas, U.S.A.); T) *O. dunklei* (FHSM VP-13210, rostral tooth from Kansas, U.S.A.); U) Sclerorhynchidae indet. (FHSM VP-15200, rostral tooth from Colorado, U.S.A.); V) *Cretomanta canadensis* Case, Tokaryk, and Baird (FHSM VP-15100, tooth from Colorado, U.S.A.). Orientations: A–D, F, H-M, P, left (or top) = lingual view, right (or bottom) = labial view; E, G, from left to right = lingual, profile, labial views; N, S, top = lingual view, bottom = occlusal view; O, R, clockwise from top left = lingual, labial, basal, and occlusal views; Q, clockwise from left = occlusal, basal, labial, and profile views; L, from left to right = lingual, profile, occlusal views; T, left = dorsal view, right = anterior view; U, from left to right = dorsal, anterior, ventral views; V, left = lingual view, right = profile view. Scale: all 1 mm.

4. Discussion

4.1. Taxonomic composition

Russell (1988, 1993) reviewed published records of North American marine Cretaceous vertebrate assemblages and introduced the concept of North American Marine Vertebrate Ages "in the hope that they might serve as conceptual guides for the future elucidation of the evolution of marine vertebrate faunas" (Russell, 1988, 1993, p. 667). The faunas discussed here correspond to Russell's (1993) 'Woodbinian Age' based on the marine vertebrate assemblage of the Woodbine Group of north-central Texas that is approximately middle Cenomanian in age. Russell (1988, 1993) characterized his 'Woodbinian Age' largely by faunal absences rather than presence, by describing that ichthyosaurs had already become extinct (e.g., Shimada, 1996), mosasaurs had not yet appeared (e.g., Polcyn et al., 2008), and hybodont sharks and durophagous fishes such as pycnodonts and semionotids were not as diverse as they had been earlier (e.g., Barck, 1992; Cicimurri, 2000; Everhart, 2004). At the time of Russell's (1988) compilation, the Woodbine Group of Texas represented the most taxonomically rich middle Cenomanian vertebrate fauna reported from North America, consisting of almost 40



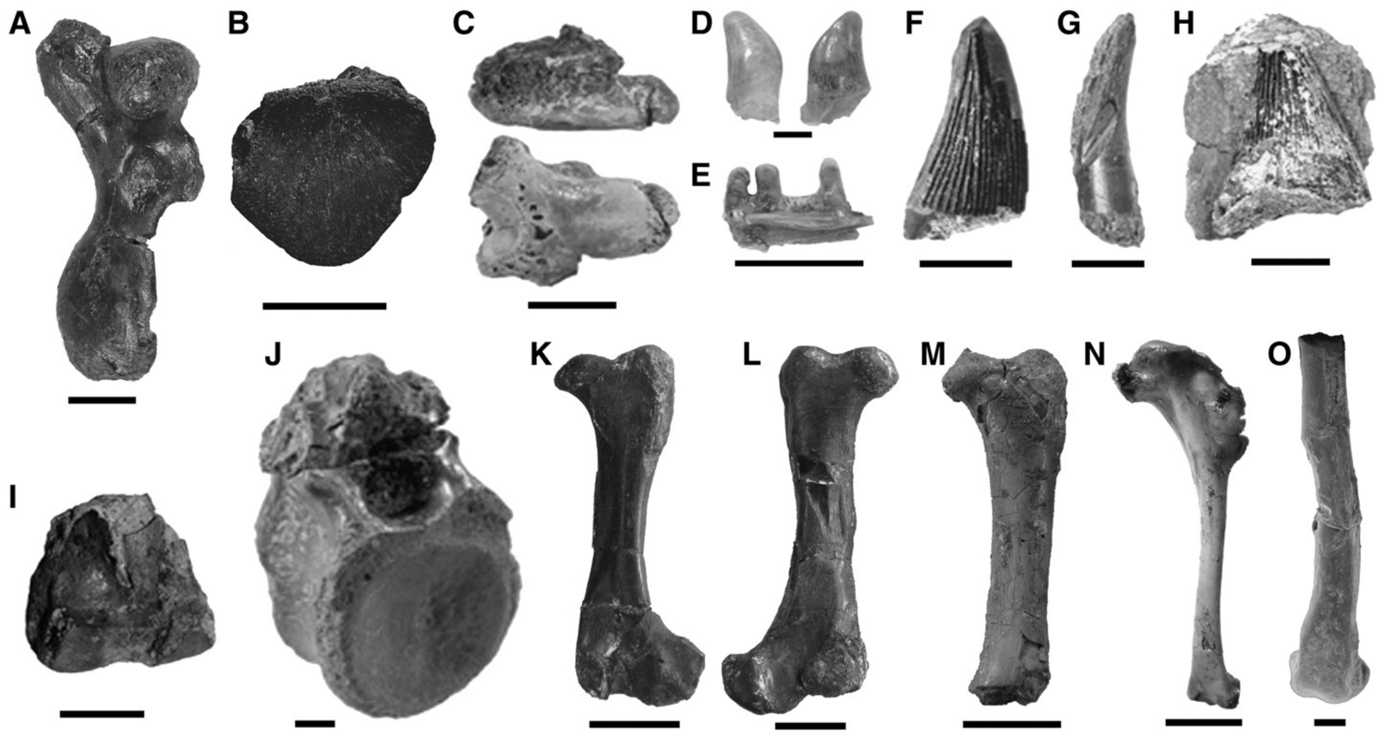


Fig. 6. Representative specimens of mid-Cenomanian tetrapods of North American Western Interior Sea. A) Protostegidae indet. (RSM P2077.64, right humerus from Saskatchewan, Canada: dorsal view); B) Testudines indet. (RSM P2989.42, pygal from Saskatchewan, Canada: dorsal view); C) *Coniasaurus crassidens* Owen (FHSM VP-15113, vertebra from Colorado, U.S.A.: top = left lateral view; bottom, ventral view); D) *C. crassidens* (FHSM VP-15270, tooth from Colorado, U.S.A.: left = anterior view; right = labial view); E) of Squamata(?) indet. (RSM P2626.26, partial right mandible with three teeth from Saskatchewan, Canada: lingual view); F) *Brachauchenius lucasi* Williston (one of two teeth in FHSM VP-14782 from Kansas, U.S.A.: profile view); G) Elasmosauridae indet. (RSM P2409.416, tooth from Saskatchewan, Canada: profile view); H) Polycotylidae indet. (RSM P2467.9, tooth in matrix from Saskatchewan, Canada: profile view); I) Pterodactyloidea indet. (FHSM VP-13998, distal end of right femur from Kansas, U.S.A.: posterior view); J) Ornithischia indet. (RSM P2409.415, vertebra from Saskatchewan, Canada: oblique view); K) *Pasquiaornis hardiei* Tokaryk, Cumbaa and Storer (SMNH P2077.60, right femur from Saskatchewan, Canada: posterior view); L) *P. tankei* Tokaryk, Cumbaa and Storer (SMNH P2077.108, left femur from Saskatchewan, Canada: posterior view); M) Hesperornithiformes indet. (RSM P2988.1, right femur from Saskatchewan, Canada: posterior view); N) *Ichthyornis* sp. (RSM P2988.8, right humerus from Saskatchewan, Canada: lateral view); O) Enantiornithine? indet. (SMNH P2077.66, distal half of metatarsal from Saskatchewan, Canada: dorsal view). Scale: A, B, F–*N* = 10 mm; C, E = 5 mm; D, O = 1 mm.

vertebrate taxa (including terrestrial mammals). However, as pointed out by Shimada et al. (2006), the reported 'Woodbine fauna' must be regarded as a significantly time-averaged assemblage because the fossils come from multiple stratigraphic horizons at multiple localities, likely formed under diverse depositional environments. Nevertheless, Russell's (1988, 1993) work was significant because it represented the first attempt to examine the evolution of WIS faunas, and it is still a benchmark for comparative studies of Cretaceous marine vertebrate faunas.

