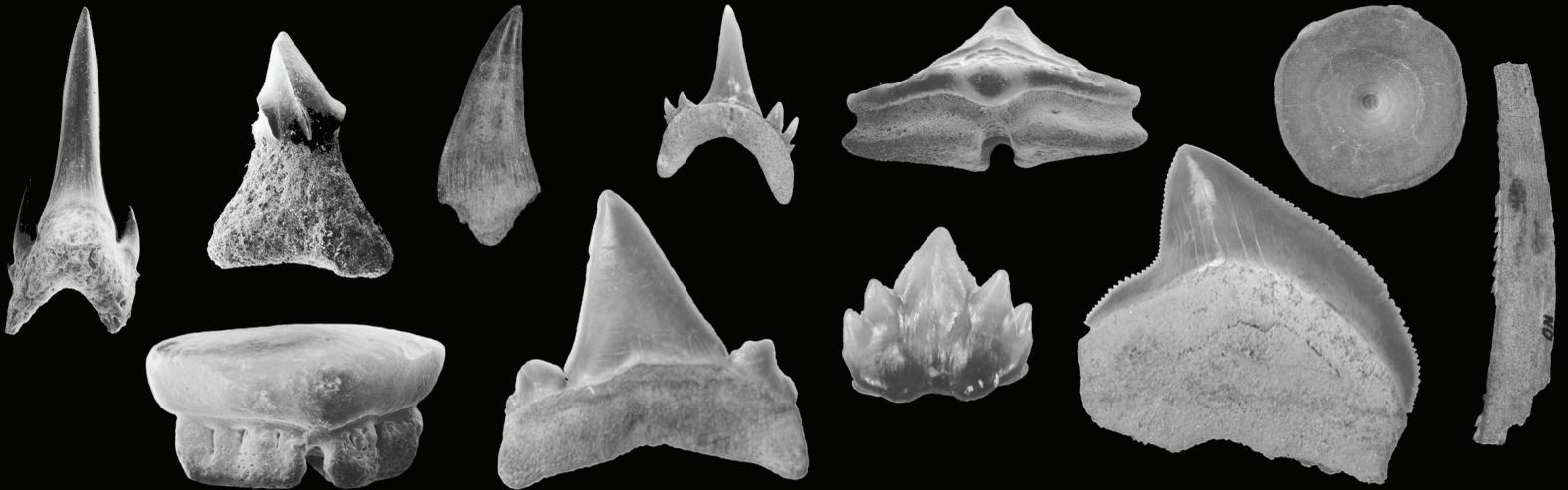


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Cover image: Examples of chondrichthyan and osteichthyan fossils from the Cretaceous Fox Hills Formation of North Dakota. Specimens not shown to scale.

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CHONDRICHTHYAN AND OSTEICHTHYAN PALEOFAUNAS FROM THE CRETACEOUS (LATE MAASTRICHTIAN) FOX HILLS FORMATION OF NORTH DAKOTA, USA: PALEOECOLOGY, PALEO GEOGRAPHY, AND EXTINCTION

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ABSTRACT

As part of a study of the Vertebrata found in the Late Cretaceous (Early Maastrichtian to Middle Late Maastrichtian) Fox Hills Formation, 48 sites in western and central North Dakota were collected to interpret the chondrichthyan and osteichthyan paleofaunas. Based mostly on teeth, 19 shark species, 16 skate and ray species, and one ratfish species were recognized. Of those, three taxa are new, including *Cretalamna feldmanni* n. sp., “*Myliobatis*” *foxhillsensis* n. sp., and *Dasyatis northdakotaensis* n. sp. New chondrichthyan species occurrences for the Fox Hills Formation include: *Squalus ballingsloevensis*, *Plicatoscyllium derameei*, *Cretorectolobus olsoni*, *Carcharias* cf. *C. tenuiplicatus*, *Cretalamna feldmanni* n. sp., *Paranomotodon toddi*, *Squalicorax pristodontus*, *Palaeogaleus navarroensis*, *Archaeotriakis rochelleae*, *Paraorthacodus andersoni*, *Synechodus turneri*, *Walteraja exigua*, *Dasyatis northdakotaensis* n. sp., *Rhombodus levis*, “*Myliobatis*” *foxhillsensis* n. sp., and morphotypes of placoid scales and dermal denticles.

Twenty species of bony fishes were identified from teeth and other skeletal parts, two were vertebral morphospecies, two were based on scales, and four were recognized from otoliths. New osteichthyan occurrences in the Fox Hills Formation include: a lepisosteid, *Melvius* sp., *Cyclurus fragosus*, *Protosphyraena* sp., *Belonostomus longirostris*, *Xiphactinus vetus*, *Paratarpon?* sp., *Pollerspoeckia siegsdorfensis*, cf. *Bathylagus* sp., *Enchodus* cf. *E. ferox*, and “*Apogonidarum*” *maastrichtiensis*.

The Fox Hills Formation is Early Maastrichtian in Bowman County, southwestern North Dakota. The Bowman County sites yielded the oldest fossils of this study. Sites in the Fox Hills type area in north-central South Dakota and south-central North Dakota are Middle Late Maastrichtian based on the presence of *Hoploscaphites nicolletii* and *Hoploscaphites nebrascensis* Ammonite Zones and the *Wodehousia spinata* Pollen Zone. Age relationships of these fossil sites suggest temporal range extensions for several of the Fox Hills fish taxa.

Fox Hills fishes were derived from deep and shallow marine, brackish, and freshwater habitats. Five groupings were identified based on qualitative assessment of these habitat preferences. These groupings are: “offshore marine,” “nearshore marine,” “brackish water/estuarine–strong tidal influence,” “brackish water/estuarine–weak tidal influence,” and “riverine/lagoonal–strong freshwater influence.” Tooth morphology and comparison to modern analogs indicate presence of the following feeding types: omnivore, general invertebrate, molluscivore, pelagic piscivore, benthic piscivore, and scavenger. Species representing all feeding types occur in each of the five habitat groupings. Feeding competition was thus partitioned by habitat preference. When coupled with paleogeographic distribution information, the Fox Hills fish fauna indicates that some taxa represent a recurring assemblage of species that have a “large-river delta” habitat preference, as found today on major deltas of most continents.

Paleogeographic conditions in the Western Interior Seaway (WIS) were dominated by the physiographic conditions of the Hell Creek Delta and Dakota Isthmus complex, which is composed of lagoons, estuaries, and barrier island shorelines. The Fox Hills fish paleofauna includes taxa restricted to the WIS and those that also occurred in the Texas Gulf Coast, Mississippi Embayment, Atlantic Coastal Plain, Greenland, and Sweden. Pelagic, deep marine lamniform species were cosmopolitan and ranged to Europe

and North Africa. The Fox Hills fish fauna is most similar to the fish faunas of the Maastrichtian Kemp Formation, Texas, Severn Formation, Maryland, and Navesink and New Egypt formations, New Jersey.

The Fox Hills paleofauna documents fish extinction at the close of the Cretaceous. None of the 36 chondrichthyan species and none of the 20 osteichthyan species recovered from the Fox Hills Formation are found in the Paleocene worldwide. 58% of Fox Hills chondrichthyan and 77% of osteichthyan genera, and 20% of chondrichthyan and 33% of osteichthyan families, did not survive after the Cretaceous. Support for this interpretation is provided by comparison of the Fox Hills paleofauna to the Paleocene Cannonball Formation paleofauna in North Dakota. None of the 13 Cannonball chondrichthyan species, nor any of the four Cannonball osteichthyan species, occur in the Fox Hills Formation. Thirteen chondrichthyan genera (*Squatina*, *Squalus*, *Ginglymostoma*, *Carcharias*, *Odontaspis*, *Cretalamna*, *Palaegaleus*, *Galeorhinus*, *Paraothacodus*, *Synechodus*, *Myliobatis*, *Dasyatis*, and *Ischyodus*) range across the K-Pg boundary.

INTRODUCTION

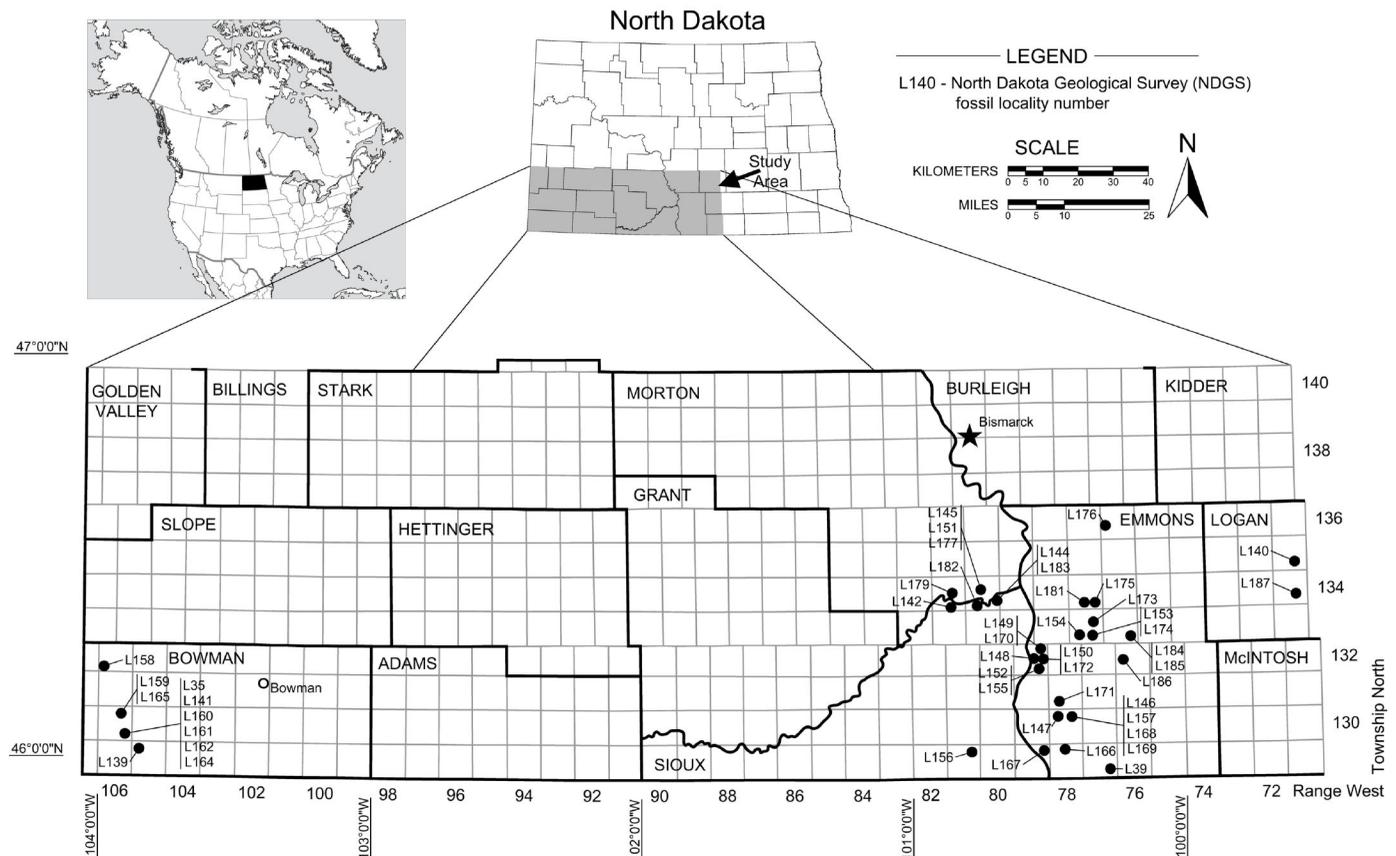
Sedimentological and paleontological signatures of the last fluctuations of the Western Interior Seaway (WIS) in the northern midcontinent during the Late Cretaceous are documented by the Fox Hills Formation, and the Breien Member and Cantapeta Tongue of the Hell Creek Formation. The Fox Hills Formation is widespread with outcrops in North Dakota, South Dakota, Montana, Wyoming, and Colorado (Text-fig. 1). Originally described as "Formation No. 5" of the Cretaceous sequence (Meek and Hayden, 1856), the historical type area lies in the Missouri River Valley and its tributaries in north-central South Dakota (Waage, 1968). Exposures of the marine Breien Member and Cantapeta Tongue of the Hell Creek Formation are restricted to the Missouri River Valley in south-central North Dakota (Hoganson and Murphy, 2002). The Fox Hills Formation and marine tongues of the Hell Creek Formation consist of poorly consolidated mudstone, siltstone, and sandstone. These represent shoreline facies of the waning Pierre-Fox Hills Sea at the end of the Late Cretaceous in the North American Midcontinent (Waage, 1968; Gill and Cobban, 1973; Erickson, 1978, 1999; Murphy et al., 2002; Hoganson and Murphy, 2002).

Fox Hills strata intercalate vertically and laterally with the complexly interbedded delta-platform facies of the Hell Creek Formation in south-central North Dakota (Text-figs. 2–4; Feldmann, 1972a; Erickson, 1992; Peppe and Erickson, 2002; Murphy et al., 2002; Hoganson and Murphy, 2002). At that time, progradation of the Hell Creek Delta and sea level fluctuations created the Dakota Isthmus across the narrow Western Interior Seaway in what is now North Dakota and South Dakota. The dynamics of this depositional system resulted in the marine tongues, including the Breien Member and Cantapeta Tongue, in the Hell Creek Formation (Hoganson and Murphy, 2002; Murphy et al., 2002) and estuarine and lagoonal facies in the underlying and lateral coastal deposits of the Fox Hills Formation (Feldmann and Palubniak, 1975; Klett and Erickson, 1976; Bouchard et al., 2002). The resulting mosaic of delta platform and marginal marine facies, and their included fossils, have been of interest and a challenge to stratigraphers and paleontologists

(Erickson, 1992; Johnson et al., 2002; Murphy et al., 2002; Hartman et al., 2014).

Numerous faunal and floral studies have been completed to help define the complex interaction of marine, marginal marine, and terrestrial communities in the Hell Creek Delta platform and Fox Hills marine setting. Fox Hills Formation marine and brackish water invertebrate faunas have been thoroughly studied beginning over 150 years ago with the exploration of Meek and Hayden (1856, 1861), that culminated in the work of Meek (1876). Several works have modernized knowledge of major invertebrate groups, including Foraminifera (Mello, 1969), Bivalvia (Feldmann, 1967, 1972a; Speden, 1970; Feldmann and Palubniak, 1975; Erickson, 1978), Gastropoda (Erickson, 1974), and Cephalopoda (Waage, 1968; Feldmann, 1972a; Landman and Waage 1993; Landman et al., 2013). Other studies that help to define the Fox Hills invertebrate fauna have included treatment of echinoids (Holland and Feldmann, 1967; Rendall et al., 2010), crabs (Feldmann et al., 1976; Tucker et al., 1987; Crawford et al., 2006), Bryozoa (Cuffey et al., 1981), and trace fossils (Daly, 1991). The megafloora of the Fox Hills Formation was identified by Peppe and Erickson (2002) and Peppe et al. (2007). Erickson et al. (2010) reported on the palynomorphs from the Linton Member of the formation.

Leonard (1912) provided the earliest report of vertebrate fossils from the Fox Hills Formation in North Dakota when he mentioned the discovery of a large fish tooth and a *Mosasaurus* tooth (identified by C. W. Gilmore) from an exposure of the formation along the Cannonball River in Sioux County. In their investigation of the paleoecology of Fox Hills oyster assemblages from Emmons County, North Dakota, Feldmann and Palubniak (1975) illustrated otoliths, a chimaeroid tritor, and crocodile remains. The amphibian, reptilian, and avian fauna of the Fox Hills Formation in North Dakota was defined by Hoganson and Erickson (2004) and Hoganson et al. (1994, 1996, 2007). Fish fossils recovered from the Fox Hills Formation in South Dakota were reported by Waage (1968), Bouchard (1990), Cicimurri (1998), Cicimurri et al. (1999), and Becker et al. (2004, 2009). Hoganson et al. (2015) described chimaeroid remains from the Fox Hills Formation in Colorado.



Text-fig. 1. Map of North Dakota indicating locations for all 48 Fox Hills Formation sites from which vertebrate materials used in this study have been collected; these include SLU, UND, NDGS, and documented student research collections. Numbers are NDGS locality numbers as used in the text and Table 2.

Preliminary assessment of the fish fauna of the Fox Hills Formation of North Dakota has been provided by Hoganson et al. (1995, 1996, 1997) and Hoganson and Erickson (2005). This contribution is a comprehensive treatment and description of that fauna. Fossils recovered for this study consist of isolated skeletal parts, primarily teeth.

Our objectives are to define the fish fauna of the Fox Hills Formation, compare this fauna to other Cretaceous faunas from the North American midcontinent and elsewhere, evaluate the paleoecological and biostratigraphic implications of the fauna, and address the importance of the fauna concerning the K-Pg boundary extinction event. The description of this fish fauna fills important temporal and paleogeographic gaps in existing knowledge of both chondrichthyan and osteichthyan fossil distributions nearest to the K-Pg boundary in the North American midcontinent.

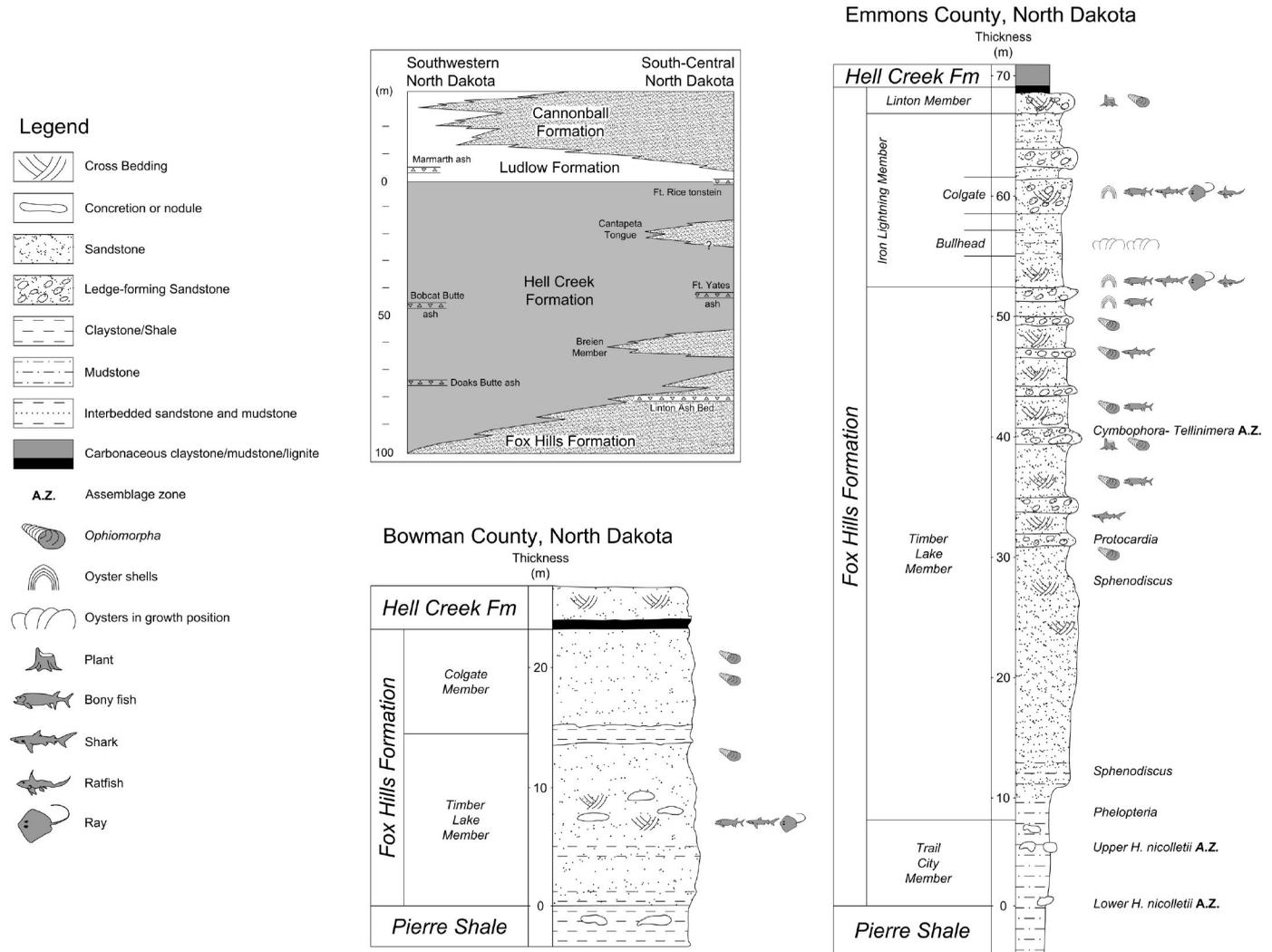
METHODS

Fossils examined for this study consist of isolated skeletal parts, primarily teeth. These fossils were obtained from two sources. The majority were collected by us over a ten-year span. The

remainder were collected by R. M. Feldmann during field work in the mid-1960s while he was in the Department of Geology at the University of North Dakota. Feldmann's collecting and ours consisted primarily of surface gleaning (Text-fig. 5). However, at locality L140 in Logan County, North Dakota, vertebrate and invertebrate fossils were concentrated in a shoreline sandstone deposit, thus allowing excavation and bulk sampling of the poorly consolidated fine-grained sandstone (Text-fig. 6). Sediment was screen-washed and sieved to isolate fossils. Specimens in this residue were removed by hand picking using magnifying glasses and microscopes. Most of that work was done by Terry Ringland, a laboratory assistant at the North Dakota Geological Survey Johnsrud Paleontology Laboratory in the North Dakota Heritage Center (State Museum), Bismarck.