Marine components of the 'Woodbine fauna' of Texas listed by Russell (1988) included 29 chondrichthyan taxa, four osteichthyan taxa, a turtle, and a crocodilian. By way of comparison, the mid-Cenomanian marine faunas reported here contain 41 chondrichthyans, 21 osteichthyans, two taxa of turtles, three plesiosaur taxa, a dolichosaur, a pterosaur, and at least four taxa of marine birds (Table 1). We did not examine the 'Woodbine fauna' to the fullest extent because of its poor constraints in spatial and stratigraphic ranges. However, from Russell's (1988) list, supplemented by data presented by Welton and Farish (1993) and Cappetta and Case (1999), the 'Woodbine fauna' and those reported here share a number of species (Table 1). Whereas only slightly less than half of the cosmopolitan chondrichthyan taxa (e.g., see Cappetta, 1987) are common to these faunas, it is clear that the osteichthyan, non-avian reptilian, and avian components are quite distinctive in the more northern faunas. For example, the following seven chondrichthyan species are reported from the Woodbine Group as well as from at least three of our five localities: *Ptychodus decurrens*, *Cretoxyrhina mantelli*, *Cretodus semiplicatus*, *Cretalamna appendiculata*, *Carcharias amonensis*,

Fig. 5. Representative specimens of mid-Cenomanian osteichthyan fishes of North American Western Interior Sea. A) *Hadrodus*(?) sp. (FHSM VP-16727, incisiform tooth from Kansas, U.S.A.); B) *Hadrodus*(?) sp. (one of two pharyngeal teeth in FHSM VP-16726 from Kansas, U.S.A.); C) *Micropycnodon kansasensis* (Hibbard and Graffham) (FHSM VP-15548, right prearticular with teeth from Kansas, U.S.A.); D) *M. kansasensis* (FHSM VP-15103, tooth from Colorado, U.S.A.); E) cf. *Palaeobalistum* sp. (RSM P2985.11, left prearticular with teeth from Saskatchewan, Canada); F) cf. *Palaeobalistum* sp. (FHSM VP-15106, tooth from Colorado, U.S.A.); G) Caturidae indet. (RSM P2983.58, premaxilla with teeth from Saskatchewan, Canada); H) *Belonostomus* sp. (RSM P2983.59, dentary with teeth from Saskatchewan, Canada); I) Actinopterygii indet. (FHSM VP-15218, tooth from Colorado, U.S.A.); J) *Protosphyraena* sp. (one of five teeth in FHSM VP-14779 from Kansas, U.S.A.); K) Plethodidae indet. (FHSM VP-15224, tooth from Colorado, U.S.A.); L) *Ichthyodectes* cf. *I. ctenodon* Cope (RSM P2995.11, left dentary from Saskatchewan, Canada); M) *Xiphactinus audax* Leidy (FHSM VP-13213, tooth from Kansas, U.S.A.); N) *Elopopsis* sp. (RSM P2626.23, right dentary with tooth from Saskatchewan, Canada); O) *Pachyrhizodus minimus* Stewart (FHSM VP-15227, tooth from Colorado, U.S.A.); P) *P. minimus* (RSM P2831.60, hypural from Saskatchewan, Canada); Q) cf. *Pachyrhizodus* sp. (FHSM VP-16752, tooth from Kansas, U.S.A.); R) cf. Albulidae (FHSM VP-15233, tooth plate without teeth from Colorado, U.S.A.); S) Salmoniformes indet. (RSM P2626.24, vertebra from Saskatchewan, Canada); T) *Enchodus* cf. *E. gladiolus* (Cope) (FHSM VP-15235, tooth from Colorado, U.S.A.); U) *E.* cf. *E. gladiolus* (FHSM VP-15110, left palatine from Colorado, U.S.A.); V) *E.* cf. *E. shumardi* Leidy (FHSM VP-15241, tooth from Colorado, U.S.A.); W) *E.* cf. *E. shumardi* (FHSM VP-15245, left palatine from Colorado, U.S.A.); X) Acanthomorpha indet. (RSM P2626.25, fin spine from Saskatchewan, Canada); Y) Teleostei indet. (Teleost A) (FHSM VP-16769, tooth from Kansas, U.S.A.); Z) Teleostei indet. (Teleost B) (one of 50 teeth in FHSM VP-16734 from Kansas, U.S.A.); AA) Teleostei indet. (Teleost C) (one of five teeth in FHSM VP-16771 from Kansas, U.S.A.); AB) Teleostei indet. (Teleost C?) (FHSM VP-16756, tooth from Kansas, U.S.A.). Orientations: A, B, J, M, O, Q, Y–AB, from left to right = labial, profile, and lingual views; C, E, R, occlusal view; D, from top to bottom = profile, oblique, occlusal views; F, from top to bottom = anterior, labial, occlusal views; G, lingual view; H, top = occlusal view, bottom = left lateral view; I, left = profile view, right = anterior view; K, left = labial view, right = profile view; L, N, P, S, U, W, lateral view; T, V, left = lingual view, right = mesial view; X, cranial view. Scale: A, B, D, F, G, I, K, O, Q, R, T–AB = 1 mm; C, E, H, J, L–N, P, S = 5 mm.

Squalicorax curvatus, and *Rhinobatos* cf. *R. incertus* (Table 1). However, an additional seven chondrichthyan and six osteichthyan species link three or more of our five localities, suggesting a possible distinct 'northern' assemblage: *Meristodonoides rajkovichi*, *Ptychodus anonymus*, *P. occidentalis*, *Carcharias saskatchewanensis*, *Archaeolamna kopingensis*, *Paleoanacorax* aff. *P. pawpawensis*, *Cretomanta canadensis*, *Micropycnodon kansasensis*, *Protosphyraena* sp., *Xiphactinus audax*, *Pachyrhizodus minimus*, *Enchodus* cf. *E. gladiolus*, and *E.* cf. *E. shumardi* (Table 1). Therefore, there are 20 species of fishes that are known from at least three of the six major mid-Cenomanian localities discussed here, including the Woodbine fauna.