Specimens were examined by light microscopy. An electron microscope, ISI-SIIIA SEM, in the Geology Department at St. Lawrence University was used for observation and imaging of small specimens. Macrophotography was done at the Johnsrud Paleontology Laboratory using Nikon cameras.

Isolated fossils were identified by comparison to described



Text-fig. 2. Stratigraphic columns of the Fox Hills Formation showing relationships between strata in western ND (Bowman Co.) and south-central ND. Materials for this study were derived from both regions. Pierre-Fox Hills formational contact is Early Maastrichtian in Bowman Co. and Early Late Maastrichtian in south-central ND. Fossiliferous horizons are symbolically indicated. Inset.—Fox Hills-Hell Creek-Fort Union stratigraphic relationships in central and western North Dakota. Note marine tongues of Fox Hills sediment in the Hell Creek Formation as the Breien Member and Cantapeta Tongue. Figure modified from Murphy et al. (2002).

taxa in the literature. Identification confirmations were obtained from other researchers when needed. Systematic arrangement of chondrichthyans follows Cappetta (2012) with few exceptions, and that of osteichthyans was determined from multiple sources as indicated in the text. Most specimens examined for this study are cataloged and housed in the North Dakota State Fossil Collection at the North Dakota Heritage Center (State Museum) in Bismarck. Type specimens, including holotypes and hypotypes, are in the North Dakota State Fossil Collection type cabinets. The Feldmann specimens are in the University of North Dakota Paleontology Collection, Grand Forks, North Dakota.

The following institutional abbreviations are used to indicate sources and repositories of specimens described, discussed,

or examined: NDGS, North Dakota Geological Survey, Bismarck; ND, North Dakota State Fossil Collection, North Dakota Heritage Center & State Museum, Bismarck; UN-PC, University of North Dakota Paleontology Collection, Grand Forks; SLU, Saint Lawrence University Paleontology Collection, Canton, New York; RF, Rodney M. Feldmann (1975), University of North Dakota, Department of Geology, dissertation field number. All specimens labeled SLU herein have been transferred to the NDGS collection.

LOCATION AND LITHOSTRATIGRAPHY

Exposures of the Fox Hills Formation in North Dakota are restricted to isolated river cut banks, road cuts, and butte outcrops in the Missouri River Trench area of south-central



*Text-fig. 3. Image of the basal contact of the Fox Hills Formation SE of Linton in Emmons Co., ND. The gradational transition from offshore silt and shale of the Pierre Formation into interlayered silt and fine- and medium-grained, ferruginous sandstone (Trail City Member) defines the beginning of subtidal Fox Hills sedimentation (yellow contact line). Sand deposition representing the Timber Lake Member is increasingly dominant in the hillslope above this site. A layer of typical fossiliferous concretions defines the upper *Hoploscaphites nicolletii* Zone of Waage (1968) at this site. The lower *H. nicolletii* Zone here is missing by non-deposition and the section is quite compressed (Erickson, 1992).*

North Dakota and in the Little Missouri River Badlands in the southwestern corner of the state. Fish fossils were collected from 48 Fox Hills Formation localities in Bowman, Morton, Sioux, Emmons, and Logan Counties (Text-fig. 1). Because of the lithologic variability and complexity of the Fox Hills Formation, stratigraphic placement of isolated outcrops within the formation is often a challenge, although placement is generally easily made where formation contacts are present with the overlying Hell Creek Formation and underlying Pierre Formation, thus allowing lithologic comparisons (Text-fig. 2).

In both south-central and southwestern North Dakota, the contact between the underlying Pierre Formation and Fox Hills Formation is evident where grey shale of the Pierre is overlain by light colored mudstone, siltstone, or sandstone of the Fox Hills (Text-fig. 3). This contact is most often gradational where the Trail City Member of the Fox Hills Formation is well defined (Waage, 1968; Erickson, 1992). In North Dakota, the most notable exposures at the base of the Fox Hills Formation, the Trail City siltstones, in both Bowman and Emmons counties, are absent or exceedingly thin suggesting non-gradational contacts in those areas (Feldmann, 1967; Erickson, 1992).

Often the upper contact of the Fox Hills Formation is also poorly defined, in this case due to the transition from the marine or estuarine deposystem of the Fox Hills into a more fluvial terrestrial system in the Hell Creek Formation. At some localities in south-central and southwestern North Dakota,



Text-fig. 4. The best exposure of the upper contact between light-colored Colgate lithofacies in the Iron Lightning Member of the Fox Hills Formation and the basal beds of the Hell Creek Formation is seen east of the town of Breien along the Cannonball River in ND. The transition here, marked by the yellow line, is from highly-fluted tidal channel sandstones through partially indurated paleosol into bedded silt and clay of deltaic plain deposits of the somber gray Hell Creek Formation. Petrified tree stumps are rooted in the basal Hell Creek beds and the soil marks the end of the Fox Hills Sea influence until a marine tongue, the Breien Member of the Hell Creek Formation (white contact line), invaded the region for a short time (Hoganson and Murphy, 2002).

the contact between the Fox Hills Formation and Hell Creek Formation is well defined. A thin (0.3–1 m-thick) carbonaceous sandstone, siltstone, or mudstone occurs at the base of the Hell Creek Formation throughout the outcrop area in North Dakota (Murphy et al., 2002). This carbonaceous bed is underlain by Fox Hills Formation sandstone (Text-fig. 4). The position of the Cretaceous-Paleogene (K-Pg) boundary has been defined in both southwestern and south-central North Dakota (Murphy et al., 2002; Hoganson and Murphy, 2002). At a measured section at the Stumpf Site Natural Area in Morton County, south-central North Dakota, the top of the Fox Hills Formation is ~65 m below the K-Pg boundary. Also at this site, the base of the marine Breien Member of the Hell Creek Formation is 4.76 m above the top of the Fox Hills Formation (Hoganson and Murphy, 2002).

REGIONAL FOX HILLS BIOSTRATIGRAPHY

Western Interior ammonite zones are continually being refined and extended toward a global model (Kennedy, 1984, 1986; Obradovich, 1993; Kennedy et al., 1992, 1995; Hancock et al., 1992; Kennedy and Cobban, 1993; Landman et al., 2004a; Landman et al., 2010, 2013). Fox Hills ammonite species from the type area of north-central South Dakota and south-central North Dakota represent the youngest marine zone fossils of the Upper Maastrichtian of the central Western Interior Seaway (Landman and Waage, 1993; Landman et al., 2013, 2018). The region does not yield the



Text-fig. 5. An indurated bed of shoreface sandstone interbedded with friable sandstone is typical of the Timber Lake Member of the Fox Hills Formation in southwestern Bowman Co., ND. Here shark and bony fish teeth are present in outcrop as seen in the inset at which worker points, as well as in shoreline lag deposits that were sieved at site NDGS L35 nearby. This bed is approximately 20 meters above the gradational contact with the Pierre Formation.

latest Maastrichtian ammonites such as *Discoscaphites iris*, *D. menardi*, or *D. newjerseyensis*, recognized by Landman et al. (2004a, b) and Landman et al. (2004a,b; 2010) from the Atlantic Coast and the Mississippi Embayment, nor does it contain ammonite species demonstrative of the latest Maastrichtian of Europe (Christensen, 1975; Machalski, 2005; Machalski et al., 2007) although belemnites and species of *Hoploscaphites* are present.

Fossil sharks and bony fish have not commonly been related stratigraphically to the traditional marine Cretaceous ammonite indices. In the Missouri River Valley of south-central North Dakota, all exposed Fox Hills strata lay above the base of the *Hoploscaphites nicolletii* Range Zone. The Timber Lake Member contains the zone ammonites *H. nicolletii* and *Hoploscaphites nebrascensis* of the Late Maastrichtian. However, in southwestern North Dakota where the formation comes to the surface along the flanks of the Cedar Creek Anticline, no *Hoploscaphites* species are present in sections of the Timber Lake Member, but Pierre Shale collections below the Fox Hills contact include “*Jeletzkytes*” *nodosus*. This suggests that the Fox Hills Formation is Late Campanian to Early Maastrichtian in that area.

Fox Hills-Hell Creek Relationships on Cedar Creek Anticline, ND and MT

Bishop (1973) mapped the upper Pierre Shale and base of the Fox Hills Formation on the northwest end of the Cedar Creek Anticline near Glendive, Montana. There he recorded *Baculites eliasi* followed by a zone of no fossils and then



Text-fig. 6. NDGS Site L140, Logan Co., ND, which is composed of friable, fine- and medium-grained Fox Hills sandstone, was gridded and excavated. Sediment was sieved and about 800 Kg of coarse fraction material were returned to the NDGS Johnsrud Paleontology Laboratory for picking. Invertebrate and vertebrate fossils were present in similar numbers. This site contains a mixed marine and estuarine fauna previously studied by Feldmann and Palubniak (1975), Erickson (1974), and Hoganson and Erickson (2005).

a “combined zone” of *B. baculus* and *B. grandis*. The latter zones began approximately 21.3 m (70 ft.) below the contact with the Fox Hills Formation and were mapped as ending at the top of the Pierre Shale. In Bishop’s interpretation, the *B. eliasi* zone was Campanian and ended at the top of a barren concretion zone 30.9 m (130 ft.) below the Fox Hills contact and within the Campanian, implying 21.3 m (70 ft.) of Lower Maastrichtian Pierre Shale was deposited prior to Fox Hills deposition using the zonation of Kennedy et al., 1998.

In Bowman County, North Dakota, the Pierre-Fox Hills sedimentary transition is rapid and not well documented by ammonites. Tucker et al. (1987) discussed ammonites from the upper 16 m of Pierre Shale, including *B. reesidei*, *B. eliasi*, and *B. grandis*, as well as *Didymoceras cheyense*, and *Oxybeloceras meekorum*. Applying the current scheme of Kennedy et al. (1998), the top of the Pierre Shale lies just above the Campanian-Maastrichtian boundary, placing the thin Fox Hills Formation of the region in the lower Maastrichtian section.

Approximately 160 km southeast from Glendive, Montana, along strike of the anticline, the Pierre Shale-Fox Hills contact is exposed in a cut bank along Little Beaver Creek in Bowman County. No ammonites were found during our research in the immediate area. Our composite section (Text-fig. 2) indicates proximity of sampling localities to the Pierre-Fox Hills contact. Fossils from this section are no older than the Early Maastrichtian *Baculites grandis* Zone and seemingly no younger than the *B. clinolobatus* Zone of the Late

Early Maastrichtian, a zone which occurs in the Mobridge Member of the Pierre Shale of the Missouri River Valley section (Stoffer et al., 1998; Kennedy et al., 1998; Landman et al., 2013; see also discussion in Landman et al., 2017). The Fox Hills fish fauna in southwestern North Dakota is thus older than the fish fauna in south-central North Dakota where the entire formation is Late Maastrichtian in age (Erickson et al. 2010).

An unconformable relationship between the Fox Hills and Hell Creek formations has long been recognized in the Hell Creek type area in eastern Montana (Leonard, 1906; Brown, 1907; Calvert, 1912; Clemens and Hartman, 2014), but it is of such variable and local occurrence and placement that it has often confused efforts to make long distance correlations. These relationships have recently been summarized by Hartman et al. (2014) during the process of redefining and formalizing lectotype sections for the Hell Creek Formation in its type area in Garfield County, Montana. In the Hell Creek type area, there is little character to the Fox Hills Formation that can be considered “typical” in its own type area of the Missouri River Valley of South Dakota and North Dakota (Waage, 1968; Feldmann, 1972a; Erickson, 1992). Probably, because of the close proximity of economic lignite in the Hell Creek and Fort Union Group, too much significance has been given to the nature of the Fox Hills stratigraphy in the region in the absence of the more complete relationships to be seen farther east.

The Pierre-Fox Hills contact is sometimes recognized as gradational in both western and central North Dakota (Waage, 1968; Feldmann, 1972a; Cvanara, 1976), although the vertical transition from distal to proximal shoreface conditions was much more rapid in the west (Hartman et al., 2014) than in the Missouri River Valley of South Dakota where the formation goes through multiple sand-silt-shale interbeds (Trail City Member) before the shoreface sandstone of the Timber Lake Member dominated deposition.

The Fox Hills-Hell Creek contact is more abrupt throughout the western North Dakota region. In the Glendive area of eastern Montana, the erosional complexities and depth of incision of the Fox Hills-Hell Creek contact increases toward the northwest (Hartman et al., 2014; Arens and Allen, 2014; Arens et al., 2014) which strongly implies increasing paleoelevation and thus penecontemporaneous active uplift of the region at the close of Fox Hills deposition. Specifically, the transition has often been considered disconformable because the ferruginous Fox Hills Sandstone is seen to have been eroded prior to Hell Creek (Lance) deposition at sites on the Cedar Creek Anticline along Little Beaver Creek in Bowman County, North Dakota (Leonard, 1911; Calvert, 1912; Feldmann, 1972a; Daly, 1991). This relationship suggests that the southeast end of the Cedar Creek Anticline was

a positive feature, although perhaps only a few meters above sea level, at the time of the Pierre/Fox Hills-Hell Creek transition from marine to continental deposition (Text-fig. 2). The syndepositional structure and geomorphology of southwestern North Dakota and southeastern Montana influenced depositional rates, facies, and faunas significantly as the Fox Hills shoreline prograded across the present Hell Creek type area and the ancestral Cedar Creek Anticline.

Fox Hills Strata in the Missouri River Valley Type Area, South Dakota

Waage (1961, 1968) and his students produced the first thorough biostratigraphic study of the Fox Hills Formation—since the work of Meek (1876)—where it is thickest in its type area of north-central South Dakota. There the transition from the Pierre Formation is represented by thick (64 m, 210 ft.) prodeltaic, interbedded clay, silt and very-fine sand beds defined as the Trail City Member. These sediments include multiple concretion layers, the lowest of which contains *Hoploscaphites nicolletii* and is early Late Maastrichtian in age (Landman and Waage, 1993; Landman et al., 2010, 2013). Higher in the Trail City Member a second concentration of *H. nicolletii*, the Upper *nicolletii* Zone of Waage (1968), includes some forms of *Hoploscaphites* that vary from the type morphology (Landman et al., 2013), but they are not recognized as conspecific with any younger Atlantic Coast hoploscaphitids (Landman et al., 2004a,b, 2007). Recognition of the Trail City Member in North Dakota is always problematic because it thins rapidly to the north and northeast (Feldmann, 1972a; Erickson, 1974, 1978, 1992).

The Timber Lake Member, which is 15–33 m (50–110 ft.) thick, is composed of very-fine to medium-grained sandstone that prograded into South Dakota from the north (Waage, 1968; Erickson, 1992); this represents shoreface deposition around the margins of the Hell Creek Delta platform. It contains *Sphenodiscus lobatus* and *Hoploscaphites nebrascensis*, the latter of which marks the youngest ammonite zone documented in the region. Landman et al. (2013) places this in the early to middle Late Maastrichtian. Some concretions in this unit also contain unusual geographically restricted belemnites (Landman et al., 2013).

Fox Hills Strata in the Missouri River Valley of North Dakota

Into North Dakota, the Trail City Member thins, whereas the Timber Lake sandstone thickens somewhat (Erickson, 1992). Situations of thin Fox Hills deposition and rapid transition, similar to those noted in the Hell Creek type area in Montana (Hartman et al., 2014), resulted from very localized structural highs in the Missouri River Valley Region (Erickson, 1992). Away from structural highs the majority of lower Fox Hills de-

position in the Missouri River Valley resembled that described for the type area in South Dakota by Waage (1968), including presence of defined ammonite zones. Northwestward and westward of the exposed Fox Hills beds lies a complex of facies in the subsurface that is not well understood (Erickson, 1992).

Above the marine sandstone of the Timber Lake Member, clay and silt laminated beds of estuarine deposition (Bullhead lithofacies) and white tidal channel sandstone (Colgate lithofacies) comprise the Iron Lightning Member (Waage, 1968). This unit represents deposition landward of the Timber Lake barrier island and beach complex (Feldmann, 1972a) of the Western Interior Seaway (Text-fig. 2). Iron Lightning sediments contain mixed estuarine and shallow marine fossil assemblages often dominated by the oyster *Crassostrea subtrigonalis*. No identifiable ammonites are known from this unit, however small fragments of shell are present.

The uppermost beds of the formation, which lie above the Iron Lightning Member, are described as the Linton Member from the stratigraphic sections around Linton in Emmons County, North Dakota. There, this butte-capping bed is a ferruginous, subarkosic sandstone containing a flora of palmetto, *Pandanus* sp., and *Equisetum* sp. (Klett and Erickson, 1976; Erickson, 1999), and the occasional *Ophiomorpha*-like crab or shrimp burrow. Just below, or perhaps partially lateral to, that indurated unit are siltstone facies containing a diverse flora similar to that described as the zonal flora Hell Creek III by Johnson (2002) in Bowman County, North Dakota. This flora (Peppe, 2003) served as additional evidence of the diachronous relationship between deposition on the Cedar Creek Anticline and that in the Missouri River Valley. Furthermore, a study of pollen from the plant-rich bed indicated early-middle Late Maastrichtian palynomorphs (Erickson et al., 2010) of the *Wodehousia spinata* pollen zone, including *W. spinata* and *Tsudyipollis* spp. (Nichols and Fleming, 1990; Nichols et al., 1990).

Sandstone tongues of the Fox Hills Formation are interbedded with the delta platform facies of the Hell Creek Formation perpendicular to an estuary shoreline that traversed from southwest to northeast through north-central South Dakota to south-central North Dakota. The oldest tongue, the Breien Member (Laird and Mitchel, 1942; Frye, 1964; Hoganson and Murphy, 2002) crops out in Sioux, Emmons, and Morton counties, North Dakota. Fossils of various estuarine organisms are present, including chondrichthyan teeth and other vertebrates, invertebrates (including two types of oysters), *Ophiomorpha* burrows, and the partial body chamber of a scaphitid ammonite (Frye, 1964; Hoganson and Murphy, 2002; Hartman and Kirkland, 2002; Smrecak et al., 2005). The ammonite specimen is an internal mold that Hoganson and Murphy (2002) referred to as *Jeletzkytes* cf. *J. nebrascensis*,

although the poorly preserved specimen had also been identified as *Discoscaphites* cf. *D. conradi* by Kennedy et al. (1998). *Jeletzkytes* has subsequently been declared a junior subjective synonym of *Hoploscaphites* by Landman et al. (2010). One of us has indicated that some of the Breien fossil material may represent a lag accumulation of Fox Hills fossils mixed with Breien mollusks that were members of the *in situ* estuarine fauna (Erickson, 1999). This ammonite body fragment has been reported by several researchers (Kennedy et al., 1998; Hoganson and Murphy, 2002) as the highest occurrence of the *H. nebrascensis* Zone, but the fragment might be reworked from lower strata (Erickson, 1992).

Higher marine tongues—including the Cantapeta Tongue described by Murphy et al. (2002) and one or more unnamed tongues—occur in Morton County, North Dakota (personal communication, Murphy 2017), where only *Ophiomorpha* sp. have thus far been found to indicate the marine connections. The upper Fox Hills beds in North Dakota (Iron Lightning and Linton Members) and the tongues in the Hell Creek may belong to higher zones for which terrestrial indices will need to be assigned. Pollen identified as middle Late Maastrichtian age from the Linton Member noted above began this process (Erickson et al., 2010).

Eastward into Logan and McIntosh counties (Text-fig. 2) lies exposed Fox Hills sandstone that is characterized by estuarine faunas and marine-estuarine mixed assemblages that document proximity to coastal conditions and reduced salinity (Feldmann and Palubniak, 1975). No traditional facies of the Iron Lightning Member are present, thus making determination of the precise stratigraphic position of the thin outcrops impossible. The top of the section is missing due to glacial removal and the thickness of the unit is not known (Feldmann, 1972a). Fine, slightly glauconitic, unconsolidated sandstone suggestive of a very broad, shallow marine intertidal sand plain remains in some areas. Oyster “reefs”, once tidal-channel fills, stand in relief more than 20 m high, suggesting a minimum thickness for these marginal marine beds (Feldmann and Palubniak, 1975; Erickson, 1992, 1999). Fragments identifiable as *Sphenodiscus lobatus* occur in this fine sandstone with mixed faunal communities, but to date no scaphitid zonal ammonites have been found.

Fox Hills Across the Sioux Arch

The axis of the Sioux Arch projects southwestward across South Dakota from the northeast edge of the state. Across the arch lie strata that historically have been assigned to both the Pierre Shale and Fox Hills formations. Studies have disclosed an ammonite fauna from the upper portion of this Cretaceous stratigraphic section south of the arch (Kennedy et al., 1998).