One may postulate that the combination of all the 20 fish species may be used to characterize the 'Woodbinian Age.' However, a number of these species, or closely related species, are also known to occur in the WIS at least into Russell's (1988, 1993) succeeding North American Marine Vertebrate Age, the 'Niobrara Age' that spans the interval from the late Cenomanian through early Campanian. Such taxa include *Ptychodus occidentalis, Cretoxyrhina mantelli, Archaeolamna kopingensis*, *Micropycnodon kansasensis*, *Xiphactinus audax*, *Pachyrhizodus minimus*, *Enchodus gladiolus*, and *E. shumardi* (Stewart, 1990; Martin et al., 1998; Shimada and Fielitz, 2006). Some of these species persisted at least into the mid-Campanian, such as *A. kopingensis*, *X. audax*, *P. minimus*, and *E. gladiolus* (e.g., Beavan and Russell, 1999; Carpenter, 2003).

Several taxa among the 20 listed fish species are much more common in mid-Cenomanian deposits than in any other stratigraphic levels. They include the following eight chondrichthyan species: *Ptychodus decurrens*, *P. occidentalis*, *Squalicorax curvatus*, *Cretodus semiplicatus*, *Carcharias amonensis*, *C. saskatchewanensis*, *Eostriatolamia tenuiplicatus*, and *Cretomanta canadensis* (see also Shimada et al., 2006). Most of these species were uncommon or had not yet appeared prior to the mid-Cenomanian, when non-ptychodontid hybodonts dominated the marine regime (e.g., see Russell, 1988, 1993; Welton and Farish 1993; Shimada et al., 2006). Therefore, the combination of these eight taxa may be used as a primary taxonomic component to characterize the 'Woodbinian Age.' However, because of a large number of commonalities in fish taxa shared between the 'Woodbinian Age' and the 'Niobrara Age' that followed, mid-Cenomanian time, or the 'Woodbinian Age,' can also be characterized by the onset of the 'Niobraran fauna.' This onset of the Niobraran fauna was marked by an increase in the taxonomic diversity of both chondrichthyan and osteichthyan fishes, at a time when ichthyosaurs had already become extinct, and mosasaurs had not yet appeared.

4.2. Paleobiogeography and paleoecology

Paleobiogeographical studies of the WIS have utilized mostly invertebrate faunas. These include Jeletzky's (1968, 1971) cephalopod studies and the work of Sohl (1967, 1971), Kauffman (1973, 1977, 1984) and Scott and Taylor (1977), all of whom used mollusks to propose biogeographical subdivisions of the Seaway. One of the most extensive paleobiogeographical zonation studies was performed by Kauffman (1984). Using macroinvertebrate and foraminiferal distributions, Kauffman subdivided the WIS into multiple subprovinces. From north to south, these biotic units included: the cool temperate 'Northern Interior Subprovince,' the mild temperate 'Central Interior Subprovince,' the warm temperate 'Southern Interior Subprovince,' and the subtropical 'Gulf and Atlantic Coast subprovinces.'

In contrast to the studies on invertebrates, relatively fewer paleobiogeographical studies have been conducted using WIS vertebrate faunas. Building on the invertebrate paleobiogeographic studies, Nicholls and Russell (1990) studied the paleobiogeography of the WIS, using the vertebrate record from early Campanian localities in Alabama, Kansas, South Dakota, Wyoming, southern Manitoba, and the Northwest Territories of Canada near the Arctic coast. Their study emphasized tetrapods, because they considered fish specimens in museum collections to be under-represented, by virtue of taphonomic and other biases (see also Russell, 1988, 1993). They nevertheless detected an overall drop in fish diversity with increasing latitude, especially in shark taxa. For tetrapods, they noted increased percentages of hesperornithiform birds and plesiosaurs in the fauna with increasing latitude, but higher percentages of ichthyornithiform birds and turtles in southern latitudes. These trends were attributed to cooler water temperatures in the north. They concluded by postulating two vertebrate biogeographic subprovinces, the 'Northern Interior Subprovince' and a 'Southern Interior Subprovince,' with the line dividing the two roughly comparable to the southern border of Kansas with Oklahoma. Between-sample temporal and facies (habitat) differences were examined, but Nicholls and Russell (1990) ultimately discounted such biases for the observed trends. It is noteworthy that their two early Campanian vertebrate faunal subprovinces corresponded well to the paleogeographic division proposed by Sohl (1971) for gastropods (Nicholls and Russell, 1990).

The localities in Alberta, Saskatchewan, the Black Hills region (South Dakota and Wyoming), Kansas, and Colorado we examined here are separated by as much as 18° latitude, a north–south distance of more than 2300 km. However, all five of these mid-Cenomanian faunas (Fig. 1A) lie spatially within Nicholls and Russell's (1990) Northern Interior Subprovince. Nicholls and Russell's (1990) study was based on faunas that are about 12 million years younger (early Campanian) than the mid-Cenomanian ones analyzed here. Although the tetrapod components of the Alberta and Black Hills faunas need further examination, one geographic trend that is strikingly similar between our study and Nicholls and Russell's (1990) work is the abundance of bird taxa in the Saskatchewan fauna and the dearth of bird fossils in our extensively examined southern vertebrate assemblages in Kansas and Colorado. Although a hesperornithiform bird element has been recovered from central Kansas to add to its mid-Cenomanian fauna (Everhart and Bell, 2009), bird fossils remain as exceptionally rare components of the Kansas fauna of this age.

Other possible clinal trends include more diverse faunas of benthic chondrichthyans mixed with dolichosaurid lizards to the south (e.g., Kansas and Colorado) compared to the north (Alberta and Saskatchewan). For example, the southern faunas contain more batomorph (ray) taxa in rajiform and sclerorhynchiform groups than the northern faunas. Extant rays are more taxonomically diverse in warmer waters (Compagno, 1999), and it is probable that was also true of rays in Cretaceous seas. Simons et al. (2003) demonstrate that the water column in the northern part of the WIS (e.g., Canada) was less oxygenated in the Cenomanian and Turonian than in much of the United States. The relative rarity of these benthic taxa in the northern localities may be a reflection of the low oxygen level, and thus the relative inhospitability of those waters. *Coniasaurus crassidens*, a small (<1 m in length) dolichosaurid lizard, possibly evolved in Europe (Caldwell and Cooper, 1999) and may have followed the westward, warm, circum-global ocean currents through the Tethys Seaway, across the then-narrow Atlantic Ocean, and into the WIS. Sea-surface temperatures along the route probably ranged between 20 and 30 °C (Jacobs et al., 2005). The presence of *C. crassidens* in our southern faunas and its absence in our northern faunas suggest the possibility that this aquatic reptile preferred a warmer environment.

The aforementioned clinal trends must be viewed as hypotheses. One of the difficulties associated with evaluating such clinal trends is the fact that the two northernmost localities, situated in Alberta and Saskatchewan, likely represent nearshore environments, whereas the other three localities situated in the Black Hills region, Kansas and Colorado, are thought to represent offshore environments during the mid-Cenomanian (Fig. 1A). The presence or absence of certain marine taxa at a given locality may reflect the difference in proximity to the coastline, and thus water depth and substrate preferences, rather than simply the difference in water temperature caused by latitudinal or current flow differences. For example, non-ptychodontid hybodonts (e.g., *Hybodus* and *Meristodonoides*) are commonly regarded as nearshore sharks (Welton and Farish, 1993; Cicimurri, 2001b), and our data (Table 1) can be interpreted to support this notion because the localities situated in Kansas and Colorado, unlike those localities in Alberta and Saskatchewan, have not yielded any hybodont material despite the extensive collecting efforts those sites received. Hybodont shark teeth are known from Kansas in older WIS sediments (upper Dakota Formation, lower Graneros Shale); however, those deposits reflect nearshore or shallow water habitat (e.g., Everhart et al., 2004). The hybodont occurrence in the Black Hills is intriguing, but because non-ptychodontid hybodonts (e.g., *Hybodus* and *Meristodonoides*) are also known from the Woodbine Group of Texas, the distribution cannot be explained by the geographic differences between the north and south. However, as has been postulated (Cicimurri, 2001a; Cumbaa et al., 2006), the basin-wide effect of lowstands would have temporarily created shallow water habitat in all but the deepest parts of the Western Interior Basin. Hattin (1965), for example, suggested that water depth in Kansas during the deposition of the mid-Cenomanian Graneros Shale ranged from less than 30 ft (<9.2 m) early on to about 100 ft (ca. 30 m) at the end of the depositional cycle. Nevertheless, there are differences between 'shallow water' and 'nearshore' habitat that go beyond simple water depth.

An additional noteworthy difference between the northern and southern faunas is with the conspicuous lamniform *Cardabiodon venator*. This species is relatively abundant in the southern faunas, but has not often been reported in the northern faunas. Because teeth of this shark are relatively large, collecting bias is unlikely, but whether or not the difference is due to the geographic trend, habitat (nearshore vs. offshore), or yet another reason, cannot be determined from the present fossil record.

To further complicate the matter, another factor that could have affected the distribution of organisms is water circulation within the WIS. Some paleo-oceanographic reconstructions include gyre concepts (Kauffman, 1977; Slingerland et al., 1996; Kump and Slingerland, 1999), where such a water circulation system might have pulled cooler boreal waters south down the western coast, and warmer Tethyan waters north up the shallow eastern margin. The Slingerland et al. (1996) and Kump and Slingerland (1999) models, however, are early Turonian backcasts.

Interpreting the environmental preferences of each taxon is difficult, but Table 1 also reveals another important aspect of the examined mid-Cenomanian vertebrate faunas: overall, they show strong taxonomic homogeneity. For example, the following chondrichthyans are known from four of the five faunas: *Ptychodus anonymus*, *P. occidentalis*, *Cretoxyrhina mantelli*, *Cretodus semiplicatus*, *Archaeolamna kopingensis*, *Squalicorax curvatus*, *Rhinobatos* cf. *R. incertus*, and *Cretomanta canadensis*. Osteichthyans reported from all three of our localities for which the bony fishes have been studied include: *Micropycnodon kansasensis*, *Protosphyraena* sp., Plethodidae indet., *Xiphactinus audax*, *Pachyrhizodus minimus*, *Enchodus* cf. *E. gladiolus*, and *Enchodus* cf. *E. shumardi*.

A few of the chondrichthyan species were cosmopolitan in both warm and temperate waters, such as *Ptychodus decurrens*, *Cretoxyrhina mantelli*, and *Cretalamna appendiculata* (Cappetta, 1987; Williamson et al., 1993; Underwood and Cumbaa, 2010). This observation implies passage throughout the seaway and beyond, through connections to both the Boreal and Tethys oceans. In addition to genera and species which appear to be endemic to the WIS, including *Ptychodus rhombodus*, *Telodontaspis*, *Eostriatolamia*, *Squalicorax curvatus*, and *Cretomanta canadensis* (Carpenter, 2003; Underwood and Cumbaa, 2010) and those named above which have a global distribution in both warm and temperate waters, we report *Microcorax*, *Rhinobatos*, and *Onchopristis* which appear to have primarily Tethyan distributions, and *Edaphodon*, *Meristodonoides*, *Pararhincodon*, *Protolamna*, *Carcharias*, *Roulletia*, *Archaeolamna*, *Orectoloboides*, and *Cretorectolobus* which could be considered to have primarily more northern affinities or distributions (Werner, 1990; Williamson et al. 1993; Underwood and Cumbaa, 2010). Few of these taxa are exclusively northern or southern in distribution; for example, *Rhinobatos* is present in our Saskatchewan localities, but exceedingly rare, while it is relatively common, for instance, in Texas localities of the same age (Welton and Farish, 1993).

Although the fossil record of osteichthyan taxa needs more attention relative to the chondrichthyan record, this study demonstrates high osteichthyan diversity, not only in the southern faunas, but also in the northern faunas of the WIS (Table 1). The northern portion of the WIS was once thought to have supported only a depauperate, cold-adapted fauna (Nicholls and Russell, 1990). None of the osteichthyan taxa reported here have a primarily Tethyan distribution; a few are endemic (e.g., *Micropycnodon*), but most have a global distribution in warm temperate–cool temperate waters (e.g., *Enchodus*, *Pachyrhizodus*, *Ichthyodectes*, and *Elopopsis*).

As discussed above, a minimum of 20 fish species are known from at least three of the six major mid-Cenomanian localities in the WIS, including the Woodbine fauna. Those fish taxa include small to medium carnivores (e.g., *Carcharias*, *Enchodus*, and *Pachyrhizodus*), large predators (e.g., *Cretoxyrhina*, *Archaeolamna*, *Cretodus*, and *Xiphactinus*), scavengers (e.g., *Squalicorax*), and durophagous forms (e.g., *Ptychodus* and *Micropycnodon*) (e.g., see discussion on paleoecology by Shimada et al., 2006). Because there are many other marine taxa known from each fauna (Table 1), including various tetrapods such as turtles, lizards, plesiosaurs and birds, from multiple localities, ecosystem structure and dynamics during the mid-Cenomanian across the WIS were undoubtedly more complex than we can ascertain from fossils alone.

5. Conclusions

It is premature to discuss reasons for the presence or absence of particular taxa from any of these faunas, although the faunal variation may reflect a difference in preferred environments—a combination of factors including water depth, water temperature, salinity, distance from shore, and substrate as well as trophic structure. Most of the vertebrate faunas discussed here, especially those from localities where fossils were collected from bonebeds or calcarenites, were probably deposited during a general trend of transgression, which was punctuated by a series of fairly dramatic lowstands that created basin-wide, shallow water habitat in the middle to late Cenomanian in North America.