Kennedy et al. (1998) have reported an occurrence of *Jeletzkytes* (= *Hoploscaphites*) *nebrascensis* with *Eutrephoceras*

dekayi, *Sphenodiscus lobatus*, *Hoploscaphites comprimus*, *Baculites* sp. and *Belemnitella* cf. *B. bulbosa* from lithologies in sandy silt facies in extreme southeast South Dakota and northeast Nebraska. Those 24.4 m of strata were included by Searight (1937) in the Fox Hills Formation although Kennedy et al. (1998) accepted the combination of these strata by Stevenson and Carlson (1951) into the Elk Butte Member of the Pierre Shale, now considered by Martin et al. (2007, fig. 3, pp. 11, 12) as the Elk Creek Formation in South Dakota. In the same study, Kennedy et al. (1998) argued that the base of the Maastrichtian be taken at the base of the *B. eliasi* Zone in the Western Interior of North America. By doing so, they expanded downward the stratigraphic extent of the Maastrichtian in the Missouri River Valley type area of the Fox Hills Formation as used in the classic literature (Waage, 1968). This usage includes zones from *B. eliasi* upward (*B. baculus*, *B. grandis*, and *B. clinolobatus*) in the Lower Maastrichtian and thereby places the entire Elk Butte Member and most of the Mobridge Member of the Pierre Shale into the Lower Maastrichtian (Cobban et al., 2006). Such a placement requires that the upper 76 m of Pierre Shale—and conservatively 76 m of the Fox Hills Formation and 50 m of the Hell Creek Formation in the Fox Hills type area and northward into North Dakota—is Upper Maastrichtian in position.

Fox Hills Relationships in the South Dakota Badlands Region

Since the work of Pettyjohn (1967), who defined Fox Hills stratigraphic units in Meade and Pennington counties, South Dakota, little attention was paid to the stratigraphy or biozonation of the formation. In the past two decades interest in K-Pg boundary issues has spawned several studies that help to place the formation in biostratigraphic context (Chamberlain et al., 2001; Stoffer et al., 2001; Stoffer, 2003; Terry et al., 2001; Landman and Cobban, 2003; Landman et al., 2010, 2013) in and north of the badlands which lie north of the Sioux Arch and southwest of the Fox Hills type area. Pettyjohn (1967) recognized that Fox Hills deposits in this region were distinct from those in the type area; in particular, they were shallow water sand and gravelly sand, as well as lignites and carbonaceous units with strong terrestrial and lagoonal overprints and lacking significant marine molluscan faunas. These units are distinct from the Iron Lightning Member of the type area and are likely older.

Stoffer et al. (1998) outlined the biostratigraphy of upper Pierre Formation and Fox Hills sections parallel to the axis of the Sioux Arch. They correlated those sections to the Mobridge area of the Missouri River Valley, and in that process, they demonstrated structural control and the diachroneity of the Pierre-Fox Hills contact, and postulated the presence of four erosional intervals within the Fox Hills section.

Recently, the biozonation of the Fox Hills Formation in the Badlands National Park region of western South Dakota has been discussed by Landman et al. (2013). They again pointed out the diachroneity and that the formation becomes younger to the east. The disturbed upper portion of the shortened section has been termed the “disturbed layer” or “disturbed zone” by Stoffer et al. (2001). In this region of South Dakota, Pettyjohn (1967) described Fox Hills stratigraphy containing shoreface deposits of the Fairpoint Member and the Stoneville facies including coal, which we consider characteristic of interdistributary bay deposits. Some stratigraphers considered the coal to mark the base of the Hell Creek Formation (Cvancara, 1976). These were produced in a shallowing embayment of the Fox Hills Sea that was being overcome by Hell Creek deltaic deposition prograding into the region from the west or northwest. It is from the Fairpoint Member that Becker et al. (2004, 2009) have described both osteichthyan and chondrichthyan faunas.

Landman et al. (2013) demonstrated that the Pierre-Fox Hills transition in that region took place during the occurrence of *H. melloi* within the *Hoploscaphites birkelundi* Zone deposition during the early Late Maastrichtian. The type area of the Fox Hills Formation was still receiving silt and clay at that time, marking the transition into silt and fine sand of the Trail City Member. The *Hoploscaphites nicolletii* Zone first occurs 70 m above the last occurrence of *Baculites clinolobatus*. The first occurrence of *H. nicolletii* marks the middle Late Maastrichtian (Kennedy et al., 1998; Landman and Cobban 2003; Landman et al., 2013).

The highest documented ammonite zone in the Fox Hills Formation is the *Hoploscaphites nebrascensis* Zone as used by Landman et al. (2013). This ammonite is found in concretions above the base of the Timber Lake Member in the type area of South Dakota and North Dakota. Landman et al. (2013) believed the zone to be 70 m thick. In North Dakota the precise thickness is unknown, but it may extend as far as the Breien Member of the Hell Creek Formation (Hoganson and Murphy, 2002). Localities in this report that lie in and east of the Missouri River Valley (Text-fig. 1) occur within the *H. nebrascensis* Zone, thus making it the youngest marine Cretaceous fish fauna known from the Western Interior Seaway.

SYSTEMATIC PALEONTOLOGY

- Class **CHONDRICHTHYES** Huxley, 1880
- Subclass **ELASMOBRANCHII** Bonaparte, 1838
- Cohort **EUSELACHII** Hay, 1902
- Subcohort **NEOSELACHII** Compagno, 1977
- Order **HYBODONTIFORMES** Maisey, 1975
- Superfamily **HYBODONTOIDEA** Owen, 1846

Family **HYBODONTIDAE** Owen, 1846
Genus **HYBODUS** Agassiz, 1843

Type species.—*Hybodus reticulatus* Agassiz, 1837.

?*Hybodus* sp.
Text-figs. 7.1–7.3

Description.—Dorsal fin spine of a hybodontid shark having two parallel rows of basally-directed, thorn-like denticles, evenly sized and paired throughout the length. Spine is smooth on lateral flanks, gently curving and lacks both distal and proximal terminations. Lateral flanks are nearly parallel, converging only slightly toward the tip, which is missing. The flat, posterior surface is flanked by two gently-curving lateral sides converging to an anterior, sub-rounded margin, producing a subtriangular cross-section with a shallow furrow between the rows of teeth.

Material.—ND 07-77.1, a single, incomplete specimen from NDGS L143, is 37.7 mm long, 6.6 mm wide, and 3.6 mm thick, is broken at each end, and is the most complete specimen (Table 1 and Table 2). A second fragment of spine (NDGS 4063) with the same tooth pattern is 1 cm long and adds nothing to the description. No *Hybodus* sp. teeth are included in our collections.

Remarks.—Hybodontid spines are rare in most chondrichthyan faunas and most are found as solitary occurrences where their size makes them more obvious. The spine and fragment we describe are a solitary find. This spine (ND 07-77.1) has been reported before (Hoganson et al., 1997), but the present report is the first to illustrate it as the only known specimen from the Fox Hills Formation in North Dakota. Because no teeth of *Hybodus* species were recovered, this specimen is potentially significant.

Bouchard (1990) reported two cephalic clasper hooks of species of *Hybodus* from the Fairpoint Member of the formation in Meade County, South Dakota. *Hybodus* remains

have been recorded from the Western Interior, and Gulf and Atlantic coast sites of Cretaceous age. In the literature, teeth are more common fossils than are cephalic claspers or spines. In Canada, species of *Hybodus* have been recognized in the marine and transitional beds of the Lethbridge Coal zone below the Bearpaw Formation (Brinkman et al., 2005), from the Dinosaur Park Formation (Brinkman, 2004), and from the marine facies of the Foremost Formation of the Campanian Belly River Group (Beavan, 1995; Peng et al., 2001). A tooth was also reported by Cook et al. (2008) from the Cenomanian Dunvegan Formation of Alberta. Underwood and Cumbaa (2010) created a new genus, *Meristodonoides*, for some of the Cenomanian fossils from Canadian sites based on teeth, but no spines were described.

Case (1978, 1987) described *Hybodus montanensis* from the Judith River Formation of Montana. Claspers and teeth were noted from the Blufftown Formation of Georgia (Case and Schwimmer, 1988). Two types of spines were illustrated by Robb (1989) from the Campanian Black Creek Formation of North Carolina. Robb also illustrated one fragment of a chimaeriform fin spine that is less tapered than the *Hybodus* spines. This has a double row of paired barbs, as does the specimen we have assigned here. It may be that the spine we illustrate in Text-figs. 7.1–7.3 would be better placed in the ratfish. However, Robb's description clearly states that his spine has a single row of barbs, whereas our specimen has a double row of barbs with a furrow between them. Species of *Lonchidion* also show a single row of denticles (Cook et al., 2014).

Kirkland et al. (2013) discussed *Hybodus* teeth and fin spines from the upper Cenomanian and Campanian of Utah. Although their fossils were from freshwater facies, these authors point out the primarily marine nature of *Hybodus*. Texas strata contain records of species of *Hybodus* throughout the Cretaceous (Welton and Farish, 1993; Cappetta and Case, 1999) in nearshore and brackish-water facies. The Maastrichtian Kemp Clay contains a species of the hybodontoid genus *Lissodus* (= *Lonchidion*), but no species of *Hybodus* were recorded (Case and Cappetta, 1997).

Text-fig. 7. Spines and teeth of Fox Hills sharks. 7.1–7.3, ?*Hybodus* sp. spine (ND 07-77.1). 7.4–7.7, *Synechodus turneri* Case, 1987, posterior tooth (ND 95-13.71). 7.8–7.13, 7.16–7.19, *Squalus ballingsloevensis* Siverson, 1993; 7.8, 7.9, lateral tooth (ND 99-5.3); 7.10, 7.11, lateral tooth (ND 99-5.4); 7.12, 7.13, lateral tooth (ND 07-75.7); 7.16, 7.17, lateral tooth (ND 99-5.5); 7.18, 7.19, posterior tooth (ND 95-13.70). 7.14, 7.15, 7.20–7.25, *Squalus* sp.; 7.14, 7.15, antero-lateral tooth (ND 99-5.6); 7.20, 7.21, anterior tooth (NDGS 1692); 7.22, 7.23, antero-lateral tooth (NDGS 1693); 7.24, 7.25, lateral tooth (NDGS 1694). 7.26–7.29, *Squatina hassei* Leriche, 1929; 7.26–7.28 (ND 07-74.1) [NB image of left tip of root is cropped]; 7.29 (ND 94-38.2). 7.30–7.33, *Plicatoscyllium derameei* Case and Cappetta, 1997 (ND 99-5.7). 7.34–7.37, *Ginglymostoma* sp. (ND 94-38.5). 7.38–7.46, *Cretorectolobus olsoni* (Case, 1978); 7.38, 7.39 (ND 94-38.4); 7.40–7.44 (ND 95-13.90); 7.45–7.46 (ND 94-38.3). 7.47–7.48, *Carcharias* cf. *C. tenuiplicatus* (Cappetta and Case, 1975b), (ND 94-36.1). 7.49–7.61, *C. samhammeri* (Cappetta and Case, 1975a); 7.49, 7.50, lateral tooth (ND 95-13.88); 7.51–7.53, anterior tooth (ND 95-13.85); 7.54, 7.55, posterior tooth (ND 95-13.87); 7.56, 7.57, postero-lateral tooth (ND 95-13.86); 7.58, 7.59 symphyseal tooth (ND 99-6.14); 7.60, 7.61, anterior tooth (ND 95-11.1). Scale bars are 5 mm except 7.20, 7.21 = 3 mm, 7.26–7.28, 7.40–7.42, 7.60, 7.61 = 2.5 mm, and 7.29, 7.38, 7.39 = 1 mm. SEM images include 7.8–7.19, 7.26–7.29, 7.38, 7.39, 7.45, and 7.46.

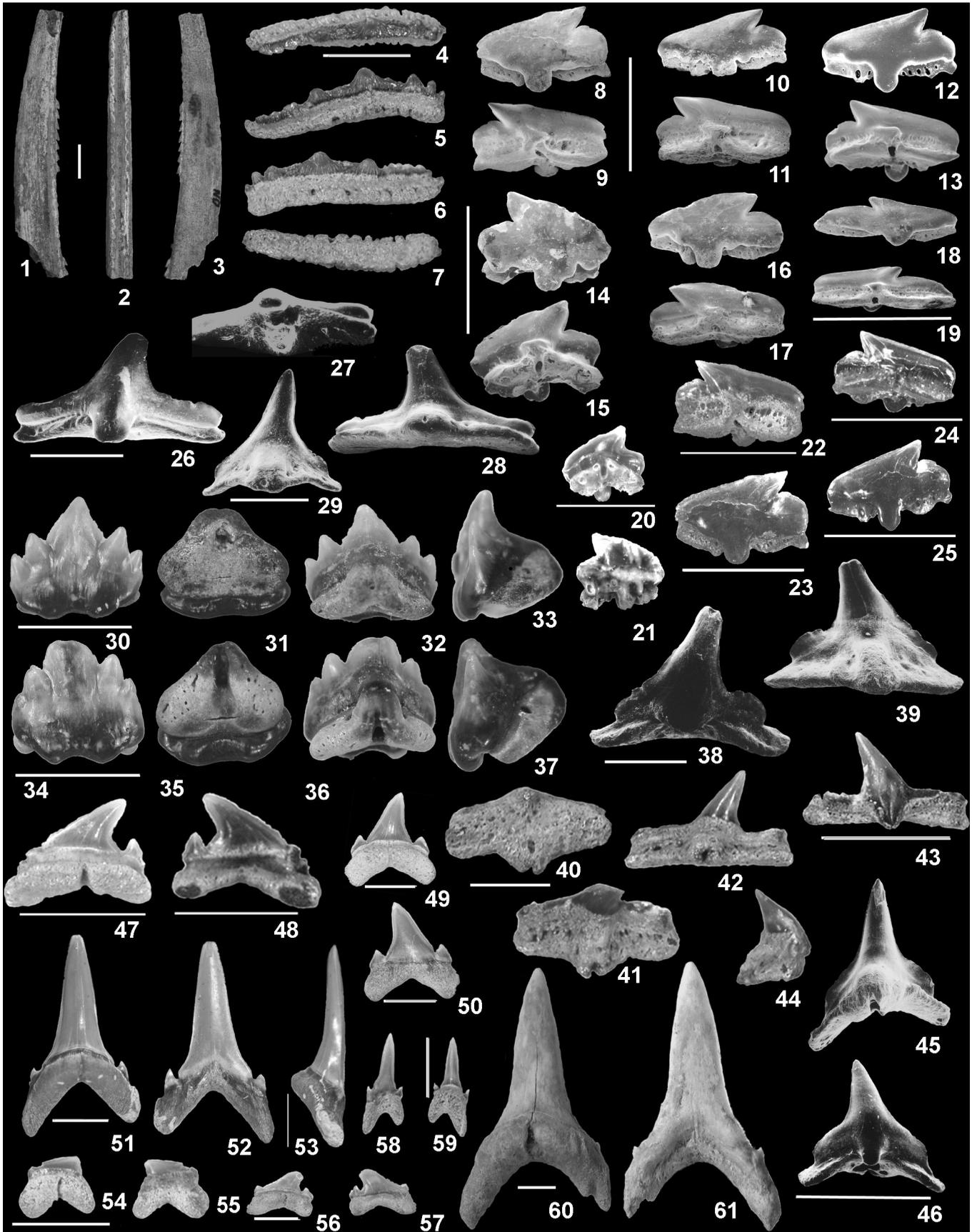


Table 1.—Taxonomic list of chondrichthyan and osteichthyan remains from the Fox Hills Formation, North Dakota.

+ = First systematic report of taxon from the Fox Hills Formation of North Dakota.

* = First systematic report of taxon from the Fox Hills Formation.

CLASS Chondrichthyes

SUBCLASS Elasmobranchii

ORDER Hybodontiformes

FAMILY Hybodontidae

? *Hybodus* sp. +

ORDER Hexanchiformes

FAMILY Paraorthacodontidae

Paraorthacodus andersoni (Case, 1978) +*

ORDER Squaliformes

FAMILY Squalidae

Squalus ballingsloevensis Siverson, 1993 +**Squalus* sp. +*

ORDER Squatiniformes

FAMILY Squatinidae

Squatina hassei Leriche, 1929 +

ORDER Orectolobiformes

FAMILY Ginglymostomatidae

Plicatosyllium derameei Case and Cappetta, 1997 +**Ginglymostoma* sp. +

FAMILY Orectolobidae

Cretorectolobus olsoni Case, 1978 +*

ORDER Lamniformes

FAMILY Odontaspidae

Carcharias cf. *C. tenuiplicatus* (Cappetta and Case, 1975b) +**Carcharias samhammeri* (Cappetta and Case, 1975a) +**Odontaspis aculeatus* (Cappetta and Case, 1975a) +

FAMILY Otodontidae

Cretalamna feldmanni n. sp. +*

FAMILY Serratolamnidae

Serratolamna serrata (Agassiz, 1843) +

FAMILY Anacoracidae

Squalicorax pristodontus (Agassiz, 1843) +*

Lamniformes incertae familiae

Paranomotodon toddi (Case and Cappetta, 1997) +*

ORDER Carcharhiniformes

FAMILY Triakidae

Palaeogaleus navarroensis Case and Cappetta, 1997 +**Galeorhinus girardoti* Herman, 1977 +*Archaeotriakis rochelleae* Case, 1978 +*

ORDER Synechodontiformes

FAMILY Palaeospinacidae

Synechodus turneri Case, 1987 +*

Indetermined shark centrum

Species A. Indetermined shark centrum

SUPERORDER Batomorphii

ORDER Rajiformes

SUBORDER Rhinobatoidei

FAMILY Rhinobatidae

Myledaphus sp. +

Rhinobatoidei incertae familiae

Protoplatyrhina renae Case, 1978 +*Pseudohypolophus mcultyi* (Thurmond, 1971) +

Species B. Indetermined rhinobatoid centrum

SUBORDER Rajoidei

FAMILY Rajidae

Walteraja exigua Siverson and Cappetta, 2001 +*

Table 1 (continued).

	SUBORDER Sclerorhynchoidei
	FAMILY Sclerorhynchidae
	<i>Ischyrhiza avonicola</i> Estes, 1964 +
	FAMILY Ptychotrygonidae
	<i>Ptychotrygon winni</i> Case and Cappetta, 1997 +*
	<i>Ptychotrygon greybullensis</i> Case, 1987 +*
	ORDER Myliobatiformes
	SUPERFAMILY Dasyatoidea
	FAMILY Dasyatidae
	<i>Dasyatis northdakotaensis</i> n. sp. +*
	SUPERFAMILY Myliobatoidea
	FAMILY Myliobatidae
	“ <i>Myliobatis</i> ” <i>foxbillsensis</i> n. sp. +*
	FAMILY Rhombodontidae
	<i>Rhombodus levis</i> Cappetta and Case, 1975a +*
	<i>Rhombodus</i> sp.
	Elasmobranchii Placoid Scale Morphotype 1
	Elasmobranchii Dermal Denticle Morphotype 1
	Elasmobranchii Dermal Denticle Morphotype 2
	Elasmobranchii Dermal Denticle Morphotype 3
	SUBCLASS Holocephali
	ORDER Chimaeriformes
	FAMILY Callorhynchidae
	<i>Ischyodus raybassi</i> Hoganson and Erickson, 2005
CLASS Osteichthyes	
	ORDER Lepisosteiformes
	FAMILY Lepisosteidae
	Genus and species indetermined
	ORDER Amiiformes
	FAMILY Amiidae
	SUBFAMILY Vidalamiinae
	<i>Melvius</i> sp. +*
	SUBFAMILY Amiinae
	<i>Cyclurus fragosus</i> (Jordan, 1927) +*
	Species C. Indetermined teleost tooth
	ORDER Pachycormiformes
	FAMILY Pachycormidae
	<i>Protosphyraena</i> sp. +*
	ORDER Aspidorhynchiformes
	FAMILY Aspidorhynchidae
	<i>Belonostomus longirostris</i> (Lambe, 1902) +*
	ORDER Ichthyodectiformes
	FAMILY Ichthyodectidae
	<i>Xiphactinus vetus</i> (Leidy, 1856) +*
	ORDER Elopiformes
	FAMILY Elopidae
	<i>Paratarpon?</i> sp. +*
	FAMILY Phyllodontidae
	<i>Paralbula casei</i> Estes, 1969 +
	ORDER Albuliformes
	FAMILY Pterothrissidae
	<i>Pollerspoeckia siegsdorfensis</i> Schwarzhans, 2010 +*
	ORDER Siluriformes
	FAMILY Ariidae
	<i>Vorbisia vulpes</i> Frizzell, 1965
	ORDER Argentiniformes
	FAMILY Microstomatidae
	cf. <i>Bathylagus</i> sp. +*

Table 1 (continued).