Therefore, the faunas, particularly those that come from what we consider to be lag deposits, represent at least minimally time-averaged accumulations, which could have resulted from sequential paleoenvironmental conditions as the sea level rose and fell. As an example of this cumulative habitat mixing, the Saskatchewan bonebeds record terrestrial taxa such as dinosaur, lizard and probable enantiornithine bird taxa, in addition to shallow-water mollusk grazers such as pycnodonts, and more pelagic species such as ichthyodectids. These bioaccumulations are located far away from any reconstructed Cenomanian WIS shorelines, but from sedimentological and faunal evidence, it is likely that mid-Cenomanian lowstands effectively, and significantly, changed the configuration of coastlines.

In spite of the fact that these localities represent to at least some degree time-averaged accumulations, we believe that the faunas are generally representative of the marine vertebrates living in the areas at approximately the same geologic time (e.g., see discussion on time-averaging by Shimada et al., 2006). Therefore, the data presented here are thought to provide, if not a 'snapshot,' then at least a reasonable composite image of the vertebrate fauna of the WIS during the mid-Cenomanian. Together these data help elucidate the evolutionary history of the vertebrate faunas, paleoenvironments, and paleoecology of the WIS. Building on previous studies, our work demonstrates that fish communities, including elasmobranchs as well as osteichthyans, had already achieved high diversity by the mid-Cenomanian in the WIS, and that a number of these taxa persisted at least into the early Campanian. The majority of the taxa reported here have been reported widely throughout WIS deposits, but some have also been linked globally, primarily to European and Eurasian faunas, presumably through Boreal connections.

In general, our vertebrate data support the concept of a WIS Northern Interior Subprovince as postulated by Nicholls and Russell (1990) and others. However, we have shown the abundant and species-rich faunal composition of the WIS and the biogeography of the fauna during mid-Cenomanian times to be different in many respects from what might have been predicted from Nicholls and Russell's (1990) observations of the early Campanian WIS, particularly in northern North America. Our study also shows that the ecosystem trophic structure and dynamics of this early Late Cretaceous seaway were complex indeed, even comparatively early on in the Seaway's evolutionary history.

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References

Antunes, M.T., Cappetta, H., 2002. Sélaciens du Crétacé (Albien–Maastrichtien) d'Angola. Palaeontographica Abteilung A 264, 85–146.

Barck, A., 1992. Paleontology of the Glen Rose Formation (Lower Cretaceous), Hood County, Texas. Texas Journal of Science 44, 3–24.

Beavan, N.R., Russell, A.P., 1999. An elasmobranch assemblage from the terrestrial marine transitional Lethbridge Coal Zone (Dinosaur Park Formation: Upper Campanian, Alberta, Canada). Journal of Palaeontology 73, 494–503.

Bhattacharya, J.P., Walker, R.G., 1991. Allostratigraphic subdivision of the Upper Cretaceous Dunvegan, Shaftesbury and Kaskapau formations in the northwestern Alberta subsurface. Bulletin of Canadian Petroleum Geology 39, 145–164.

Bilelo, M.A.M., 1969. The fossil shark genus Squalicorax in north-central Texas. Texas Journal of Science 20, 339–348.

Bloch, J., Schröder-Adams, C.J., Leckie, D.A., McIntyre, D.J., Craig, J., Staniland, M., 1993. Revised stratigraphy of the lower Colorado Group (Albian to Turonian), Western Canada. Bulletin of Canadian Petroleum Geology 41, 325–348.

Cadrin, A.A.J., 1992. Geochemistry and paleoenvironmental reconstruction of the Cretaceous Greenhorn marine cyclothem in the Western Interior Basin of Canada. Ph.D. Thesis, University of Saskatchewan, Canada.

Caldwell, M.W., 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in squamates. Journal of Vertebrate Paleontology 20, 720–735.

Caldwell, M.W., Cooper, J., 1999. Redescription, palaebiogeography, and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the English Chalk (Cretaceous; Cenomanian). Zoological Journal of the Linnean Society 127, 423–452.

Caldwell, M.W., Lee, M.S.Y., 1997. A snake with legs from the marine Cretaceous of the Middle East. Nature 386, 705–709.

Caldwell, W.G.E., North, B.R., Stelck, C.R., Wall, J.H., 1978. A foraminiferal zonal scheme for the Cretaceous System in the Interior Plains of Canada. In: Stelck, C.R., Chatterton, B.D.E. (Eds.), Western and Arctic Canadian Biostratigraphy: Geological Association of Canada, Special Paper, 18, pp. 495–575.

Cappetta, H., 1980a. Les sélaciens du Crétacé supérieur du Liban. II: Batoïdes. Palaeontographica Abteilung A 168, 149–229.

Cappetta, H., 1980b. Les sélaciens du Crétacé supérieur du Liban. I: Requins. Palaeontographica Abteilung A 168, 69–148.

Cappetta, H., 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. In: Schultze, H.P. (Ed.), Handbook of Paleoichthyology, vol. 3B. Gustav Fischer Verlag, Stuttgart, pp. 1–193.

Cappetta, H., Case, G.R., 1999. Additions aux faunes de sélaciens du Crétacé du Texas (Albien supérieur–Campanien). Palaeo Ichthyologica 9, 5–111.

Carpenter, K., 2003. Vertebrate biostratigraphy of the Smoky Hill Chalk (Niobrara Formation) and the Sharon Springs Member (Pierre Shale). In: Harries, P.J. (Ed.), Approaches in High-Resolution Stratigraphic Paleontology. Kluwer Academic Publishers, Amsterdam, pp. 421–437.

Case, G.R., 2001. A new selachian fauna from the Coleraine Formation (Upper Cretaceous/ Cenomanian) of Minnesota. Palaeontographica Abteilung A 261, 103–112.

Case, G.R., Tokaryk, T.T., Baird, D., 1990. Selachians from the Niobrara Formation of the Upper Cretaceous (Coniacian) of Carrot River, Saskatchewan, Canada. Canadian Journal of Earth Sciences 27, 1084–1094.

Cicimurri, D.J., 2000. Early Cretaceous elasmobranchs from the Newcastle Sandstone (Albian) of Cook County, Wyoming. Mountain Geologist 37, 101–107.

Cicimurri, D.J., 2001a. Fossil selachians from the Belle Fourche Shale (Cretaceous, Cenomanian), Black Hills region of South Dakota and Wyoming. Mountain Geologist 38, 181–192.

Cicimurri, D.J., 2001b. Cretaceous elasmobranchs of the Greenhorn Formation (middle Cenomanian–middle Turonian), western South Dakota. In: Santucci, V.L., McClelland, L. (Eds.), Proceedings of the Sixth Fossil Resource Conference: Geologic Resources Division Technical Report. U.S. National Forest Service, Washington, D.C, pp. 27–43.

Cobban, W.A., 1951. Colorado Shale of central and northwestern Montana and equivalent rocks of the Black Hills. American Association of Petroleum Geologists 35, 2170–2198.

Cobban, W.A., Merewether, E.A., Fouch, T.D., Obradovich, J.D., 1994. Some Cretaceous shorelines in the Western Interior of the United States. In: Caputo, M.V., Peterson, J.A., Franczyk, K.J. (Eds.), Mesozoic Systems of the Rocky Mountain Region, USA: Rocky Mountain Section, SEPM (Society for Sedimentary Geology), Denver, CO, pp. 393–414.