ORDER Aulopiformes	
FAMILY Enchodontidae	
	<i>Enchodus dirus</i> Leidy, 1857 +*
	<i>Enchodus</i> cf. <i>E. ferox</i> Leidy, 1855 +*
ORDER Perciformes	
FAMILY Apogonidae	
	" <i>Apogonidarum</i> " <i>maastrichtiensis</i> (Nolf and Stringer, 1966) +*
TELEOST <i>incertae sedis</i>	
	Species D. Indetermined teleost? Bone fragment
	Species E. Vertebral Morphoserries Type IB-2 of Brinkman and Neuman, 2002
	Species F. Vertebral Morphoserries Type IIIA-1 of Brinkman and Neuman, 2002
	Species G. Indetermined teleost scale
	Species H. Indetermined teleost scale

Maastrichtian *Hybodus* material was noted by Bouchard (1990) from the Fairpoint Member of the Fox Hills Formation in South Dakota and from the Navesink Formation in New Jersey by Becker et al. (2002). In particular, Becker et al. (2002, fig. 3D–G) illustrate in fig. 3E a worn fragment with a double row of teeth having a groove between them which they discuss as their "(*Hybodus* type B)." This most resembles the material in our collection.

Hybodontoid spines are illustrated in some of these works (Becker et al., 2002; Brinkman, 2004; Case, 1978, 1987), although none seems to be as well preserved as the specimen illustrated herein. Spines with a tuberculate surface or with longitudinal striae are illustrated in several reports. Case (1978) described as *Hybodus montanensis* a striated spine in a fauna that included teeth and compared it with a tuberculate form from the Navesink of New Jersey. Two striated, perhaps weakly tuberculate, fragmental specimens have been illustrated from the Campanian Teapot Sandstone of the Big Horn Basin under the name *Hybodus wyomingensis* (Case 1987, pl. 1, fig. 4a, c). In all of these specimens denticles are arranged in a single file, but in alternating positions along the posterior face of the spine. Brinkman (2004) illustrated similar material from the Dinosaur Park Formation of Alberta and Brinkman et al. (2005) do the same for marine shale units of the Lethbridge Coal zone below the Bearpaw Formation. None of their specimens appear to have had a double file of teeth flanking a central, smooth region as found in our specimen. We have not seen the material of an unassigned species of *Hybodus* discussed by Rees (1999), which includes a fragment with a double file of teeth from the Campanian of Sweden.

Case (1987) illustrated the dorsal fin spine of a species of the polyacrodontid hybodont *Lissodus* possessing tuberculate denticles offset in alternating fashion along a single row. These are considerably more comparable to many of the patterns shown on specimens mentioned above, and they are distinctly different from those on the Fox Hills specimen. We have pro-

visionally assigned this spine to ?*Hybodus* sp. because it has two well-defined rows of thorn-like denticles, unlike members of the polyacrodont genus *Lissodus* (= *Lonchidion*).

A specimen identified as *Lissodus* (= *Lonchidion*) *selachos* from the Hell Creek Formation was illustrated by Murphy et al. (1995, fig. A). That specimen (ND 93-77.5) has a single row of teeth overlapping slightly in an alternating fashion along the center of the spine. No axial groove is present, and it is incomplete at each end. Dorsal fin spines of *Lonchidion selachos* were illustrated by Kirkland et al. (2013, fig. 9.5J–M), showing a single row of teeth similar to the Hell Creek specimen. They do not resemble our Fox Hills specimen.

We are aware that chimaeroid dorsal spines may also occur in the fossil record (Robb 1989, p.89, fig. 13B, C) and that they have similar morphology, but we have followed the discussion by Becker et al. (2002, pp. 284–286) when provisionally accepting our Fox Hills specimen as ?*Hybodus* sp.

Catfish, too, have toothed fin spines. We have examined a fin spine of *Ictalurus punctatus*, the channel catfish of North America. It is typical of more than 1000 species having dorsal and pectoral fins that are toothed by bony extensions along both margins of the spine. This construction is markedly different from the individual, inset, enamel-like teeth of our Fox Hills specimen. Our spine is not from a catfish.

We also suggest that the practice of describing teeth and spines under the same name when they have not been found in skeletal association should probably be abandoned because teeth must be the primary nomenclatorial tools for fossil selachians in the absence of context.

Order **HEXANCHIFORMES** Buen, 1926

Family **PARAORTHACODONTIDAE** Glikman, 1958

Genus **PARAORTHACODUS** Glikman, 1957

Type species.—*Sphenodus recurvus* Trautschold, 1877.

Paraorthacodus andersoni (Case, 1978)

Text-figs. 8.29–8.33

- Synechodus andersoni* Case, 1978: p. 184, pl. 2, figs. 2, 3.
Synechodus striatus Case, 1978: p. 185, pl. 2, fig. 4.
Paraorthacodus andersoni (Case). Cappetta, 1987a: p. 129, figs. 109c, d.
Paraorthacodus andersoni (Case). Siverson, 1992b: p. 996, figs. 3.1–3.12.
Paraorthacodus andersoni (Case). Adolfsen and Ward, 2014: p. 595, figs. 2C–G.

Description.—Teeth large for the genus. Width of nearly complete root of the largest tooth is 15.1 mm. Even though only the base of the cusp is present on both specimens, it can be determined that it was large and flanked by three pairs of cusplets. The two cusplets which are preserved on each tooth indicate that they were high, conical, apically curved toward the cusp, and separated from the cusp and one another. Parallel coarse ridges extend from base of cusplets to apex. Labial face of cusp is flat with indistinct ridges at base and the lingual face is strongly convex.

Pseudopolyaulacorhize root is robust and extends beyond the basal margin of the cusplets. Basal margin of root is gently arched in labial view. Basal face of root has two large and deep grooves positioned beneath the cusp. Large foramina occupy each groove. These grooves are also evident in labial view, where the root and basal part of the cusp form a flat surface. Two pairs of incipient grooves occur on either side of the large grooves. Foramina are present on the large lingual protuberance and lingual face of the root.

Material.—Two broken anterior teeth from NDGS L140 (ND 95-13.74, ND 95-13.75). One tooth has a nearly complete root, only half the root is preserved on the other. Bases of the cusp and cusplets are present on the roots. The cusps are not preserved on either specimen, but two cusplets are preserved on each specimen. The larger specimen (ND 95-13.75; Text-figs. 8.29–8.31), with one root tip missing, is 5.1 mm wide and 5.3 mm high from the base of the root to the top of the second cusplet, but the crown on both teeth is missing.

Remarks.—*Paraorthacodus andersoni* was originally described by Case (1978) as a species of *Synechodus*. The reassignment of the species to *Paraorthacodus* by Cappetta (1987a, p. 129) was accepted by Siverson (1992b). *Paraorthacodus andersoni* is separated from *P. conicus*, a similar species, by its flat and weakly ornamented basal labial cusp face. The flat labial face of the cusp and labial face of the root form a continuous flat plain (Siverson, 1992b). This condition permits identification of *P. andersoni* even if the specimens are incomplete.

Paraorthacodus andersoni, initially reported from the Campanian Judith River Formation of Montana (Case, 1978), also occurs in the Coniacian and/or Early Santonian (possibly Cenomanian) to Early Campanian (possibly Early Maastrichtian) of Sweden (Siverson, 1992b). It has also been reported from the Maastrichtian of Denmark (Adolfsen and Ward, 2014). This is the first record of *Paraorthacodus* from the Fox Hills Formation, and it extends the range of *P. andersoni* into the Late Maastrichtian. Cvancara and Hoganson (1993) reported *P. eocaenus* from the Paleocene Cannonball Formation of North Dakota. Cretaceous distributions seem to suggest a species preferring the higher latitudes; however, it has not been noted in Canadian strata.

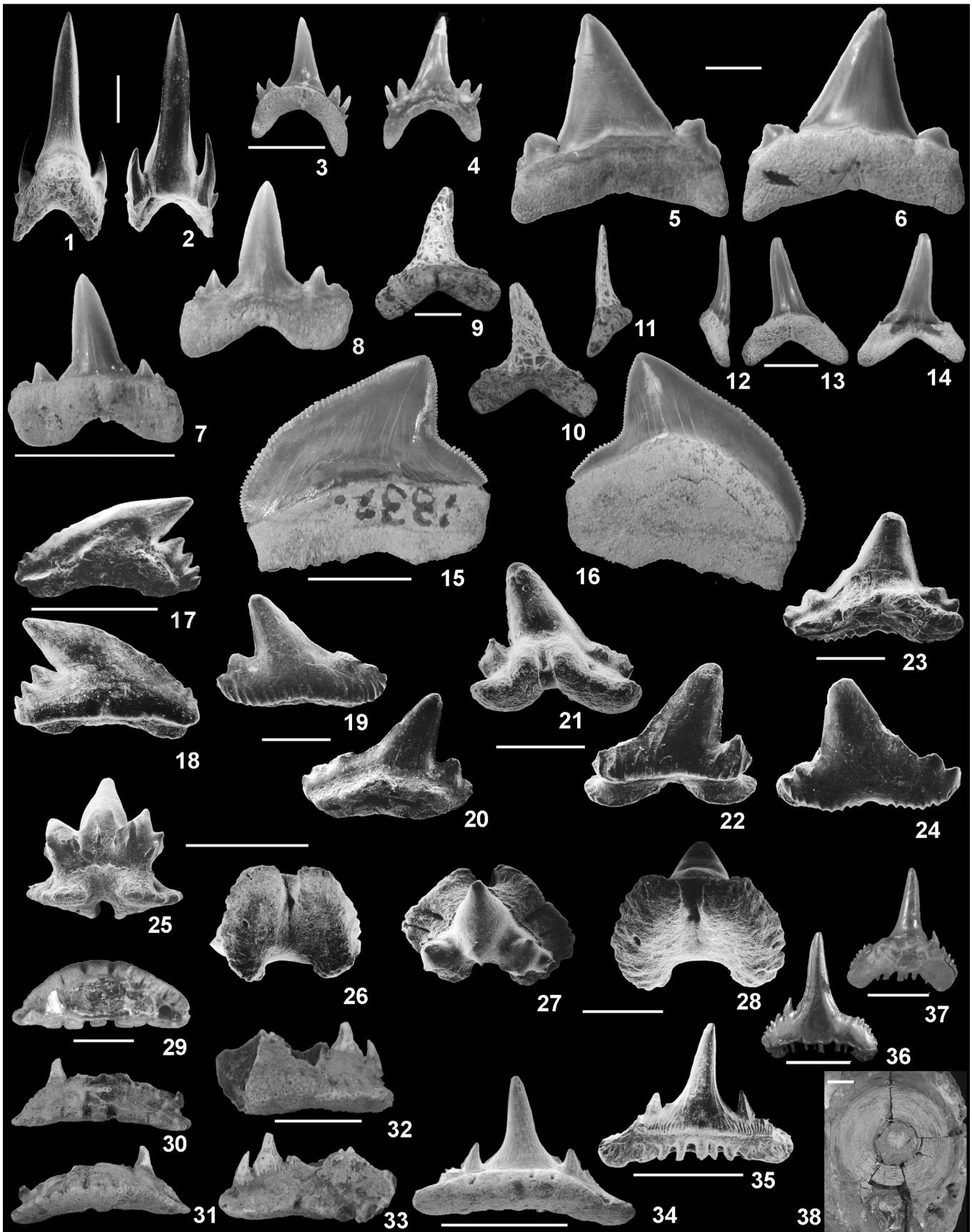
Superorder **SQUALOMORPHII** Compagno, 1973Order **SQUALIFORMES** Goodrich, 1909Family **SQUALIDAE** Bonaparte, 1834Genus **SQUALUS** Linnaeus, 1758**Type species.**—*Squalus acanthias* Linnaeus, 1758.***Squalus ballingsloevensis*** Siverson, 1993

Text-figs. 7.8–7.13, 7.16–7.19

Squalus ballingsloevensis Siverson, 1993: p. 6, pl. 1, figs. 1–8.

Description.—Large *Squalus* teeth averaging more than 5 mm in width. Mesial cutting edge straight to slightly convex. Distal heel large and markedly convex. Apron centrally located and well developed with parallel sides. Base of apron observable beneath basal root face from lingual side. Basal face of root flat to slightly concave. Uvula overhangs large infundibulum.

Text-fig. 8.—Teeth and centrum of Fox Hills sharks. 8.1–8.4, *Odontaspis aculeatus* (Cappetta and Case, 1975a); 8.1, 8.2, symphyseal tooth (ND 94-37.1); 8.3, 8.4, antero-lateral tooth (ND 95-13.89). 8.5, 8.6, holotype, *Cretalamna feldmanni* n. sp., upper left lateral (UND-PC 15903); 8.5, labial view; 8.6, lingual view. 8.7, 8.8, *Serratolamna serrata* (Agassiz, 1843), lateral tooth (ND 99-6.5). 8.9–8.14, *Paranomotodon toddi* (Case and Cappetta, 1997) lateral teeth, 8.9–8.11 (ND 95-13.72), 8.12–8.14 (ND 95-13.73). 8.15, 8.16, *Squalicorax pristodontus* (Agassiz, 1843), (NDGS 1695). 8.17, 8.18, *Galeorhinus girardoti* Herman, 1977, lateral teeth (NDGS 1002). 8.19–8.24, *Palaeogaleus navarroensis* Case and Cappetta, 1997; 8.19, 8.20, antero-lateral tooth (ND 94-38.7); 8.21, 8.22, antero-lateral tooth (ND 94-38.6); 8.23, 8.24 lateral tooth (ND 94-38.8). 8.25–8.28, *Archaeotriakis rochelleae* Case, 1978; 8.25, 8.26 (ND 94-38.10); 8.27, 8.28 (ND 94-38.9). 8.29–8.33, *Paraorthacodus andersoni* (Case, 1978); 8.29–8.31 (ND 95-13.74); 8.32, 8.33 (ND 95-13.75). 8.34–8.37, *Synechodus turneri* Case, 1987; 8.34, 8.35 lateral teeth (ND 95-13.76); 8.36, 8.37, anterior tooth (ND 99-6.6). 8.38, Species A, indetermined lamniform shark centrum, (ND 07-76.1). Scale bar = 5 mm except 8.1, 8.2, 8.19–8.28 = 1 mm; 8.17, 8.18 = 2.5 mm; 8.7, 8.8, 8.15, 8.16, and 8.38 = 1.0 cm. SEM images include 8.1, 8.2, 8.17–8.28, and 8.35.



Numerous lingual and labial marginal foramina. Posterior, or juvenile, teeth elongated with crowns much shorter than in lateral teeth. Sides of aprons in posterior teeth are triangular, not parallel. Basal margin of cusp on labial side is sinuous.

Material.—Included in the Fox Hills material are 153 specimens of *Squalus ballingsloevensis* from sites NDGS L140, and NDGS L142 (Table 2). Illustrated material includes NDGS specimens ND 99-5.3 (Text-figs. 7.8, 7.9; H. 3.7 mm, W. 5.7 mm), ND 99-5.4 (Text-figs. 7.10, 7.11; H. 3.4 mm, W. 6.0 mm), ND 07-75.7 (Text-figs. 7.12, 7.13; H. 3.5 mm, W. 5.0 mm), ND 99-5.5 (Text-figs. 7.16, 7.17), and ND 95-13.70 (Text-figs. 7.18, 7.19; H. 1.8 mm, W. 5.6 mm).

Remarks.—Our specimens compare well with the *Squalus ballingsloevensis* holotype figured by Siverson (1993) from the earliest Maastrichtian *Belemnitella lanceolata* Zone in the Kristianstad Basin of southern Sweden.

Squalus has previously not been reported from the Fox Hills Formation. *Squalus minor* was documented previously from the Paleocene Cannonball Formation in North Dakota (Cvancara and Hoganson, 1993) and a distinctive undescribed *Squalus* was identified from the DeGrey Member of the Pierre Formation in North Dakota (Hoganson et al., 1999). *Squalus minor* of the Cannonball Formation is distinctly different from *Squalus ballingsloevensis* by being notably mesial-distally compressed and by having a much higher crown. The apron of *S. minor* is shorter than in *Squalus ballingsloevensis* and it extends from the crown mesial of center. The basal cusp margin on the labial side of *S. minor* is much more irregular than in *Squalus ballingsloevensis*.

Squalus huntensis, described by Case and Cappetta (1997) from the Late Maastrichtian Kemp Clay of Texas, falls within the size range and is morphologically similar to juvenile specimens of *Squalus ballingsloevensis* reported by Siverson (1993). It may well be the same species. *Squalus ballingsloevensis* differs from *Squalus* sp. (Text-figs. 7.14, 7.15, 7.20, and 7.21) by having a more centrally located apron with parallel sides and a basal face of root that is flat compared to the distinctly concave basal face of these specimens. The basal cusp margin on the labial side is more sinuous and less distinct and the uvula is reduced on the lingual side of these specimens.

Siverson (1993) suggested that *Squalus ballingsloevensis* inhabited shallow, temperate coastal waters of the Kristianstad Basin during the earliest Maastrichtian. Today squalids live in boreal, temperate, and tropical waters down to considerable depths (600 to 1450 m). They primarily eat bony fishes, but also feed on other sharks, various invertebrates, and even marine mammals (Compagno et al., 2005). Evolution of the squalids, including their adaptation to deep water, has been examined by researchers during the past decade (Adner and

Cappetta, 2001; Krewit and Klug, 2009; Klug and Krewit, 2010).

Dogfish sharks are noted scavengers. Their teeth are often found in large numbers associated with skeletons of marine reptiles. Hoganson et al. (1999) noted that a *Squalus* sp. from the North Dakota Pierre Formation was a scavenger of the carcass of the mosasaur *Plioplatecarpus*. This behavior was also noted by Cicimurri et al. (1999) and Bardet et al. (1998).

Squalus sp.

Text-figs. 7.14, 7.15, 7.20, 7.21, 7.22–7.25

Description.—Teeth of *Squalus* sp. differ from those of *S. ballingsloevensis*. Specimens ND 99-5.6 (Text-figs. 7.14, 7.15) and NDGS 1692 (Text-figs. 7.20, 7.21) are distinctly more equidimensional than the antero-lateral teeth of *S. ballingsloevensis* as illustrated by Siverson (1993). They differ from *Squalus ballingsloevensis* in having a higher cusp, apron with edges that are non-parallel, and a much more irregular basal cusp margin on the labial side. The root is deeply concave.

Specimens NDGS 1693 (Text-figs. 7.22, 7.23) and NDGS 1694 (Text-figs. 7.24, 7.25) are slightly more lateral than ND 99-5.6 and NDGS 1692, but they still show more complex root aprons and less prominent uvulae than are illustrated for *S. ballingsloevensis* (Siverson, 1993).

Material.—This species is represented by specimens ND 99-5.6 (Text-figs. 7.14, 7.15; H. 3.2 mm, W. 3.4 mm), NDGS 1692 (Text-figs. 7.20, 7.21; H. 3.1 mm, W. 2.7 mm), NDGS 1693 (Text-figs. 7.22, 7.23; H. 3.9 mm, W. 6.0 mm), and NDGS 1694 (Text-figs. 7.24, 7.25; H. 3.5 mm, W. 4.9 mm), all from site NDGS L140.

Remarks.—In our opinion, the descriptions above distinguish these forms from the teeth of *S. ballingsloevensis*. Fox Hills specimens from site L140 are Early Late Maastrichtian in age, somewhat younger than the type material of *S. ballingsloevensis*, which is—according to Siverson (1993)—from the *Belemnitella lanceolata* Zone of the earliest Maastrichtian.

Order **SQUATINIFORMES** Buen, 1926

Family **SQUATINIDAE** Bonaparte, 1838

Genus **SQUATINA** Dumeril, 1806

Type species.—*Squalus squatina* Linnaeus, 1758.

Squatina hassei Leriche, 1929

Text-figs. 7.26–7.29

- Squatina hassei* Leriche, 1929: pp. 206–208, figs. 1–3.
Squatina hassei Leriche. Herman, 1977: pp. 124, 125, pl. 5, fig. 3.
Squatina hassei Leriche. Manning and Dockery, 1992: p. 26, pl. 4, figs. 8a–d.
Squatina hassei Leriche. Welton and Farish, 1993: p. 77, figs. 1, 2.
Squatina hassei Leriche. Case, 1995: pp. 78, 80, pl. 3, figs. 7–11.
Squatina hassei Leriche. Hoganson et al., 1995: p. 60.
Squatina hassei Leriche. Hoganson et al., 1996: p. 41A.
Cretorectolobus cf. *olsoni* Case, 1978. Case and Cappetta, 1997: p. 138, pl. 5, figs. 3, 4.
Squatina hassei Leriche. Hartstein et al., 1999: pl. 1, fig. 8.
Squatina hassei Leriche. Peng et al., 2001: pp. 10, 11, pl. 2, figs. 7–9.
Squatina hassei Leriche. Case et al., 2001b: pp. 115, 116, pl. 1, figs. 3–18.
Squatina hassei Leriche. Becker et al., 2004: p. 783, figs. 4a–d.
Squatina hassei Leriche. Brinkman et al., 2005: p. 240, fig. 26.2F.
Squatina hassei Leriche. Vullo, 2005: p. 612, fig. 3A, B.
Squatina hassei Leriche. Becker et al., 2006: pp. 701, 702, figs. 3.3–3.5.
Squatina (*Cretascyllium*) *hassei* Leriche. Guinot et al., 2012: pp. 540–544, figs. 8a–u.
(See also synonymy in Guinot et al., 2012.)