Cobban, W.A., Walaszczyk, I., Obradovich, J.D., McKinney, K.C., 2006. A USGS Zonal Table for the Upper Cretaceous middle Cenomanian–Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages. United States Geological Survey Open-File Report 2006, 1250, p. 45.

Compagno, L.J.V., 1999. Checklist of living elasmobranchs. In: Hamlett, W.C. (Ed.), Sharks, Skates and Rays: The Biology of Elasmobranch Fishes. Johns Hopkins University Press, Baltimore, pp. 471–498.

Cook, T.D., Wilson, M.V.H., Murray, A.M., 2008. A middle Cenomanian euselachian assemblage from the Dunvegan Formation of northwestern Alberta. Canadian Journal of Earth Sciences 45, 1185–1197.

Cumbaa, S.L., Bryant, H.N., 2001. Stratigraphic position of a Late Cretaceous (Cenomanian) bonebed, east-central Saskatchewan. In: Christopher, J.E., Gilboy, C.F., Haidl, F.M., Kreis, L.K. (Eds.), Summary of Investigations 2001, Volume1: Saskatchewan Geological Survey, Saskatchewan Energy Mines, Miscellaneous Reports 2001, 1, pp. 121–124. 4.

Cumbaa, S.L., Tokaryk, T.T., 1999. Recent discoveries of Cretaceous marine vertebrates on the eastern margins of the Western Interior Seaway. In: Christopher, J.E., Delaney, G.D., Gilboy, C.F., Haidl, F.M., Harper, F.M., Paterson, D.F. (Eds.), Summary of Investigations 1999, Volume 1: Saskatchewan Geological Survey, Saskatchewan Energy Mines, Miscellaneous Reports, pp. 57–63. 1.

Cumbaa, S.L., Schröder-Adams, C.J., Day, R.G., Phillips, A.J., 2006. Cenomanian bonebed faunas from the northeastern margin, Western Interior Seaway, Canada. In: Lucas, S.G., Sullivan, R.M. (Eds.), Late Cretaceous Vertebrates from the Western Interior. New Mexico Museum of Natural History and Science, Bulletin 35, Albuquerque, NM, pp. 139–155.

Dyman, T.S., Cobban, W.A., Fox, J.E., Hammond, R.H., Nicholls, D.J., Perry, W.J., Porter, K.W., Rice, D.D., Setterholm, D.R., Shurr, G.W., Tysdal, R.G., Haley, J.C., Campen, E.B., 1994. Cretaceous rocks from southwestern Montana to southwestern Minnesota, northern Rocky Mountains, and Great Plains region. In: Shurr, G.W., Ludvigson, G.A., Hammond, R.H. (Eds.), Perspectives on the eastern margin of the Cretaceous Western Interior Basin: Geological Society of America Special Paper 287, Boulder, CO, pp. 5–26.

Eaton Jr., T.H., 1960. A new armored dinosaur from the Cretaceous of Kansas. Vertebrata, 8. University of Kansas Paleontological Contributions, pp. 1–24.

Everhart, M.J., 2004. First record of the hybodont shark genus, "*Polyacrodus*" sp. (Chondrichthyes; Polyacrodontidae). Transactions of Kansas Academy of Science 107, 83–87.

Everhart, M.J., 2005. Oceans of Kansas — A Natural History of the Western Interior Sea. Indiana University Press, Bloomington.

Everhart, M.J., 2009. First occurrence of marine vertebrates in the Early Cretaceous of Kansas: Champion Shell Bed, basal Kiowa Formation. Transactions of the Kansas Academy of Science 112, 201–210.

Everhart, M.J., Bell, A., 2009. A hesperornithiform limb bone from the basal Greenhorn Formation (Late Cretaceous; Middle Cenomanian) of north central Kansas. Journal of Vertebrate Paleontology.

Everhart, M.J., Everhart, P.A., Ewell, K., 2004. A marine ichthyofauna from the Upper Dakota Sandstone (Late Cretaceous). Abstracts of oral presentations and posters. Joint Annual meeting of the Kansas and Missouri Academies of Science, p. 48.

Forey, P.L., Yi, L., Patterson, C., Davies, C.E., 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. Journal of Systematic Palaeontology 1, 227–330.

Fox, R.C., 1984. *Ichthyornis* (Aves) from the early Turonian (Late Cretaceous) of Alberta. Canadian Journal of Earth Sciences 21, 258–260.

Glickman, L.S., Shvazhaite, R.A., 1971. Sharks of the family Anacoracidae from Cenomanian and Turonian of Lithuania, Pre-Volga's Region and Middle Asia. Paleontologiia i Stratigraphiia Pribatltiki Belorussii 3, 185–192 (In Russian).

Hancock, J.M., 2003. Lower sea levels in the Middle Cenomanian. Carnets de Géologie/ Notebooks on Geology, Letter 02, 1–6 2003.

Hattin, D.E., 1965. Stratigraphy of the Graneros Shale (Upper Cretaceous) in central Kansas. Kansas Geological Survey, Bulletin 178, 1–83.

Hattin, D.E., 1975. Stratigraphy and depositional environment of Greenhorn Limestone (Upper Cretaceous) of Kansas. Kansas Geological Survey, Bulletin 209, 1–128.

Hattin, D.E., 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. Kansas Geological Survey, Bulletin 225, 1–108.

Hattin, D.E., Siemers, C.T., Stewart, G.F., 1987. Upper Cretaceous stratigraphy and depositional environments of western Kansas. Kansas Geological Survey, Guidebook Series Number 3, 1–102.

Hay, M.J., Cumbaa, S.L., Murray, A.M., Plint, A.G., 2007. A new paraclupeid fish (Clupeomorpha, Ellimmichthyiformes) from a muddy marine prodelta environment: middle Cenomanian Dunvegan Formation, Alberta, Canada. Canadian Journal of Earth Sciences 44, 775–790.

Jacobs, L.L., Polcyn, M.J., Taylor, L.H., Ferguson, K., 2005. Sea-surface temperatures and palaeoenvironments of dolichosaurs and early mosasaurs. Netherlands Journal of Geosciences 84, 269–281.

Jeletzky, J.A., 1968. Macrofossil zones of the marine Cretaceous of the Western Interior of Canada and their correlation with the zones and stages of Europe and the Western Interior of the United States. Geological Survey of Canada Paper 67–72, 1–66.

Jeletzky, J.A., 1971. Marine Cretaceous biotic provinces and paleogeography of Western and Arctic Canada, illustrated by a detailed study of Ammonites. Geological Survey of Canada Paper 70–22, 1–92.

Jordan, T., 1981. Thrust loads and foreland basin evolution, Cretaceous, Western United States. American Association of Petroleum Geologists, Bulletin 65, 2506–2520.

Kauffman, E.G., 1973. Cretaceous bivalvia. In: Hallam, A. (Ed.), Atlas of Paleobiogeography. Elsevier, Amsterdam, pp. 353–384.