Description.—Small teeth averaging 1.6 to 3.6 mm in height and 1.8 to 5.6 mm in width. Anterior and lateral teeth present. Teeth trigonal in shape with wide base. Cusps of anterior teeth short, slender, and erect. Those of lateral teeth inclined posteriorly. Mesial and distal heels blade-like and forming a continuous cutting edge with cusp. Heels on anterior teeth strongly sloping. Mesial and distal heels of lateral teeth elongate, as long as height of cusp and parallel with base of root. Lateral teeth broader than high, having relatively long and low mesial and distal heels with sharp cutting edges. Apron distinct with parallel to subparallel edges. Root is thin, flat, triangular, and perpendicular to crown. Base of root is flat in lateral teeth and distinctly concave in anterior teeth. Small foramina on lingual protuberance. Lingual and labial cusp faces smooth, labial bulge of crown distinct. Cutting edges of crown and heels continuous. Root triangular in basal outline and projecting lingually at right angle to crown. Central foramen on lingual protuberance of root. Root hemiaulacorhizous. Basal attachment surface of root at right angles to cusp. Strong labial flange present.

Material.—Fifty-two specimens have been examined, including illustrated specimen ND94-38.2 (Text-fig. 7.29) from site NDGS L35, and specimen ND 07-74.1 (Text-figs. 7.26, 7.28) from NDGS L141. As indicated in Table 2, the species is present in collections from both the central and western outcrop areas.

Remarks.—Leriche (1929) named *Squatina hassei* based on specimens from the Maastrichtian type area in Holland. Teeth of *Squatina hassei* are similar to teeth of *Cretorectolobus olsoni* in the Fox Hills fauna, but they do not have cusplets and the root is hemiaulacorhizous. The *Cretorectolobus* cf. *C. olsoni* illustrated by Case and Cappetta (1997) from the Kemp Clay (Maastrichtian, Texas) is *Squatina hassei* for reasons that are discussed under *Cretorectolobus* herein.

Determination of generic assignments of these teeth became more complicated after the erection of *Cederstroemia* by Siverson (1995) for very similar teeth, but teeth twice, or more, as wide as high and having a subtriangular, hemialacorhizous to holaulacorhizous root. Siverson placed *Cederstroemia* species in the orectolobiform sharks, or wob-begongs, whereas *Squatina* is a genus of squatiniform shark belonging to the angle sharks. Additionally, Guinot et al. (2012) noted that some of their *Squatina* teeth were similar to members of *Cretascyllium*, a genus described by Müller and Deidrich in 1991, but again an orectolobiform genus. They reduced the rank of *Cretascyllium* to subgenus and assigned the types of both *S. cranei* Woodward, 1888, the nominal species, and *S. hassei* Leriche to this subgenus in the belief that *Cretascyllium* teeth were but anterior teeth of squatinid sharks (Guinot et al., 2012, p. 531). Our study does not contribute to this systematic discussion, therefore we have followed the more conservative course, and we do not recognize the subgenus *S. (Cretascyllium)* herein.

Hoganson et al. (1995, 1996) first reported *S. hassei* from the Fox Hills Formation in North Dakota, where it has been recovered from three localities (Table 2). *Squatina hassei* was also identified from the Fairpoint Member of the Fox Hills Formation in northwestern South Dakota by Becker et al. (2004). A well preserved tooth illustrated by them (fig. 4A–D) has a wide root heel that seems more related to *Cederstroemia* Siverson (1995), as was suggested by Guinot et al. (2012), but the type of nutritive groove is not described. Therefore, we cannot be certain and we retain the identification of Becker et al. (2004). Cicimurri (1998) recognized two *Squatina* species, *S. sp. 1* and *S. sp. 2*, from the Fairpoint Member as well. His two *Squatina sp. 2* teeth may be lateral teeth or anterior teeth of *S. hassei*. His two *S. sp. 1* teeth may possibly be anterior teeth of *S. hassei*, but they are incomplete and probably not identifiable.

Becker et al. (2006) reported the occurrence of *S. hassei* from the Upper Maastrichtian Arkadelphia Formation from Hot Springs County, Arkansas based on poorly preserved teeth. Our feeling is that the illustrated specimen (Becker et al. 2006, figure 3.3–3.5) is probably too abraded to assign with certainty. Again, Guinot et al. (2012) suggested it was related to *Cederstroemia*.

Welton and Farish (1993) reported *S. hassei* from the Campanian Pecan Gap and Ozan formations of Texas and the Maastrichtian Kemp Clay, Escondido and Littig formations of Texas. Leriche (1929) cited Wade (1926) as having *S. hassei* from the Maastrichtian Ripley Formation of Tennessee, but the specimen illustrated by Wade does not seem to be a *Squatina*. Case et al. (2001a) reported *S. hassei* from the Upper Cretaceous (Early to Middle Santonian) Eutaw Formation of Georgia. In New Jersey, *Squatina hassei* was reported from the lower and middle Maastrichtian Mt. Laurel and Navesink formations (Case, 1995) and was also noted from the Upper Maastrichtian New Egypt Formation (Case et al., 2001b). This taxon has also been recorded from the Upper Cretaceous Demopolis Formation of Mississippi (Manning and Dockery, 1992). This species also occurs in the Upper Campanian Donoho Creek Formation in South Carolina (Cicimurri, 2007). A fauna from the Campanian Black Creek Formation of North Carolina contained *S. hassei* as reported by Robb (1989); this species of angel shark is also reported by Peng et al. (2001) from the Campanian Foremost Formation of southeastern Alberta. A specimen of *Squatina* illustrated by Brinkman et al. (2005, fig. 26.2F, p. 490) from the marine shales of the Lethbridge Coal below the Bearpaw Formation appears to be *S. hassei*. Brinkman et al. (2004, table 3, p. 307) report it as a member of their coastal community in the Milk River study area of the Judith River Formation.

Globally the species is widely reported. Herman (1977) indicated that it is known from the Maastrichtian of Holland, Belgium, and Morocco. Guinot et al. (2012a, p. 542) confirmed these occurrences and further noted presence of *S. (C.) hassei* from the Santonian of southern England and northern France, the latter being considered the oldest occurrence of the species and its earliest appearance in the London-Paris Basin. Vullo (2005), using the same criteria as we have done above, distinguished *S. hassei* from *Cederstroemia* and *Cretorectolobus* in the Campanian of western France.

The wide distribution of this and other Campanian and Maastrichtian taxa is likely an artifact of the proximity of paleo-continent, whereas the modern distributions of species of *Squatina* are more restricted. Stelbrink et al. (2010) point out that these sharks are coastal, bottom-hugging ambush predators whose molecular systematics indicate modern presence of four geographic clades, including a Europe-North Africa-Asia clade, a South African clade, an Australian clade, and a fourth clade comprising all North and South American species. Their work suggests that speciation of modern *Squatina* resulted from fragmentation of the Tethyan coastline as the Atlantic opened, the Tethys closed, and finally the Panamanian Isthmus formed. Furthermore, they suggest this phylogeographic distribution is an example of vicariance, or the separation of species into two or more parts by divi-

sion of their geographic range after creation of a barrier or barriers as defined by de Queiroz (2005) (Stelbrink et al., 2010). We note that this process must have begun during the Maastrichtian Fox Hills Sea as the Dakota Isthmus closed to divide the Western Interior Seaway into northern and southern portions (Erickson 1978, 1999).

The study of node development of squatiniforms by Klug and Kriwet (2013), based on fossil body remains rather than teeth, suggested that squatiniforms underwent a secondary radiation during the Cretaceous and were little affected by end-Cretaceous extinctions. Another radiation event in the Oligocene established the basis of the modern fauna.

Order **ORECTOLOBIFORMES** Applegate, 1972

Family **GINGLYMOSTOMATIDAE** Gill, 1862

Genus **PLICATOSCYLLIUM** Case and Cappetta, 1997

Type Species.—*Plicatoscyllium derameei* Case and Cappetta, 1997.

Plicatoscyllium derameei Case and Cappetta, 1997

Text-figs. 7.30–7.33

Ginglymostoma lehneri Leriche. Welton and Farish, 1993: p. 83, figs. 1–5.

Plicatoscyllium derameei Case and Cappetta, 1997: pp. 137, 138, pl. 5, figs. 5–7.

Plicatoscyllium derameei Case and Cappetta. Hartstein et al., 1999: p. 18, pl. 2, figs. 16, 17.

Description.—Medium-sized, symmetrical rasping teeth with two cusplets flanking each side of a central cusp. Labial crown face having a median crest. Lingual crown face with a protuberance that overhangs the root. Apron slightly concave and heart-shaped root with an apical foramen and two smaller lateral foramina.

Material.—Five specimens of antero-lateral teeth, two with some damage. Illustrated material is the largest tooth (ND 99-5.7; Text-figs. 7.30–7.33) with a crown height of 5.64 mm and crown width 5.70 mm from site NDGS L140 (Table 2). The smallest is NDGS 1001 with crown height 4.42 mm, crown width 4.66 mm, also from site NDGS L140.

Remarks.—*Plicatoscyllium* was erected by Case and Cappetta (1997) to hold ginglymostomatid teeth (up to 7 mm) that were separated from *Ginglymostoma* by the presence of a median crest or ridge on the median cusp. In other characters, these teeth are unlikely to be separated from teeth of *Ginglymostoma* species. Size should not, of itself, be considered a generic character because its application artificially limits assignment of both specimens and species under a range of

circumstances of both growth (ontogeny) and evolutionary development.

Plicatoscyllium derameei Case and Cappetta (1997) from the Upper Maastrichtian Kemp Clay of Texas is the type species of the genus. Our report is the first recognition of the species in the Fox Hills Formation. A single specimen to be compared to *P. derameei* has also been noted by Becker et al. (2006) from the Upper Maastrichtian Arkadelphia Formation of Arkansas. Fox Hills specimens are at the upper end of the size range known for the species and the median crest is less prominent than that on the type material illustrated by the authors of the species. Defining morphology (median cusp) of *P. derameei* is present, however, and forms the basis for our assignment. A Fox Hills correlative, the Severn Formation of Maryland (Brouwers and Hazel, 1978), also contains *P. derameei* (Hartstein et al., 1999).

Several species of *Plicatoscyllium* have been recognized in the Maastrichtian of Morocco (Noubhani and Cappetta, 1997). As illustrated by Noubhani and Cappetta (1997), these species show a range of development of the ridge on the median cusp. Our specimens seem to fall within that range for *P. derameei*. We include in synonymy the specimen figured by Welton and Farish (1993, figs. 1–5) which we believe to be *P. derameei*.

Genus **GINGLYMOSTOMA** Müller and Henle, 1837

Type species.—*Squalus cirratus* Gmelin, 1789.

***Ginglymostoma* sp.**
Text-figs. 7.34–7.37

Description.—One tooth has been assigned to this undetermined species of *Ginglymostoma*. The specimen is about the size given as average by Cappetta (1987a) and crowns are somewhat worn. Crown with weak outer and strong second cusplets flanking well-developed central cusp. Labial surface with strong, bifid basal flange covering root in basal view. Lingual surface with central root protuberance containing a central groove and foramen and a pair of margino-lingual foramina at the upper edge of the root on each side of the central protuberance. Root hemiaulacorhizous with many fine foramina on basal surface. Range of the genus is Maastrichtian to Recent (Cappetta, 2012).

Material.—One antero-lateral tooth with the following measurements: H. 5.32 mm, W. 5.55 mm. This illustrated specimen (ND 94-38.5; Text-figs. 7.34–7.37) is from locality NDGS L35.

Remarks.—*Ginglymostoma* is a genus with many Late Campanian and Maastrichtian species described from North America, Europe, and countries of the Mediterranean basin. Maastrichtian occurrences include *G. lehneri* from both Morocco and Trinidad, *G. minutum* from Maastricht, Netherlands, *G. rugosum* from Morocco (Cappetta, 1987a), the Kemp Clay of northern Texas (Case and Cappetta, 1997), four teeth from the Arkadelphia Formation of Arkansas (Becker et al., 2006), and a single tooth from the Fairpoint Member of the Fox Hills Formation in South Dakota as reported by Bouchard (1990) and Cicimurri (1998). In contrast with the Maastrichtian which had several species, the modern family Ginglymostomatidae contains only three monospecific genera.

Teeth of *Ginglymostoma*, a nurse shark, are usually described as rare elements of shark faunal studies (Case, 1987; Case and Schwimmer 1988; Case and Cappetta, 1997; Cicimurri, 1998). They are also scarce in the North Dakota material. Nurse sharks are subtropical to tropical shallow-water (0 to 130 m) species that frequent the littoral zone and feed on bottom-dwelling invertebrates and small fishes (Compagno et al., 2005). It would seem that they were an uncommon member of the Fox Hills vertebrate community in North Dakota.

Family **ORECTOLOBIDAE** Jordan and Fowler, 1903
Genus **CRETORECTOLOBUS** (Case, 1978) emend.
Siverson, 1995

Type species.—*Cretorectolobus olsoni* Case, 1978.

***Cretorectolobus olsoni* Case, 1978**
Text-figs. 7.38–7.46

Cretorectolobus olsoni Case, 1978: p. 188, [partim], pl. 3, fig. 1, text-figs. 9, 10b, non text-fig. 10a.

Cretorectolobus olsoni Case. Case, 1987: p. 18 [partim], pl. 8, fig. 6, non pl. 8, figs. 1–5, 7.

Cretorectolobus olsoni Case. Cappetta, 1987a: pp. 74, 75 [partim], figs. 68D–G, non figs. 68A–C.

Cretorectolobus olsoni Case. Siverson, 1995: pp. 978, 979, figs. 3, 1–6.

Cretorectolobus olsoni Case. Beavan and Russell, 1999: p. 496, figs. 3.3, 3.4.

Description.—Latero-posterior tooth with high labio-lingually compressed cusp directed distally and having one pair of well-developed cusplets. Lingual face concave with well-defined cutting edges on lower half of cusp. Apron short. Root thin and holaulacorhizal (or with central foramen). Basal face of root tetragonal; many foramina on lingual surface of root just beneath cusp.

Material.—Fox Hills material includes 33 specimens from both Bowman and Logan counties, ND (Tables 1, 2). Illustrated specimens include ND 94-38.4 (Text-figs. 7.38, 7.39; H. 2.2 mm, W. 2.3 mm), ND 95-13.90 (Text-figs. 7.40–7.44; H. 3.4 mm, W. 6.5 mm), and ND 94-38.3 (Text-figs. 7.45, 7.46; H. 2.5 mm, W. 2.4 mm).

Remarks.—Teeth of *C. olsoni* are superficially similar to *Squatina hassei*, but teeth of *S. hassei* do not have cusplets and are hemiaulacorhizous.

Siverson (1995) emended *Cretorectolobus* Case, 1978, wherein he determined that the type series was heterogeneous. In doing, so he clarified the difference in dental characteristics between *Cretorectolobus* and the morphologically similar *Squatina* by establishing that *Cretorectolobus* has cusplets and a holaulacorhizous root. Furthermore, he defined the new genus *Cederstroemia*, pointing out that in both *Cretorectolobus olsoni* and *Cederstroemia triangulate*, the root can be either hemiaulacorhizous or holaulacorhizous, at least in the Campanian Judith River forms (Siverson, 1995, p. 978). This places greater importance on the presence of cusplets or on the need for a large series of specimens.

Case (1978) originally described *Cretorectolobus olsoni* from the Campanian Judith River Formation, Blaine County, Montana. He later noted the presence of that taxon in the Upper Campanian Teapot Sandstone Member of the Mesaverde Formation in the Big Horn Basin of Wyoming. As our synonymy indicates, we have followed Siverson's assignments.

Bouchard (1990) identified *Cretorectolobus olsoni* from the Fairpoint Member of the Fox Hills Formation near Red Owl, northwestern South Dakota. However, she did not figure any of the three specimens. Cicimurri (1998), in his review of Fairpoint Member sharks, suggested that specimens previously identified as *C. olsoni* are *Squatina*. We cannot verify this based on the illustrations provided by Cicimurri (1998).

An antero-lateral tooth from the Turonian of Texas identified as *Cretorectolobus* sp. by Welton and Farish (1993) is believed not to belong to that genus because it lacks cusplets. Case and Cappetta (1997) described *Cretorectolobus* cf. *olsoni* from the Kemp Clay of Texas; however, the figured specimen appears to be *Squatina hassei* because it lacks cusplets and the root does not have a nutritive groove. Figures 3a–d of Case and Cappetta (1997) appear to be a lateral tooth, and figures 4a–e illustrate an anterior tooth of *S. hassei*.

Beavan and Russell (1999) report *C. olsoni* from Upper Campanian Lethbridge Coal Zone of the Dinosaur Park Formation of Alberta. Wroblewski (2004) lists *Cretorectolobus* sp. from the lower Ferris Formation (Lancian) of the western Hanna Basin, Wyoming.

Cretorectolobus olsoni is reported here from the Fox Hills Formation for the first time based on the emended definition of Siverson discussed above. It was a member of the bottom-dwelling sharks, perhaps behaving similarly to modern wobbegong sharks (Siverson, 1995), with a range from Late Campanian to Late Maastrichtian.

Order **LAMNIFORMES** Berg, 1937

Family **ODONTASPIDIDAE** Müller and Henle, 1839

Genus **CARCHARIAS** Rafinesque, 1810

Type species.—*Carcharias taurus* Rafinesque, 1810.

Carcharias cf. *C. tenuiplicatus* (Cappetta and Case, 1975b)

Text-figs. 7.47, 7.48

Description.—Teeth small, width of largest is 10.5 mm. Labial and lingual faces of triangular crown equally convex. Crown is distally directed. Base of crown broad and flanked by one pair of large, broadly-based, erect, triangular cusplets. Distinct, sharp cutting edge is continuous to base of crown where a distinct notch occurs before cutting edge continues over cusplets. Cusplets are attached to crown. Very short and closely spaced longitudinal ridges form a band at base of labial face of crown. A distinct neck or collar occurs at the base of the labial face of the crown. Root strongly bilobate. Lobes flattened and form an obtuse angle. Anterior lobe much longer than posterior lobe. Lingual root protuberance is distinct and exhibits a deep nutritive groove.

Material.—Nine latero-posterior teeth are present in the collection from NDGS L35. Illustrated is specimen ND94-36.1 (Text-figs. 7.47, 7.48) (Table 2). Additionally, seven specimens are present from NDGS L140; the largest is H. 9.73 mm, W. 10.53 mm and the smallest is H. 4.09 mm and W. 5.23 mm.

Remarks.—We follow Compagno (2002) and Compagno et al. (2005) by placing both *Carcharias* and *Odontaspis* in the family Odontaspidae.

Our specimens compare favorably with illustrations of *Carcharias tenuiplicatus* by Welton and Farish (1993, p. 90, figs. 3a, 3b) and with illustrations of *Cenocarcharias tenuiplicatus* by Cappetta and Case (1999, pl. 9). Although all of the Fox Hills specimens have short, closely spaced, longitudinal ridges at the base of the labial face of the crown, none of them has these ridges at the base of the lingual face of the crown, apparently a characteristic of *C. tenuiplicatus*. There seems to be variation in this characteristic which suggests that, rather than accepting a new genus, the more conservative approach

may be most appropriate. Because of this we have chosen to refer these specimens to *Carcharias* cf. *C. tenuiplicatus*.

Also, *Carcharias tenuiplicatus* (*sensu strictu*) has only been reported previously in Texas during the Cenomanian. We concur with Welton and Farish (1993) that this taxon should be assigned to *Carcharias* based on tooth morphology, rather than concurring with Cappetta and Case (1999) who created a new genus, *Cenocarcharias*, to accommodate this species. *Cenocarcharias* has been applied by Cumbaa et al. (2006), a position that has not yet been widely accepted (Cicimurri, 2000; Shimada et al., 2006). The teeth Cumbaa et al. (2006) described and illustrated from the Bainbridge River bonebed of Saskatchewan, Canada have enameloid ridges on both sides of the crown, but also more complicated cusplets as well.

Carcharias tenuiplicatus (*sensu strictu*) has been noted from the Cenomanian Pepper Formation, Bell Co., Texas (Welton and Farish, 1993, p. 90), Lower Arlington Sandstone Member of the Woodbine Formation, Tarrant Co., Texas (Cappetta and Case, 1975b, p. 304), and an undesignated Cenomanian Tarrant Co. interval (Cappetta and Case, 1999, p. 17). Both Cicimurri (2000) and Shimada et al. (2006) discussed it, respectively, from the Middle Cenomanian Greenhorn Formation of South Dakota and southeastern Colorado.

Carcharias samhammeri (Cappetta and Case, 1975a)
Text-figs. 7.49–7.61

Odontaspis samhammeri Cappetta and Case, 1975a: p. 18, pl. 5, figs. 11–26.

Odontaspis samhammeri Cappetta and Case. Lauginiger and Hartstein, 1983: p. 25, pl. 5, fig. 62.

Carcharias samhammeri (Cappetta and Case). Siverson, 1992a: pp. 537, 538.

Carcharias samhammeri (Cappetta and Case). Kent, 1994: p. 42, fig. 9.3A.

Carcharias sp. Hoganson et al., 1995: p. 60.