Kauffman, E.G., 1977. Upper Cretaceous cyclothems, biotas and environments, Rock Canyon Anticline, Pueblo, Colorado. In: Kauffman, E.G. (Ed.), Cretaceous Facies, Faunas and Paleoenvironments across the Western Interior Basin: Mountain Geologist, 14, pp. 129–152. 3–4.

Kauffman, E.G., 1984. Paleobiogeography and evolutionary response dynamic in the Cretaceous Western Interior Seaway of North America. In: Westermann, G.E.G., (Ed.), Jurassic–Cretaceous Biochronology and Biogeography of North America. Geological Association of Canada, Special Paper 27, pp. 273–306.

Kauffman, E.G., Sageman, B.B., Kirkland, J.I., Elder, W.P., Harries, P.J., Villamil, T., 1993. Molluscan biostratigraphy of the Cretaceous Western Interior Basin, North America. In: Caldwell, W.G.E., Kauffman, E.G. (Eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper, 39, pp. 397–434.

Kirkland, J.I., 1989. Fossil elasmobranchs from the mid-Cretaceous (Middle Cenomanian Middle Turonian) Greenhorn Cyclothem of eastern Nebraska. Proceedings of Nebraska Academy of Science 99, 1–52.

Kump, L.E., Slingerland, R.L., 1999. Circulation and stratification of the early Turonian Western Interior Seaway: sensitivity to a variety of forcings. In: Barrera, L.R., Slingerland, R.L. (Eds.), Evolution of the Cretaceous Oceaan-Climate System. Geological Society of America Special Paper, p. 332.

Liggett, G.A., Shimada, K., Bennett, C.S., Schumacher, B.A., 2005. Cenomanian (Late Cretaceous) reptiles from northwestern Russell County, Kansas. Paleobios 25 (2), 9–17.

Martin, D.J., Shimada, K., 2008. Lithostratigraphy and depositional environment of the Lincoln Limestone Member of the Greenhorn Limestone (Upper Cretaceous in Russell County, Kansas, with special reference to the basal beds). Transactions of Kansas Academy of Science 111, 79–92.

Martin, J.E., Schumacher, B.A., Parris, D.C., Grandstaff, B.S., 1998. Fossil vertebrates of the Niobrara Formation in South Dakota. Dakoterra 5, 39–54.

McNeil, D.H., Caldwell, W.G.E., 1981. Cretaceous rocks and their foraminifera in the Manitoba escarpment. Geological Association of Canada, Special Paper 21, 1–439.

Nicholls, E.L., Russell, A.P., 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79, 149–169.

Obradovich, J.D., 1993. A Cretaceous time scale. In: Caldwell, W.G.E., Kauffman, E.G. (Eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper, 39, pp. 379–396.

Pereira, A.A., Medeiros, M.A., 2008. A new sclerorhynchiform (Elasmobranchii) from the middle Cretaceous of Brazil. Revista Brasileira de Paleontologia 11, 207–212.

Petsch, B.C., 1949. North part of the Whitewood anticline. South Dakota State Geological Survey Report of Investigations 65, 1–30.

Plint, A.G., 2000. Sequence stratigraphy and paleogeography of a Cenomanian deltaic complex: the Dunvegan and lower Kaskapau formations in subsurface and outcrop, Alberta and British Columbia, Canada. Canadian Petroleum Geology, Bulletin 48, 43–79.

Polcyn, M.J., Bell Jr., G.L., Shimada, K., Everhart, M.J., 2008. The oldest North American mosasaurs (Reptilia: Squamata) from the Turonian (Upper Cretaceous) of Kansas and Texas with comments on the radiations of major mosasaur clades. In: Everhart, M.J. (Ed.), Proceedings of the Second Mosasaur Meeting, Fort Hays Studies Special Issue 3. Fort Hays State University, Hays, Kansas, pp. 137–155.

Price, R.A., 1973. Large-scale gravitational flow of supracrustal rocks, southern Canadian Rockies. In: Delong, K.A., Scholten, R. (Eds.), Gravity and Tectonics. J. Wiley Publishing, NY, pp. 491–502.

Russell, D.A., 1988. A check list of North American marine Cretaceous vertebrates including fresh water fishes. Occasional Paper of Tyrrell Museum of Palaeontology 4, 1–57.

Russell, D.A., 1993. Vertebrates in the Cretaceous Western Interior Sea. In: Caldwell, W.G.E., Kauffman, E.G. (Eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper, 39, pp. 665–680.

Rylaarsdam, J.R., Varban, B.L., Plint, A.G., Buckley, L.G., McCrea, R.T., 2006. Middle Turonian dinosaur paleoenvironments in the Upper Cretaceous Kaskapau Formation, North East British Columbia. Canadian Journal of Earth Sciences 43, 631–652.

Sato, T., Storrs, G.W., 2000. An early polycotylid plesiosaur (Reptilia: Sauropterygia) from the Cretaceous of Hokkaido, Japan. Journal of Paleontology 74, 907–914.

Schröder-Adams, C.J., Cumbaa, S.L., Bloch, J., Leckie, D.A., Craig, J., Seif El-Dein, S.A., Simons, D.J.H.A.E., Kenig, F., 2001. Late Cretaceous (Cenomanian to Campanian) paleoenvironmental history of the eastern Canadian margin of the Western Interior Seaway: bonebeds and anoxic events. Palaeogeography, Palaeoclimatology, Palaeoecology 170, 261–289.

Schumacher, B.A., 2008. On the skull of a pliosaur (Plesiosauria; Pliosauridae) from the Upper Cretaceous (Early Turonian) of the North American Western Interior. Kansas Academy of Science Transactions 111, 203–218.

Scott, S.M., Taylor, A.M., 1977. Early Cretaceous environments and paleocommunities in the Southern Western Interior. In: Kauffman, E.G. (Ed.), Cretaceous Facies, Faunas and Paleoenvironments across the Western Interior Basin. Mountain Geologist, 14, pp. 155–168. 3–4.

Shimada, K., 1996. Ichthyosaur (Reptilia: Ichthyosauria) vertebra from the Kiowa Shale (Lower Cretaceous: Upper Albian), Clark County, Kansas. Transactions of Kansas Academy of Science 99, 39–44.

Shimada, K., 2007. Mesozoic origin for megamouth shark (Lamniformes: Megachasmidae). Journal of Vertebrate Paleontology 27, 512–516.

Shimada, K., Fielitz, C., 2006. Annotated checklist of fossil fishes from the Smoky Hill Chalk of the Niobrara Chalk (Upper Cretaceous) of Kansas. New Mexico Museum of Natural History and Science, Bulletin 35, 193–213.

Shimada, K., Martin, D.J., 2008. Fossil fishes from the basal Greenhorn Limestone (Upper Cretaceous: Late Cenomanian) in Russell County, Kansas. In: Farley, G.H., Choate, J.R. (Eds.), Unlocking the Unknown: Papers Honoring Dr. Richard J. Zakrzewski: Fort Hays Studies Special Issue Number 2. Fort Hays State University, Hays, Kansas, pp. 89–103.

Shimada, K., Schumacher, B.A., 2003. The oldest record of the Late Cretaceous fish genus *Thryptodus* (Teleostei: Tselfatiiformes) from central Kansas. Transactions of Kansas Academy of Science 106, 54–58.

Shimada, K., Ystesund, T.K., 2007. A dolichosaurid lizard, *Coniasaurus* cf. *C. crassidens*, from the Upper Cretaceous Carlile Shale in Russell County, Kansas. Transactions of Kansas Academy of Science 110, 236–242.

Shimada, K., Schumacher, B.A., Parkin, J.A., Palermo, J.M., 2006. Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: Middle Cenomanian) in southeastern Colorado. Journal of Paleontology Memoir 63, 1–45.

Simons, D.-J.H., Kenig, F., Schröder-Adams, C.J., 2003. An organic geochemical study of Cenomanian–Turonian sediments from the Western Interior Seaway, Canada. Organic Geochemistry 34, 1177–1198.

Singh, C., 1983. Cenomanian microfloras of the Peace River area, northwestern Alberta. Alberta Research Council, Bulletin 44, 1–322.

Siverson, M., 1996. Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia. Palaeontology 39, 813–849.

Siverson, M., 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. Transactions of Royal Society of Edinburgh: Earth Sciences 90, 49–65.

Siverson, M., Lindgren, J., Kelley, L.S., 2007. Anacoracid sharks from the Albian (Lower Cretaceous) Pawpaw Shale of Texas. Palaeontology 50, 939–950.

Slingerland, R., Kump, L.R., Arthur, M.A., Fawcett, P.J., Sageman, B.B., Barron, E.J., 1996. Estuarine circulation in the Turonian Western Interior seaway of North America. Geological Society of America, Bulletin 108, 941–952.

Smith, A.B., Batten, D.J., 2002. In: Smith, A.B., Batten, D.J. (Eds.), Fossils of the Chalk, second ed. Palaeontological Association, London.

Smith, A.G., Smith, D.G., Funnell, M., 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge. pp. 1–99.

Sohl, N.F., 1967. Upper Cretaceous gastropod assemblages of the Western Interior of the United States. In: Kauffman, E.G., Kent, H.C. (Eds.), Paleoenvironments of the Cretaceous Seaway — a Symposium. Colorado School of Mines, Special Publication, pp. 1–37.

Sohl, N.F., 1971. North American Cretaceous biotic provinces delineated by gastropods. In: Yochelson, E.L. (Ed.), Proceedings of North American Paleontological Convention, Chicago, 2. Allen Press, Lawrence, Kansas, pp. 1610–1637.

Stelck, C.R., Wahl, J.H., Wetter, R.E., 1958. Lower Cenomanian foraminifera from Peace River area, western Canada. Alberta Research Council, Geological Division, Bulletin 2 (1), 1–35.

Stewart, J.D., 1990. Niobrara Formation vertebrate stratigraphy. In: Bennett, S.C. (Ed.), Niobrara Chalk excursion guidebook. University of Kansas Museum of Natural History and Kansas Geological Survey, Lawrence, pp. 19–30. Open-file Report 90-60.

Stott, D.F., 1967. The Cretaceous Smoky Group, Rocky Mountain Foothills, Alberta and British Columbia. Geological Survey of Canada, Bulletin 132, 1–133.

Stott, D.F., 1982. Lower Cretaceous Fort St. John Group and Upper Cretaceous Dunvegan Formation of the foothills and plains of Alberta, British Columbia, District of Mackenzie and Yukon Territory. Geological Survey of Canada, Bulletin 328, 1–124.

Tokaryk, T.T., Cumbaa, S.L., Storer, J.E., 1997. Early Late Cretaceous birds from Saskatchewan, Canada: the oldest diverse avifauna known from North America. Journal of Vertebrate Paleontology 17, 172–176.

Tyagi, A., Plint, A.G., McNeil, D.H., 2007. Correlation of physical surfaces, bentonites, and biozones in the Cretaceous Colorado Group from the Alberta Foothills to southwest Saskatchewan, and a revision of the Belle Fourche–Second White Specks formational boundary. Canadian Journal of Earth Sciences 44, 871–888.

Underwood, C.J., Cumbaa, S.L., 2010. Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. Palaeontology 53, 903–944.

Underwood, C.J., Mitchell, S.M., 1999. Albian and Cenomanian selachian assemblages from north-east England. Palaeontology 60, 9–66 Special Papers in Palaeontology.

Varban, B.L., Plint, A.G., 2005. An allostratigraphic correlation of the Kaskapau Formation (Cenomanian–Turonian) in subsurface and outcrop: NE British Columbia and NW Alberta, Western Canada Foreland Basin. Bulletin of Canadian Petroleum Geology, Bulletin 53, 357–389.

VonLoh, J.P., Bell, G.L., 1998. Fossil reptiles from the Late Cretaceous Greenhorn Formation (Late Cenomanian–Middle Turonian) of the Black Hills region, South Dakota. Dakoterra 5, 29–38.

Vullo, R., Néraudeau, D., Videt, B., 2003. Un faciès de type falun dans le Cénomanien basal de Charente-Maritime (France). Annales de Paléontologie 89, 171–189.

Vullo, R., Néraudeau, D., Allain, R., Cappetta, H., 2005. Un nouveau gisement à microrestes de vértebrés continentaux et littoraux dans le Cénomanien inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). Comptes Rendus Palevol 4, 95–107.

Vullo, R., Bernárdez, E., Buscalioni, A.D., 2009. Vertebrates from the middle?–late Cenomanian La Cabaña Formation (Asturias, northern Spain): palaeoenvironmental and palaeobiogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 276, 120–129.

Welton, B.J., Farish, R.F., 1993. The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas. Before Time, Lewisville, Texas.

Werner, C., 1990. Biostratigraphic results of investigations on the Cenomanian elasmobranchian fauna of Bahariya Oasis, Egypt. Berliner Geowissenschaft Abhandlungen, Reihe A 120 (2), 943–956.

Williamson, T.E., Kirkland, J.I., Lucas, S.G., 1993. Selachians from the Greenhorn Cyclothem ("Middle" Cretaceous: Cenomanian–Turonian), Black Mesa, Arizona, and the paleogeographic distribution of Late Cretaceous selachians. Journal of Paleontology 67, 447–474.

Williston, S.W., 1906. American amphicoelian crocodiles. Journal of Geology 14, 1–17.

Wilson, M.V.H., Chalifa, Y., 1989. Fossil marine actinopterygian fishes from the Kaskapau Formation (Upper Cretaceous: Turonian) near Watino, Alberta. Canadian Journal of Earth Sciences 26, 2604–2620.

Witzke, B.J., Ludvigson, G.H., 1994. The Dakota Formation in Iowa and its type area. In: Shurr, G.W., Ludvigson, G.A., Hammond, R.H. (Eds.), Perspectives on the eastern margin of the Cretaceous Western Interior Basin. Geological Society of America, Special Paper, 287, pp. 43–78.