Carcharias sp. Hoganson et al., 1996: p. 41A.

Odontaspis sp. 2 Cicimurri, 1998: p. 116, pl. 14, figs. 14–17.

Carcharias samhammeri (Cappetta and Case). Hartstein et al., 1999: p. 18, pl. 2, fig. 36.

Carcharias heathi Case and Cappetta, 1997: pp. 140, 141, pl. 7, figs. 7–9.

Carcharias sp. Hoganson and Murphy, 2002: p. 265, figs. 12R, S.

Carcharias cf. *C. samhammeri* Becker et al., 2004: p. 785, figs. 4G–L.

Description.—Teeth medium to large in size. Crown of anterior teeth very high and slender. Lateral view of anterior crown only slightly sigmoid. Labial face weakly convex, lingual face strongly convex. Cutting edge sharp and continuous. In labial view, the cutting edges of the cusp are variable from concave to convex approaching the base of the cusp and before reaching marginal cusplets. Basal margin of labial cusp face invert-

ed, v-shaped, and bulging at foot of crown. Lingual dental band (or neck) well developed on anterior and lateral teeth.

Crown flanked by one pair of erect, slightly divergent cusplets. Cusplets are large, triangular to nearly conical, and attached to long labial enameled shoulders of the crown. A notch occurs between crown and cusplets which also have continuous cutting edges. Interlobe area of roots is tightly v-shaped, lobes slightly asymmetrical, lingual root protuberance quite pronounced and bisected by distinct nutritive groove.

Crown of lateral tooth triangular and much lower than anterior tooth and proportionately broader at base. Cusplets on lateral tooth are erect, triangular, and broader at base than at anterior. Crown of lateral tooth distally directed. Root lobes of lateral tooth somewhat flattened (spatulate) and are more widely divergent than in anterior teeth. Interlobe areas on lateral teeth v-shaped but broader than anterior teeth. Lingual root protuberance not as large as in anterior teeth, but also has a distinct nutritive groove.

Material.—Symphysial, anterior, lateral, and posterior teeth are included in the 637 specimens of this species in the Fox Hills collection. The figured specimens include: lateral tooth ND 95-13.88 (Text-figs. 7.49, 7.50; H. 10.57 mm, W. 9.41 mm); anterior tooth ND 95-13.85 (Text-figs. 7.51–7.53; H. 20.67 mm, W. 11.98 mm); posterior tooth ND 95-13.87 (Text-figs. 7.54, 7.55; H. 3.03 mm, W. 4.09 mm); posterolateral tooth ND 95-13.86 (Text-figs. 7.56, 7.57; H. 5.75 mm, W. 7.87 mm); symphysial tooth ND 99-6.14 (Text-figs. 7.58, 7.59; H. 8.49 mm, W. 3.60 mm); anterior tooth ND 95-11.1 (Text-figs. 7.60, 7.61; H. 20.41 mm, W. 11.87 mm). This species was dominant in the collection and particularly abundant at site NDGS L140. It was present at 27 sites (Table 2). Numerous fragments from various sites reside in the North Dakota Geological Survey State Fossil Collection as *Carcharias* sp. and have not been counted.

Remarks.—*Carcharias samhammeri* differs from *C. holmdelenensis* and *Odontaspis hardingi*—described from the Monmouth Group (Campanian–Maastrichtian) from New Jersey by Cappetta and Case (1975a, p. 45, pl. 17)—by not having folds on the lingual crown faces. Case and Cappetta (1997, p. 140) also described a new species, *Carcharias heathi*, from the Maastrichtian Kemp Formation of Texas. They remarked that *C. heathi* differs from *C. samhammeri* in the following ways: *C. heathi* is smaller than *C. samhammeri*, has smaller and narrower lateral cusplets, its basal limit of the labial face is strongly angular medially, its lingual protuberance is less well developed, and the cutting edges at the base of the cusp are concave rather than convex as in *C. samhammeri*. After examining the Fox Hills collections, we have found that characters used by Case and Cappetta (1997) to distinguish these

two species are variable through the size range of these specimens, and we have chosen to assign all to the prior species, *Carcharias samhhammeri*.

The largest Fox Hills specimen of *C. samhhammeri* is an anterior tooth that has small cusplets (Text-figs. 7.60, 7.61). This specimen resembles *Carcharias* sp. B of Welton and Farish (1993, p. 92, figs. 1a–1c), but that specimen has fine, parallel, longitudinal ridges extending from the crown foot almost to the apex of the lingual crown face, whereas our specimen is smooth, as are all in our collection. We believe the Welton and Farish (1993) specimen is better assigned to *C. holmdelensis*.

Carcharias samhhammeri is here newly reported from the Fox Hills Formation. Becker et al. (2004) described and figured a specimen they referred to as *Carcharias* cf. *C. samhhammeri* from the Fairpoint Member of the Fox Hills Formation in South Dakota. Our specimens appear to be the same taxon as their figured teeth. Cicimurri (1998) also described similar teeth from the Fairpoint Member, referring to them as *Odontaspis* sp. 2. From his description and line drawings it appears likely that they are also *C. samhhammeri*. *Carcharias* sp. reported from the Fox Hills Formation of North Dakota by Hoganson et al. (1995) is also *C. samhhammeri*, as is the specimen illustrated by Hoganson and Murphy (2002) from the Breien Member of the Hell Creek Formation in North Dakota.

Carcharias samhhammeri was initially placed in *Odontaspis* by Cappetta and Case (1975a) based on specimens from the Monmouth Group (Campanian–Maastrichtian) of New Jersey. Lauginiger and Hartstein (1983) reported *O. samhhammeri* from the Marshalltown (Campanian?) and Mt. Laurel (Maastrichtian) formations of Delaware. Siverson (1992a) and Kent (1994) assigned *O. samhhammeri* to *Carcharias* and listed its occurrence in the Marshalltown (Campanian), Mount Laurel (Maastrichtian), and Severn (Maastrichtian) formations in the Chesapeake Bay Region. Later Case (1995) accepted the reassignment based on specimens from the Maastrichtian of Monmouth County, New Jersey. Case and Cappetta (1997) provisionally reassigned a single tooth from the Late Maastrichtian Kemp Formation in Texas to *C. samhhammeri*. It has also been reported from a lag accumulation surface on a local sand unit at the base of the Maastrichtian Severn Formation in Maryland by Hartstein et al. (1999). The specimen identified by Retzler et al. (2013, fig. 3G) as *C. samhhammeri* seems to be too poorly preserved to be assigned to that species with certainty.

Genus *ODONTASPIS* Agassiz, 1843

Type species.—*Squalus ferox* Risso, 1810.

Odontaspis aculeatus (Cappetta and Case, 1975a) Text-figs. 8.1–8.4

Hypotodus aculeatus Cappetta and Case, 1975a: p.16, pl. 6, figs. 1–9.

Odontaspis aculeatus (Cappetta and Case). Kent, 1994: p. 39, pl. 9.1 A.

Odontaspis sp. Hoganson et al.: 1995, p. 60.

Odontaspis sp. Hoganson et al.: 1996, p. 41A.

Odontaspis aculeatus (Cappetta and Case). Hartstein et al., 1999: p. 18, pl. 1, fig. 9.

Odontaspis aculeatus (Cappetta and Case). Beavan and Russell, 1999: p. 499, figs. 2.7, 2.8.

Odontaspis aculeatus (Cappetta and Case). Becker et al., 2004: p. 783, figs. 4e, f.

Odontaspis aculeatus (Cappetta and Case). Becker et al., 2006: p. 703, figs. 3.16, 3.17.

Odontaspis aculeatus (Cappetta and Case). Brinkman et al., 2005: p. 490 fig. 26.2E.

Description.—Teeth small, nearly symmetrical with finely attenuated central cusp and two or more pairs of cusplets directed slightly toward the central cusp. Sharp cutting edges of cusp lie along labial margin and are nearly parallel in the lower half of the cusp on anterior teeth (Text-fig. 8.1) and divergent with cusp margin on lateral teeth. Teeth smoothly sigmoid in shape from cusp tip to root, emphasized by a strong lingual protuberance and the very fine longitudinal striae on the base of the labial face. Enameloid of the labial face with numerous short folds along entire base on lateral teeth and weakly so on anterior teeth. The slightly asymmetrical, deeply curved roots are smoothly rounded. Nutritive groove well developed on mature teeth and undeveloped on unemergent anterior teeth (such as in Text-fig. 8.1), as has been illustrated among the smaller specimens of various *Odontaspis* species (Cappetta and Case, 1975a).

Material.—Three teeth. Symphyseal tooth ND 94-37.1 (Text-figs. 8.1, 8.2; SEM; H. 5.2 mm, W. 2.31 mm) and antero-lateral tooth ND 95-13.89 (Text-figs. 8.3, 8.4; H. 7.3 mm, W. 3.7 mm), both from NDGS L35. Lateral tooth NDGS 4064 from NDGS L140 (H. 9.2 mm, W. 6.51 mm). One partial tooth from NDGS L35 is included in the collection (Table 2).

Remarks.—Among all lamniform specimens collected, these three teeth have the unique characteristics of multiple, inwardly directed cusplets, small size, a delicate attenuated central cusp, labial folds, and a nutritive groove which distinguish them from teeth of *Carcharias* species.

Odontaspis species are uncommon but persistently occurring in Maastrichtian shark assemblages of the Western Interior Seaway (Cicimurri et al., 1999; Hoganson and Murphy, 2002; Becker et al., 2006). *O. aculeatus* was identified from marine shale of the Lethbridge Coal zone of the Dinosaur Park

Formation by Brinkman et al. (2005). A single tooth illustrated as *O. aculeatus* in Case and Cappetta (1997, pl. 4, fig. 4) is incomplete and difficult to assess. If it is this species, a single tooth still suggests rarity in the WIS. The species is somewhat more common in the Campanian and Maastrichtian of the Gulf and Atlantic Coastal Plains. It was described as *Hypotodus aculeatus* by Cappetta and Case (1975a) from rocks designated as Late Campanian from Willow Brook, New Jersey. New Jersey strata thought to have been Upper Campanian have been recently reevaluated and are now assigned to the Maastrichtian (Becker et al., 2002; Landman et al., 2004a, b). Hartstein et al. (1999) figured a specimen of *O. aculeatus* from the Severn Formation of Maryland. Most recently this species has been considered *Odontaspis* (Kent, 1994) and has been found in the Maastrichtian Arkadelphia Formation of Arkansas (Becker et al., 2006). *Odontaspis* was not included in the Paleocene shark fauna of the Cannonball Formation of North Dakota (Cvancara and Hoganson, 1993).

A Fox Hills Formation *Odontaspis aculeatus* was described by Becker et al. (2004) in the Fairpoint Member southwest of the formation type area of Waage (1968). The genus was noted by Bouchard in her 1990 study, with the suggestion that *O. aculeatus* may be the species in question, but no assignment was made. Cicimurri (1998) mentioned two *Odontaspis* specimens from the Fairpoint Member. By the poor condition of the specimens shown in his illustrations, we concur with him that they are unassignable to species. He noted that some of the *Cretodus* sp. teeth in Bouchard (1990) are characteristic of odontospidids but no reassignment of these was made. The earliest record of the genus in the Fox Hills Formation of North Dakota was made by Hoganson et al. (1995) based on material here assigned to *O. aculeatus*.

Family **OTODONTIDAE** Glikman, 1964
Genus **CRETALAMNA** Glikman, 1958

Type species.—*Otodus appendiculatus* Agassiz, 1843.

Cretalamna feldmanni n. sp.
Text-figs. 8.5, 8.6

Holotype.—*Cretalamna feldmanni* Hoganson, Erickson, and Holland, UND-PC 15903 (Text-figs. 8.5, 8.6).

Diagnosis.—Known only from upper left lateral tooth characterized by prominent central cusp flanked on each side by single well-developed cusplets possessing basal extensions of the enamel cutting surface just beyond the edge of the root. Entire crown margin is a smooth cutting edge having cusplets separated from cusp only by deep groove that is nearly covered by enamel at top of cusps. Entire crown surface is non-

striated. Upper one-third of cusp gently flexed lingually, no prominent central lingual bulge. Root with insignificant central foramen. Root has characteristic quadrate shape formed by distinct, straight-sided lobes at anterior and posterior tips, anterior being longer, from which lower margins of root converge on mesial position of the root, forming distinct straight V-shaped lower edge of tooth. Tooth large, only slightly wider than long.

Description.—Single left lateral upper tooth from approximately position L4 of Shimada (2002) in nearly pristine condition. Tooth large and nearly equidimensional in lingual and labial views. Crown high, slightly distally directed, smooth and broad at base. Crown gently convex labially and more strongly convex lingually, slightly sinuous in profile and bent lingually. One pair of broad, triangular divergent cusplets are attached to cusp. Cutting edges of cusp are continuous along cusp margin; cutting edges of cusplets are also continuous along cusplet margins. Cutting tip of anterior cusplet missing. Root bilobate and rectangular in outline in lingual and labial views. Interlobe area is a very wide V-shape. Lingual protuberance is very weak and penetrated by an indistinct, centrally located foramen. A post-mortem fracture of root tip has been repaired. The labial surface of the cusp is marked by more than 22 transverse grooves in the enamel (feeding damage?).

Material.—Holotype is a single well-preserved upper left lateral tooth. The illustrated specimen is UND-PC 15903 (Text-figs. 8.5, 8.6; H. 18.77 mm, W. 19.84 mm) from NDGS L165, Bowman Co., North Dakota (Table 2). It is housed in the paleontological collection of the University of North Dakota, Grand Forks, ND.

Etymology.—This species is named for Dr. Rodney M. Feldmann of Kent State University, who collected the type specimen.

Remarks.—Cappetta (2012) did not recognize Mesozoic members of Otodontidae; rather he assigned *Cretalamna* to Cretoxyrinidae Glikman, 1958. We follow Siversson et al. (2015) by assigning *Cretalamna* to the Otodontidae. We are also following Shimada (2007) and Siversson et al. (2015) regarding the spelling of “*Cretalamna*” rather than the emended “*Cretolamna*” advocated by Cappetta (2012).

This tooth belonged to a large lamniform shark most similar to members of the genus *Cretalamna*. Past usage would have subsumed it in the form species *C. appendiculata* (Agassiz, 1843). However, this taxon has recently been the subject of significant research in part based on the morphology and systematic implications of dental reconstructions of a Lower Campanian partial skeleton (Los Angeles County

Natural History Museum 128126) from the Niobrara Chalk of Kansas by Shimada (2007). Siversson et al. (2015) re-examined LACM 128126 along with numerous additional specimens from other localities of importance, including probable topotype specimens in the British Museum from the Turonian type locality of *Otodus appendiculatus*. This work concluded that *C. appendiculata*, as it has been applied in the literature, includes a large number of species rather than simply one long-ranging taxon, and they described eight new species from the Cenomanian and Campanian strata of Australia, Europe, and North America.

The specimen from the Smokey Hill Member of the Niobrara Chalk of Kansas studied by Shimada (2007) was selected as the type for *Cretalamna hattini* (Siversson et al. 2015). In that same work, other forms that had been referred to *C. appendiculata* s.l. for many years were illustrated and re-described within *Cretalamna*; they were further organized into species morphogroups which Siversson et al. (2015) used to characterize mid-paleolatitude Cenomanian and Campanian *Cretalamna*. Our tooth is somewhat similar to those of *C. catoxodon* and *C. hattini*, but the cusplets and the root morphology clearly do not match those taxa precisely, prompting the need for a new species. Our specimen does not resemble any of the material illustrated by Vullo (2005), nor is it similar to that illustrated as *Cretalamna* [sic] *appendiculata* by Retzler et al. (2013, fig. 3a) from the Campanian of Israel, which seems to have a nutritive groove and is perhaps a *Carcharias*.

The very broad, shallow, V-shaped intra-root-lobe area is wider, and each side is decidedly more linear than typical dentition teeth of *C. appendiculata sensu lato*, appearing somewhat more like those of *Serratolamna serrata*. Our tooth differs, however, from species of *Serratolamna* in having only one pair of lateral cusplets and by not having a nutritive groove on the lingual root protuberance. We found no other teeth with the combination of characters that include the following: complete cutting edge, no lingual bulge, cusplets with lateral extensions beyond root margin, and a V-shaped root embayment with straight rather than curved margin. All others have an arched embayment, even if they produce a small “v” at the peak of the basal root arch. In the manner of Siversson et al. (2015), these may distinguish a unique *Cretalamna* group of which *C. feldmanni* n. sp. is the first recognized species.

Hoganson and Murphy (2002) reported *C. appendiculata* from the Maastrichtian Breien Member of the Hell Creek Formation in south-central North Dakota, an assignment we accept questionably. That specimen has a narrower crown and relatively wider root than antero-lateral teeth of any of the recently defined species. For the present it should be considered *Cretalamna* sp.

As mentioned, Siversson et al. (2015) have pointed out that *Cretalamna appendiculata* s.l. has a long (50 million years)

temporal range (Albian–Ypresian) and has been found nearly worldwide (Shimada et al., 2006). Kriwet and Benton (2004) noted that Cretaceous neoselachian diversity was greatest in the Maastrichtian before the loss of seven families, 62 genera, and 182 species at the K–Pg boundary. Although assignments to *C. appendiculata* have been made into the Ypresian, none of these taxa were addressed by Siversson et al. (2015). The numerous Maastrichtian assignments available in the literature would suggest that further revision of the species is necessary. We suggest that such an effort may indicate species of *Cretalamna* to be useful biostratigraphic indices when completed.

Cretalamna is here newly reported from the Fox Hills Formation based on the single specimen of *C. feldmanni* n. sp. No other occurrences of *C. feldmanni* n. sp. have been identified. Other Maastrichtian occurrences of the genus as “*C. appendiculata*” are: Texas (Welton and Farish, 1993); Selma Formation (Alabama), Belgium, Holland, and Morocco (Herman, 1975 [1977]); Monmouth Group (Campanian–Maastrichtian) New Jersey, (Fowler, 1911; Cappetta and Case, 1975a); Cretaceous of Japan (Itoigawa et al., 1977); Peedee Formation (Late Maastrichtian) of Duplin County, North Carolina (Case, 1979); Severn Formation, Big Brook, New Jersey (Lauginiger, 1986); Severn Formation, Prince Georges County, Maryland as *C. appendiculata pachyrhiza* Herman (Hartstein and Decina, 1986); Maastrichtian Mt. Laurel Formation, Delaware (Lauginiger and Hartstein, 1983); Maastrichtian of Morocco (Arambourg, 1952); Raritan Formation, New Jersey (Case, 1989); Mt. Laurel and Navesink formations, New Jersey (Case, 1995); Navesink Formation, Monmouth County, New Jersey (Becker et al., 2002). Also, Case (2001) has illustrated a specimen from the Coleraine Formation, Cenomanian of Minnesota, an assignment that should be reviewed.

Family **SERRATOLAMNIDAE** Landemaine, 1991

Genus **SERRATOLAMNA** Landemaine, 1991

Type species.—*Otodus serratus* Agassiz, 1843.

Serratolamna serrata (Agassiz, 1843)

Text-figs. 8.7, 8.8

Otodus serratus Agassiz, 1843: v. 3, p. 272, fig. xxxii.

Cretalamna serrata (Agassiz). Case, 1979: p. 84, figs. 1.21, 1.22.

Cretalamna serrata (Agassiz). Hartstein and Decina, 1986: p. 90, pl. 1, fig. 4.

Serratolamna serrata (Agassiz). Welton and Farish, 1993: p. 112, figs. 1–6.

Serratolamna serrata (Agassiz). Kent, 1994: p. 53, figs. 10.2 H, I.

Serratolamna serrata (Agassiz). Hoganson et al., 1995: p. 60.

Serratolamna serrata (Agassiz). Hoganson et al., 1996: p. 41A.

- Serratolamna serrata* (Agassiz). Case and Cappetta, 1997: p. 139, pl. 3, figs. 5–8.
- Serratolamna serrata* (Agassiz). Hartstein et al., 1999: p. 18, pl. 1, fig. 3.
- Serratolamna serrata* (Agassiz). Underwood and Mitchell, 2000, pp. 26–28, figs. 4A–E.
- Serratolamna serrata* (Agassiz). Case et al., 2001b: p. 118, pl. 2, figs. 21, 22.
- Serratolamna serrata* (Agassiz). Hoganson and Murphy, 2002: p. 263, figs. 12L, M.
- Serratolamna serrata* (Agassiz). Becker et al., 2004: p. 785, figs. 4M, N.
- Serratolamna serrata* (Agassiz). Becker et al., 2006: p. 705, figs. 3.20, 3.21.
- Serratolamna serrata* (Agassiz). Shimada and Brereton, 2007: pp. 105–109, figs. 2A–G.
- (Please refer also to the synonymy provided in Arambourg, 1952.)

Description.—Crown is labio-lingually compressed with a wide base. Lingual and labial faces of crown are convex, lingual face more so than labial face. Both faces are smooth. Cutting edge continuous from apex to base of crown. Generally two pairs of asymmetrical, diverging cusplets on the shoulders. The pair closest to crown are triangular and much larger than second pair. Distal cusplets are directed distally and often consist of three or more cusplets compared to two mesial cusplets, thereby making the tooth distinctively asymmetrical. Labial crown foot forms a slight basal ledge. Root lobes are compressed labio-lingually and spatulate with a pronounced u-shaped basal margin and are distinctly asymmetrical in anteriolateral teeth with the distal lobe longer than the mesial lobe. This asymmetry is less pronounced in the more anterior teeth. A well-developed nutritive groove is situated on a large lingual protuberance.

Material.—Twenty anterior and antero-lateral teeth from seven sites; illustrated specimen is a lateral tooth (ND 99-6.5; Text-figs. 8.7, 8.8; H. 13.58 mm, W. 13.69 mm) from NDGS L140. The largest (NDGS 4065) is from NDGS L139 (Table 2) and measures 21.98 mm high and 28.34 mm wide.

Remarks.—*Serratolamna serrata* is one of the most easily recognizable lamniform sharks in the Fox Hills Formation because of its distinctive tooth asymmetry, multiple divergent cusplets on the mesial and distal shoulders, and smooth labial and lingual crown faces. *Serratolamna serrata* was first reported from the Fox Hills Formation in North Dakota by Hoganson et al. (1995). Becker et al. (2004) reported this species from the Fairpoint Member of the Fox Hills Formation in South Dakota. The Maastrichtian marine Breien Member of the Hell Creek Formation vertebrate fauna in south-central North Dakota also contains this taxon (Hoganson and Murphy, 2002). Other Maastrichtian or Late Cretaceous

occurrences are in: the Arkadelphia Formation, Hot Spring County, Arkansas (Becker et al., 2006); Maastrichtian Peedee Formation, Duplin County, North Carolina (Case, 1979); Maastrichtian Severn Formation, Maryland (Hartstein and Decina, 1986; Kent, 1994); Campanian Merchantville Formation, Graham Brickyard locality, New Jersey; Maastrichtian of New Jersey (Case, 1995); Late Maastrichtian New Egypt Formation of New Jersey (Case et al., 2001b); ?late Campanian–Maastrichtian Kemp, Escondido, Littig and upper Taylor marls in Texas (Welton and Farish, 1993); Maastrichtian Kemp Clay, north-central Texas (Case and Cappetta, 1997); and Late Cretaceous Moorville Chalk, Alabama (Shimada and Brereton, 2007).

In Europe *S. serrata* has been recognized from the Late Cretaceous of France (Landemaine, 1991; Leriche, 1902, 1906); Belgium (Casier, 1943); Cretaceous of Belgium (Leriche, 1929); Tuffeau de Maastricht, Netherlands (Leriche, 1938); and Cretaceous of Holland (Geyn, 1937). In addition to occurrences in the type region of the Maastrichtian in western Europe, Arambourg (1952, p. 102) noted the presence of this species in the Cretaceous of Great Britain, Libya, Angola, Egypt, and the Congo Basin of Africa (Darteville and Casier, 1941, 1943). This taxon has also been reported from the Late Maastrichtian Guinea Corn Formation, Jamaica (Underwood and Mitchell, 2000).

Serratolamna serrata was a cosmopolitan taxon that is restricted to the Late Cretaceous and possibly to the Maastrichtian.

Family Incertae Familiae

Genus *PARANOMOTODON* Herman, 1977

Type species.—*Oxyrrhina* [sic] *angustidens* Reuss, 1845.

Paranomotodon toddi (Case and Cappetta, 1997)

Text-figs. 8.9–8.14

Oxyrrhina [sic] *angustidens* Reuss, 1845: p. 6, T. III, f. 7–13.

Paranomotodon sp. Welton and Farish, 1993: p. 114, figs. 2–5, non fig. 1.

Anomotodon toddi Case and Cappetta, 1997: pp. 142, 143, pl. 5, figs. 1, 2.

Description.—Teeth of this species in the present collection possess a single, somewhat rectangular cusp that lacks lingual folding. Mesial and distal heels on a high root with broadly v-shaped, symmetrical to slightly asymmetrical base and a well-developed lingual protuberance having a deep vertical nutritive groove.

Material.—The species is represented in the Fox Hills collection by eight specimens from four sites. Illustrated specimens

are lateral teeth that include ND95-13.72 (with numerous micro-borings; Text-figs. 8.9–8.11; H. 14.8 mm, W. 14.4 mm) and ND95-13.73 (Text-figs. 8.12–8.14; H. 13.0 mm, W. 9.8 mm). An un-illustrated specimen (ND95-13.84) is 15.61 mm high and 10.91 mm wide. All figured teeth are from NDGS L140 (Table 2).

Remarks.—North Dakota specimens closely resemble the type material of *Anomotodon toddi* of Case and Cappetta (1997) from the Upper Maastrichtian Kemp Clay of Texas, including the specimens illustrated as *Paranomotodon* sp. by Welton and Farish (1993, p. 114, figs. 2–5, *non* fig. 1) which Case and Cappetta reassigned to their species.

Cappetta (1987a) pointed out that the lingual face of *Anomotodon* is folded and the heels are extended with no lateral cusplets, whereas he recognized as a generic character of *Paranomotodon* a smooth lingual face of the cusp and heels with slight cusplets. These descriptions seem consistent with those of the authors of the two genera. In contrast, assignment of *A. toddi* to the genus *Anomotodon* violates the generic description because the assigned materials are avowed to have smooth lingual faces (Case and Cappetta, 1997). Herein we reassign the species *A. toddi* to the genus *Paranomotodon* because it has a smooth lingual surface on the cusp.

Ours is the first recorded *Paranomotodon toddi* from the Western Interior Seaway and from North Dakota.

Family **ANACORACIDAE** Casier, 1947

Genus **SQUALICORAX** Whitley, 1939

Type species.—*Corax pristodontus* Agassiz, 1843.

Squalicorax pristodontus (Agassiz, 1843)

Text-figs. 8.15, 8.16

Corax pristodontus Agassiz, 1843: p. 224, pl. 26, figs. 9–13.

Galeocerdo pristodontus (Agassiz). Cope, 1875: p. 295.

Corax pristodontus Agassiz. Fowler, 1911: pp. 64–66, figs. 29.1–23.

Corax pristodontus Agassiz. Dartevelle and Casier, 1943: p. 98, pl. 1, fig. 32, pl. II.

Corax pristodontus Agassiz. Arambourg, 1952: p. 112, pl. XX, figs. 1–10.

Squalicorax pristodontus (Agassiz). Bilelo, 1969: p. 341, figs. 2A–E.

Squalicorax pristodontus (Agassiz). Herman, 1977: pp. 110–113, pl. 4, fig. 3.

Squalicorax pristodontus (Agassiz). Case, 1979: p. 80, fig. 1-26.8.

Squalicorax pristodontus (Agassiz). Lauginiger and Hartstein, 1983: pp. 34, 35, text figs. 15a, b, pl. 1, figs. 1, 2 as “*pristodontis*”.

Squalicorax pristodontus (Agassiz). Hartstein and Decina, 1986: p. 88, 90, pl. 1, fig. 7.

Squalicorax pristodontus (Agassiz). Case, 1987: p. 12, p. 4, figs. 4a–5b.

Squalicorax pristodontus (Agassiz). Robb, 1989: p. 79, fig. 6B.

Squalicorax pristodontus (Agassiz). Manning and Dockery, 1992: pl. 5, figs. 6, 7, *non* fig. 5.

Squalicorax pristodontus (Agassiz). Welton and Farish, 1993: p. 119, figs. 1a–c, 2a, b.

Squalicorax pristodontus (Agassiz). Kent, 1994: pp. 73, 74, fig. 10.13B.

Squalicorax pristodontus (Agassiz). Case, 1995: p. 73, pl. 2, figs. 4–8.

Squalicorax pristodontus (Agassiz). Schwimmer et al., 1997a: p. 72, figs. 1L–Q.

Squalicorax pristodontus (Agassiz). Hartstein et al., 1999: p. 18, pl. 1, fig. 2.

Squalicorax pristodontus (Agassiz). Bardet et al., 2000: p. 276, figs. 4p–r.

Squalicorax pristodontus (Agassiz). Shimada and Cicimurri, 2005: fig. 7.

Squalicorax pristodontus (Agassiz). Shimada and Cicimurri, 2006: figs. 1A–C.

Squalicorax pristodontus (Agassiz). Adolfssen and Ward, 2014: p. 612, figs. 8E, F.

(Please refer also to the synonymy provided in Herman, 1977.)

Description.—A single large, unworn tooth. Root tips missing. Cusp rises at a low angle from the root. Crown crescentic, but maintaining a strong mesial angle. Serrations well preserved and unusually fine for members of the genus. Root about twice as high as the crown.

Material.—This tooth was a solitary, *in situ* find from an outcrop exposing the Pierre-Fox Hills contact in Bowman County, ND (NDGS L35). The specimen was taken from silty sandstone approximately two meters above the contact. It was transferred from field collections of the Geology Department at St. Lawrence University (SLU1832.) to the North Dakota State Fossil Collection where it is NDGS 1695. It has dimensions of H. 18.52 mm, and W. 22.4 mm (Text-figs. 8.15, 8.16).

Remarks.—We have assigned this specimen to *Squalicorax pristodontus* based on the more crescentic-shaped crown with lower (less acute) cusp angle and its overall size. The crown is typical of *S. pristodontus* and the root is too damaged to indicate otherwise. This configuration produces a ratio of root-height to crown-height that is larger than in most examples of *S. kaupi* (Case, 1978, 1987; Lauginiger and Hartstein, 1983; Siverson, 1992a; Welton and Farish, 1993), the species with which *S. pristodontus* is most likely to be compared. Although the ordinal placement of *Squalicorax* is uncertain (Shimada and Cicimurri, 2005), we have placed *Squalicorax pristodontus* in the Lamniformes.

Bilelo (1969) pointed out the importance of the apex angle for distinguishing adult teeth of species in the *Squalicorax*

complex in Texas. In the Fox Hills specimen, the mesial cutting ridge is angled more strongly than in typical *S. pristodontus*. The serrations are finer than on most examples of either species we have seen illustrated, a characteristic also noted by Schwimmer et al. (1997a) in their discussion of *Squalicorax* scavenging habits.

The Fox Hills specimen is smaller than some described *S. pristodontus* (Robb, 1989) as generally illustrated (Siverson, 1992a) and is larger than most *S. kaupi*, a relationship that accentuates the point by Siverson (1992a), and was reiterated by Adolfssen and Ward (2014), that better definition of *Squalicorax* species is necessary. *Squalicorax pristodontus* is the most appropriate designation for the Fox Hills specimen at present, but we acknowledge the possibility that an additional species of *Squalicorax* with teeth notched to a lesser degree than *S. kaupi* and greater than some *S. pristodontus* may have existed during the Late Maastrichtian. Somewhat similar ideas have been expressed by Manning and Dockery (1992) regarding *Squalicorax* species at the Frankstown Site in the base of the Demopolis Formation, Maastrichtian, Mississippi. Case (1979) recorded this as a middle and late Maastrichtian species, and Fowler (1911) recorded it from the New Jersey Greensand (Hornerstown? Marl, Late Maastrichtian) as well. Gallagher et al. (1986) and Gallagher (2003) noted it in the Navesink and basal Hornerstown formations of New Jersey. Robb (1989) found it in the Campanian Black Creek Formation of North Carolina.

Additional North American Campanian–Maastrichtian occurrences of *Squalicorax pristodontus* include: early and middle Maastrichtian of Monmouth, New Jersey Case (1995); late Campanian Mesaverde Formation, Wyoming Case (1987); early middle Maastrichtian, Severn Fm., Maryland (Hartstein and Decina, 1986; Hartstein et al., 1999); Marshalltown, Mount Laurel, and Severn formations, Chesapeake Bay Region (Kent, 1994); Campanian and Maastrichtian, Upper Taylor Marl, Kemp, Escondido and Littig formations, Texas (Welton and Farish, 1993); Late Cretaceous, Demopolis Formation, Mississippi (Manning and Dockery, 1992); Niobrara Chalk of Kansas and Pierre Formation of South Dakota (Shimada and Cicimurri, 2006).

Squalicorax pristodontus had nearly a global distribution during the Maastrichtian (Schwimmer et al., 1997a). It was recently noted in a shark assemblage from the Maastrichtian of Israel (Retzler et al., 2013), as well as in paleofaunas from Denmark (Adolphsen and Ward, 2014), Mexico (González-Barba et al., 2001; González-Rodríguez et al., 2013), France (Vullo, 2005), Tunisia (Cuny et al., 2004), Bulgaria (Jagt et al., 2006), Syria (Bardet et al., 2000), Madagascar (Gottfried et al., 2001), and India (Verma, 1965). All these finds suggest that the species roamed the WIS—Atlantic—Tethys corridors broadly.

Based on the morphology of placoid scales and analysis of skeletal remains, Shimada and Cicimurri (2005) determined that species of *Squalicorax* were capable of swimming quickly and were similar to the modern tiger shark, *Galeocerdo*, in their feeding habits. Schwimmer et al. (1997a) have suggested that members of *Squalicorax* were scavengers of Late Cretaceous (Santonian–Maastrichtian) large marine animal carcasses based on an imbedded tooth and gnaw marks on bone. They pointed out that this feeding occurred in the near-shore marine realm consistent with the Fox Hills occurrence. Shimada and Cicimurri (2005) demonstrated that *S. pristodontus* teeth were larger but less numerous than teeth in other *Squalicorax* species. Schein (2013) has reported on a pathological *S. pristodontus* tooth from the latest Maastrichtian basal Hornerstown Formation of New Jersey that seems to demonstrate both pathology and deformity as the tooth grew, perhaps in a damaged jaw. This augmented a thorough discussion of *Squalicorax kaupi* and *S. pristodontus* feeding behavior as derived from damaged teeth in the lowermost Navesink Formation of New Jersey, wherein Becker and Chamberlain (2012) documented damage to *S. pristodontus* teeth during predation/scavenging activities of the animals. Becker and Chamberlain (2012) also suggested that tooth replacement was somewhat slower in the Maastrichtian shark than in modern ecological equivalents such as *Galeocerdo cuvieri* and *Carcharodon carcharias*.

Order **CARCHARHINIFORMES** Compagno, 1973

Family **TRIAKIDAE** Gray, 1851

Genus **PALAEOGALEUS** Gurr, 1962

Type species.—*Scyllium vincenti* Daimeries, 1888.

Palaeogaleus navarroensis Case and Cappetta, 1997

Text-figs. 8.19–8.24

Palaeogaleus sp. Welton and Farish, 1993: p. 128, figs. 1a–3b.

Palaeogaleus sp. Hoganson et al., 1995: p. 60.

Palaeogaleus sp. Hoganson et al., 1996: p. 41A.

Palaeogaleus navarroensis Case and Cappetta, 1997: p. 143, pl. 4, figs. 5–9.

Description.—Lateral and antero-lateral teeth, extremely small, generally less than 3 mm in width, with thick crown and robust root. Cusps broad and inclined posteriorly in antero-lateral teeth. Two distinct to indistinct cusplets on triangular, antero-lateral teeth. Lateral teeth have indistinct mesial cusplets and distinct distal heels that may bear up to two blade-like cusplets. Labial face of crown overhangs root by a bulge that exhibits strong, but few, vertical folds which extend a short distance up the labial crown face. Root is robust and is divided into two triangular lobes by a wide and deep nutri-

tive groove that contains a pit. Base of root is flat to slightly concave. Numerous foramina on root at lingual crown base.

Material.—The Fox Hills Formation yielded 19 specimens of *Palaeogaleus navarroensis* nearly evenly divided between site NDGS L35, Bowman County, with ten and NDGS L140 in Logan County with nine teeth. The figured specimens are: antero-lateral tooth ND 94-38.7 (Text-figs. 8.19, 8.20; H. 2.1 mm, W. 2.5 mm), antero-lateral tooth ND 94-38.6 (Text-figs. 8.21, 8.22; H. 1.9 mm, W. 2.0 mm), and lateral tooth ND 94-38.8 (Text-figs. 8.23, 8.24; H. 2.4 mm, W. 2.8 mm).

Remarks.—Hoganson et al. (1995, 1996) first reported the occurrence of *Palaeogaleus* in the Fox Hills Formation of North Dakota but did not provide a specific identification. Those specimens are here identified as *P. navarroensis*. *Palaeogaleus* sp. has been noted in the Fairpoint Member of the Fox Hills Formation of South Dakota (Bouchard, 1990; Cicimurri, 1998; Becker et al., 2004). The type specimens of *P. navarroensis* are from the Maastrichtian Kemp Clay of Texas (Case and Cappetta, 1997). We concur with Case and Cappetta (1997) that the specimens illustrated by Welton and Farish (1993) from the Kemp Clay are *P. navarroensis*.

Palaeogaleus navarroensis differs from *P. vincenti* from the Paleocene Cannonball Formation in North Dakota as described by Cvanca and Hoganson (1993) in the following ways: *Palaeogaleus vincenti* teeth are more massive, particularly the root; the nutritive groove is wider in *P. vincenti*; and the cusp of *P. vincenti* is more erect in lateral teeth.

Genus *GALEORHINUS* Blainville, 1816

Type species.—*Squalus galeus* Linnaeus, 1758.

Galeorhinus girardoti Herman, 1977

Text-figs. 8.17, 8.18

Galeorhinus girardoti Herman, 1977: pp. 268, 269, pl. 12, figs. 7a–h.

Galeorhinus? sp. Hoganson et al., 1995: p. 60.

Galeorhinus sp. Hoganson et al. 1996: p. 41A.

Galeorhinus girardoti Herman. Hartstein et al., 1999: p. 18, pl. 1, figs. 10, 11.

Galeorhinus cf. *G. girardoti* Becker et al., 2004: p. 786, figs. 4Q, R.

Galeorhinus girardoti Herman. Vullo, 2005: pp. 624, 625, figs. 5C–F.

Galeorhinus girardoti Herman. Becker et al., 2006: p. 707, figs. 3.24, 3.25.

Description.—Small lateral teeth averaging 3.8 mm in length. Crown broad and thin with crown inclined posteriorly. Edge of mesial heel has crenulated cutting edge. Mesial edge is

convex. Distal heel is high and bears three distinct triangular cusplets and one minute cusplet that decrease in height to the distal edge of the crown. Edge of the labial face of crown is slightly concave and overhangs the root by a slight bulge. Labial and lingual surfaces smooth. Root thin and small compared to crown. Base of root is flat or slightly convex with a substantial nutritive groove.

Material.—The Fox Hills material includes 29 specimens of *G. girardoti*, 28 from NDGS L140, and one from NDGS L148 (Table 2). Figured specimen NDGS 1002 (Text-figs. 8.17, 8.18; H. 2.3 mm and W. 3.7 mm) is a lateral tooth and has a complete crown. Nutritive groove and root are eroded; however, other unillustrated material in the collection shows the complete root with groove. The largest (NDGS 4066) is H. 3.2 mm, W. 5.7 mm, and the smallest (NDGS 4067) is H. 2.1 mm, W. 2.0 mm.

Remarks.—The genus seems to have a distribution throughout Europe and North Africa, potentially crossing into the Cenozoic (Cappetta, 1987a; Becker et al., 2006). The small, distinctive teeth of *Galeorhinus girardoti* have been recognized from the Maastrichtian Arkadelphia Formation in the Western Interior Seaway by Becker et al. (2006) and on the Atlantic Plain by Hartstein et al. (1999) in the Severn Formation of Maryland.

In the Fairpoint Member of the Fox Hills Formation, a specimen referred to *G. cf. girardoti* by Becker et al. (2004) seems to be an upper antero-lateral tooth of the species from a position somewhat anterior to the specimen we have figured herein. We are unable to verify that the specimen illustrated by Hoganson and Murphy (2002) is this species. However, we concur with its generic placement in *Galeorhinus*.

Vullo (2005, fig. 5C–F) presented images of *G. girardoti* from the Campanian type area of France. We have accepted that specimen in synonymy, although it has a smooth cutting edge on the anterior margin of the cusp and lacks the fine cuspides shown on our specimens (Text-figs. 8.17, 8.18). The type material of Herman (1977) was from the Campanian and Maastrichtian of Belgium and includes both crenulated and smooth anterior margins. He suggested the crenulations were on upper teeth, the lowers being smooth (p. 269).

Genus *ARCHAEOTRIAKIS* Case, 1978

Type species.—*Archaeotriakis rochelleae* Case, 1978.

Archaeotriakis rochelleae Case, 1978

Text-figs. 8.25–8.28

Archaeotriakis rochelleae Case, 1978: pp. 191, 192, pl. 4, figs. 9, 10, p. 192, text-fig. 13.

Archaeotriakis rochelleae Case. Case, 1987: p. 21; p. 47, pl. 9, figs. 1, 2.

Archaeotriakis rochelleae Case. Cappetta, 1987a: p. 116, figs. 99C–E.

Archaeotriakis sp. Hoganson et al., 1995: p. 60.

Archaeotriakis sp. Hoganson et al., 1996: p. 41A.

Archaeotriakis sp. Hoganson et al., 1997: p. 53A.

Description.—Teeth very small, <2 mm in width. Conical crown is flanked by pair of large, divergent cusplets. Cusplets attached to crown, but offset labially. The large cusplets are 1/3 to 1/2 size of the crown, thereby giving the tooth a tricuspid appearance. On some teeth cusplets are split at apex. Lingual faces of the crown and cusplets are smooth. Vertical ridge extends from base of crown to apex on labial surface. Ridge may not always extend to the labial surface. One or more vertical ridges (or folds) are also present on the labial face of the cusplets. Crown is lingually inclined. Labial face of crown does not overhang root nor is there a lingual protuberance.

Root is holaulacorhize, wide, and heart shaped in basal view. The central foramen is distinct and a pair of lateral foramina are present.

Material.—Twelve teeth, six from NDGS L135 and six from NDGS L140. Figured specimens are NDGS 94-38.10 (Text-figs. 8.25, 8.26; H. 1.5 mm, W. 1.2 mm) and NDGS 94-38.9 (Text-figs. 8.27, 8.28; H. 2.1 mm, W. 1.9 mm), both from NDGS L35. The remainder of our specimens are of similar size.

Remarks.—Case (1987) described a second species of *Archaeotriakis*, *A. ornatus*, from the Campanian Mesaverde Formation of Wyoming. In that taxon, which is the same size as *Archaeotriakis rochelleae*, the labial base of the crown overhangs the root, ridges on the crown and cusplets are more complex and ornate, and the lingual face of the crown is ornamented. Our specimens exhibit none of those characteristics.

Archaeotriakis rochelleae is newly reported herein from the Maastrichtian Fox Hills Formation. Its occurrence represents a temporal range extension since it has only been reported previously from the Campanian Judith River Formation of Montana (Case, 1978) and the Late Campanian Teapot Sandstone Member of the Mesaverde Formation in the Big Horn Basin of Wyoming (Case, 1987).

Order **SYNECHODONTIFORMES** Duffin and Ward, 1993

Family **PALAEOSPINACIDAE** Regan, 1906

Genus **SYNECHODUS** A.S. Woodward, 1888

Type species.—*Hybodus dubrisiensis* Mackie, 1863.

***Synechodus turneri* Case, 1987**

Text-figs. 7.4–7.7, 8.34–8.37

Synechodus turneri Case, 1987: pp. 8, 9, pl. 2, figs. 1a–5e.

Synechodus turneri Case. Peng et al., 2001: p. 11, pl. 2, figs. 10–12.

Description.—Teeth broad with cusps flanked by wide mesial and distal heels. Anterior and lateral teeth have sharp, slender central cusps that are erect in anterior teeth (Text-figs. 8.34–8.37) and inclined distally in lateral teeth. Lingual faces of cusps are slightly more convex than labial faces. Anterior and lateral teeth have up to seven pairs of cusplets on the heels. These cusplets are connected and become progressively smaller away from the cusp. On anterior teeth a continuous cutting edge unites the cusp and cusplets. This cutting edge is indistinct on lateral and posterior teeth. The posterior tooth is grossly elongated and asymmetrical. Its central cusp is low and not much higher than the flanking three mesial and four distal cusplets. The base of the labial face of the cusp overhangs the root on all teeth, but this is most pronounced on anterior teeth. Both the lingual and labial faces of the cusps and cusplets have vertical, sinuous folds. These folds are less developed on cusps of anterior teeth and only extend a short distance up the cusp from the base. The folds are coarser and extend further toward the apex of the cusp and cusplets on lateral and posterior teeth.

Root is pseudopolyaulacorhize and robust. In lateral and posterior teeth, the root extends beyond the basal margin of the cusp. The basal margin of the root is gently arched in labial view and sinuous in the posterior tooth. The basal face of the root is flat lingually and has up to eight deep grooves separated by ridges labially. The root is flat to slightly concave at the lingual protuberance and bears many foramina.

Material.—Thirteen teeth (4 anterior, 8 lateral, 1 posterior). Largest anterior tooth ND 99-6.6 (Text-figs. 8.36, 8.37) is 10.5 mm high and 8.6 mm wide. Lateral tooth ND 95-13.76 (Text-figs. 8.34, 8.35) is 5.78 mm and 7.15 mm wide. Posterior tooth ND 95-13.71 (Text-figs. 7.4–7.7) is 3.6 mm high and 12.1 mm wide. All illustrated teeth are from NDGS L140.

Remarks.—Our Fox Hills *Synechodus turneri* teeth compare well with the type specimens illustrated by Case (1987) from the late Campanian/Maastrichtian Mesaverde Formation in Wyoming. Our specimens differ from *Paraorthacodus andersoni* because of the much smaller size and united cusplets. *Synechodus striatus* differs from the Fox Hills specimens in having more extensive folding on the cusps and lacking foramina on the lingual aspect of the roots. In clarification of the relationships of Campanian *Synechodus* species from

Montana, Siverson (1992b) synonymized *Synechodus andersoni* and *Synechodus striatus* under *Paraorthacodus andersoni*. We concur with this change. The genera of *Paraorthacodus* and *Synechodus* are easily separable by characteristics of the root as defined by Siverson (1992b) and noted herein (Text-figs. 8.29–8.33). This is the first report of *Synechodus* from the Fox Hills Formation and extends the range of *Synechodus turneri* into the Late Maastrichtian.

Peng et al. (2001 p. 45, Table 1) recognized a single tooth of *S. turneri* among microsite material from the “Milk River Region assemblage” in the lower Judith River Group, Campanian of southeast Alberta, Canada.

Indetermined Shark Centrum

Species A Text-fig. 8.38

Description.—Circular, slightly impressed centrum with concentric growth lines well displayed. Specimen has been repaired.

Material.—A single centrum (ND 07-76.1) 50.1 mm wide is preserved in a siltstone concretion from the Timber Lake Member of the Fox Hills Formation (NDGS L153), donated by A. Pamonis.

Remarks.—Shark material, other than teeth, is rare in this formation even in the well-known concretions (Waage, 1968), which represent early cementation of seafloor sediments not deeply buried (Carpenter et al., 1988). We illustrate this large centrum, belonging to a lamniform shark, for completeness. Newbrey (personal communication, 2012) has suggested it belongs to *Squalicorax* sp. because of the absence of radial lamellae, prominent circular lamellae, round shape from end view, and it may not be deeply amphicoelous (see Newbrey et al., 2015). This may well be the case, but we are reluctant to assign it herein because it is encased in concretionary sandstone, and we have no lateral view.

Superorder **BATOMORPHII** Cappetta, 1980

Order **RAJIFORMES** Berg, 1937

Suborder **RHINOBATOIDEI** Fowler, 1941

Family **RHINOBATIDAE** Müller and Henle, 1838

Genus **MYLEDAPHUS** Cope, 1876

Type species.—*Myledaphus bipartitus* Cope, 1876.

Myledaphus sp.

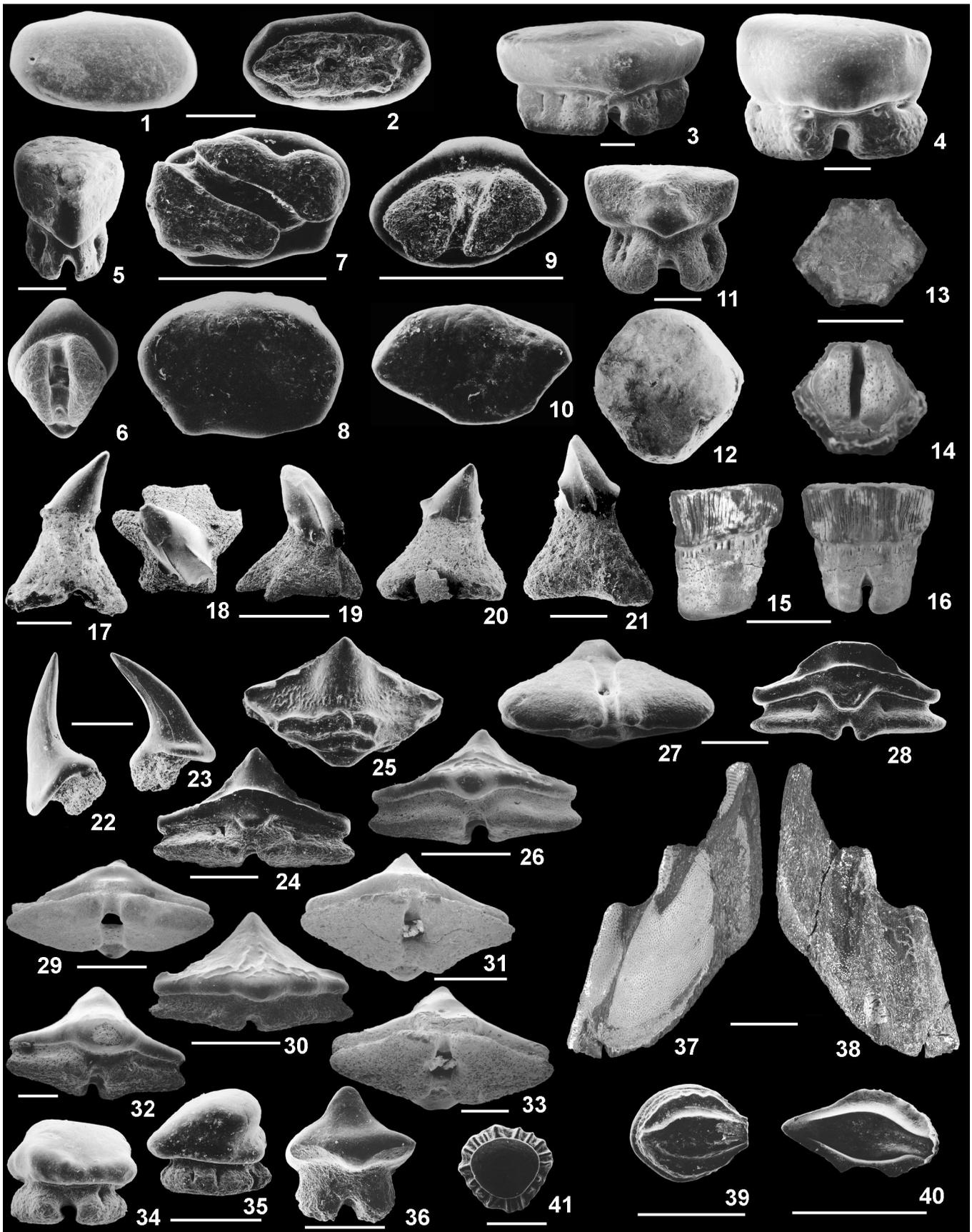
Text-figs. 9.13–9.16

Description.—Hexagonal crushing tooth with overhanging enameloid or vitrodentine crown marked around margin by numerous fine wrinkles or striations from root to occlusal surface. Overhang of crown is asymmetrical, pronounced on labial side and nearly flush on lingual side. Occlusal surface worn and rather flat. Root is tall. Band of numerous, small, elongate foramina surrounds the top of the root just below the crown. Nutritive groove large, deep, and well developed across entire base of root.

Material.—The figured specimen (UND-PC 15904; Text-figs. 9.13–9.16) is a large tooth, measuring 8.0 mm high and 7.7 mm in maximum width collected from NDGS L177. Seven additional specimens from NDGS L140 include the largest, H. 4.37 mm, W. 6.72 mm maximum width (NDGS 4068), and the smallest, H. 3.95 mm and W. 5.00 mm (NDGS 4069), from that site. All specimens have worn crowns.

Remarks.—Teeth of *Myledaphus* are easily recognizable because they are highly robust, have a hexagonal occlusal surface and possess “distinctive” vertical wrinkles on the labial, lingual, and marginal crown faces. This genus was thought to be monospecific until Brinkman et al. (2004) suggested that a second unnamed species occurs in the Campanian Foremost and lower Oldman formations in southeastern Alberta, Canada. Recently, Cook et al. (2014) described a new species, *Myledaphus pustulosus*, from the Hell Creek Formation in eastern Montana. Apparently, in an effort to include a discussion of the new species in their paper, Kirkland et al. (2013) created an invalid name, *Myledaphus “postulatus”*, intended to

Text-fig. 9.—Fox Hills skates, rays, and ratfish. 9.1, 9.2, 9.9–9.12, *Protoplatyrhina renae* Case, 1978; 9.1, 9.2 (ND 94-38.22); 9.9, 9.10 (ND 94-38.12); 9.11, 9.12 (ND 94-38.13). 9.3–9.8, *Pseudohypolophus mcultyi*; 9.3 (ND 07-74.2); 9.4 (ND 07-74.3); 9.5, 9.6 (ND 94-38.19); 9.7, 9.8 (ND 94-38.18); 9.13–9.16, *Myledaphus* sp. (UND-PC 15904). 9.17–9.21, *Ischyrrhiza avoncola* Estes, 1964; 9.17, 9.21 (ND 94-38.24); 9.18, 9.19 (ND 94-38.25); 9.20 (ND 94-38.26). 9.22, 9.23, *Walteraja exigua* Siverson and Cappetta, 2001 (ND 94-38.21). 9.24–9.31, *Ptychotrygon winni* Case and Cappetta, 1997; 9.24–9.26 (ND 94-38.27); 9.27, 9.28 (ND 94-38.28); 9.29 (ND 99-6.7); 9.30, 9.31 (ND 95-13.77). 9.32, 9.33, *Ptychotrygon greybullensis* Case, 1987, (ND 99-5.8). 9.34–9.36, *Dasyatis northdakotaensis* n. sp.; 9.34, 9.35, *holotype, probable female* (ND 94-38.20); 9.36, *allotype, probable male* (ND 94-38.11). 9.37, 9.38, *Ischyodus rayhassi* Hoganson and Erickson, 2005, *mandibular tooth plate of holotype* (ND 99-6.1). 9.39, 9.40, *Elasmobranchii placoid scale morphotype 1*; 9.39 (ND 94-38.16); 9.40 *Elasmobranchii placoid scale morphotype 1* (ND 94-38.15). 9.41, *Elasmobranchii dermal denticle morphotype 1* (ND 94-38.14). Scale bars are 1 mm except 9.13–9.16 = 5 mm; 9.22, 9.23, and 9.36 = 0.5 mm; and 9.37, 9.38 = 1 cm. All are SEM images except 9.13–9.16 and 9.37, 9.38.



represent the Cook et al. (2014) *Myledaphus pustulosus*, which was in press at the time. Note that the illustrated “typical specimen” of Kirkland et al. (2013, p. 172, fig. 12V) is not a holotype, nor is their “type specimen” (UCMP 191578) the same specimen designated by Cook et al. (2014, p. 238, fig. 4A) as the holotype of *M. pustulosus* (UCMP 197869). Note also that *M. “postulatus”* has no standing under the code in the absence of an illustrated holotype. *Myledaphus pustulosus* has a more strongly pustulose occlusal surface than *M. bipartitus*. Our crowns are worn beyond useful recognition of occlusal surface characteristics, making specific identification of the Fox Hills specimens impossible.

Sahni (1972) discussed variation of teeth between lower and upper jaws in *Myledaphus*, noting differences in tooth height and degree of consistent hexagonal shape. Characteristics of the Fox Hills illustrated specimen resemble teeth from a lower jaw. Based on a collection of centra, Wilson et al. (2013) described age and growth characteristics of the *M. bipartitus*. The species *Myledaphus bipartitus* is commonly found in Campanian and Maastrichtian freshwater and brackish water deposits in the northern latitudes of the North American midcontinent and New Jersey. It has not been reported from Gulf or south Atlantic Coastal deposits, nor outside of North America.

Kirkland et al. (2013) reported a new genus, *Pseudomyledaphus*, from the Coniacian and Santonian Straight Cliffs Formation of Utah based on *Pseudomyledaphus madseni*. Teeth of *P. madseni* do not possess labial-lingual directed folds, nor wrinkled enameloid on the vertical tooth margins except for slight crenulations on mesial lingual faces. The crown is smooth as well. Specimens from the Milk River Formation were assigned to *Pseudomyledaphus madseni* by Brinkman et al. (2017) following description of that species from Utah by Kirkland et al. (2013). Brinkman (personal communication, 2018) has also placed the *Myledaphus* specimens reported by Russell (1935) and Johnson and Storer (1974) from the Foremost Formation in *Pseudomyledaphus*. The Fox Hills teeth do not show any of the characteristics of *Pseudomyledaphus*.

Recognition of *M. pustulosus* (Cook et al., 2014), notwithstanding the “*pustulosus/pustulatus* issue,” and *Pseudomyledaphus* and *Cristomylylus* (Kirkland et al., 2013) have greatly clarified relationships among Western Interior Seaway rhinobatoid rays of the “myledaphid group.” In particular, separation of *M. pustulosus* from *M. bipartitus* (*sensu* Estes, 1964) in the Hell Creek Formation begins the process of stratigraphic distinction among these taxa, which may eventually lead to their greater chronostratigraphic utility. Sadly, our Fox Hills specimens are too worn to add more information to this process.

The specimens illustrated by Waage (1968), from the Fox Hills Formation of South Dakota, are *Myledaphus bipartitus*. A specimen of *Myledaphus bipartitus* was reported from the

Breien Member of the Hell Creek Formation in North Dakota by Hoganson et al. (1994) and Murphy et al. (1995). After reexamination, this specimen is determined to be *Myledaphus pustulosus*. Gates et al. (2019) have recorded *Myledaphus pustulosus* teeth among a suite of chondrichthyan teeth sieved from the jacketed sediment of the *Tyrannosaurus rex* specimen “Sue” from the Hell Creek Formation 4.8 m above the Fox Hills contact in Meade County, South Dakota. Numerous records from the Western Interior Seaway of *Myledaphus* will need to be reevaluated.

Estes (1964) reported that *Myledaphus bipartitus* occurs in the Wasatchian of Colorado and Holtzman (1978) reported it from the Tiffanian Tongue River Formation in North Dakota. It is likely these occurrences are reworked specimens.

Discovery of an articulated specimen of *Myledaphus bipartitus* in the fluvial beds of the Dinosaur Park Formation prompted Brinkman et al. (2005) to suggest this taxon is related to guitarfish, which are shallow water, bottom-feeding rays often found in bays and estuaries. They suggest that it was euryhaline, residing in both marine and freshwater environments.

Family Incertae Familiae

Genus *PROTOPLATYRHINA* Case, 1978

Type species.—*Protoplatyrhina renae* Case, 1978.

Protoplatyrhina renae Case, 1978

Text-figs. 9.1, 9.2, 9.9–9.12

Protoplatyrhina renae Case, 1978: pp. 193–195, text-figs. 14, 15, pl. 5, figs. 4a–d, 5a–d.

Protoplatyrhina renae Case. Cappetta, 1987a: p. 142, figs. 120a–c.

Protoplatyrhina renae Case. Case, 1987: pp. 22, 23, text-fig. 9, pl. 15, figs. 1a–6.

Protoplatyrhina renae Case. Bouchard, 1990: p. 32.

Protoplatyrhina renae Case. Welton and Farish, 1993: p. 133, figs. 1a–2d.

Protoplatyrhina renae Case. Cicimurri, 1998: pp. 125, 126, pl. 16, figs. 6, 7.

Protoplatyrhina renae Case. Case and Cappetta, 1997: p. 147, pl. 11, fig. 3.

Protoplatyrhina renae Case. Beavan and Russell, 1999: p. 500, figs. 3.20–3.23.

Protoplatyrhina renae Case. Case et al., 2001b: p. 119, pl. 3, figs. 46–49.

Protoplatyrhina renae Case. Becker et al., 2004: p. 786, figs. 4S–V.

Protoplatyrhina renae Case. Brinkman et al., 2005: fig. 26.2M, non 26.2L.

Description.—Teeth small, up to 2 mm wide, rarely up to 5 mm wide. Crown bulbous, thick, and smooth with rounded margins. Crown margin overhangs root on all sides. Weakly developed lingual protuberance. Occlusal outline subhexagonal to subrectangular. Root bilobed with triangular shaped lobes and flat basal attachment surfaces. Nutritive groove wide with large central foramina. Nutritive groove extends transversely in lateral teeth and obliquely in more posterior teeth. Small foramina occur below crown apron on root lobes. Slight concavities on crown aprons of some teeth are wear facets.

Material.—Forty-two teeth, including: ND 94-38.22 (Text-figs. 9.1, 9.2; H. 1.6 mm, W. 2.7 mm); ND 94-38.12 (Text-figs. 9.9, 9.10; H. 0.8 mm, W. 1.2 mm); and ND 94-38.13 (Text-figs. 9.11, 9.12; H. 0.6 mm, W. 1.1 mm; smallest tooth in collection). Largest unillustrated tooth (NDGS 4070) in collection is H. 3.1 mm, W. 5.5 mm.

Remarks.—*Protoplatyrhina renae* is monospecific and was first described from the Campanian Judith River Formation of Montana (Case, 1978; Cappetta, 1987a). It was first recognized in the Fox Hills Formation by Bouchard (1990) in South Dakota. Cicimurri (1998) noted the occurrence of *P. renae* in the Stoneville Coal facies (Pettyjohn, 1967) of the Fairpoint Member, Fox Hills Formation in South Dakota. Becker et al. (2004) also reported this species from the Fairpoint Member in South Dakota. Other Campanian occurrences are from the Mesaverde Formation of Wyoming (Case, 1987) and the Lethbridge Coal Zone of the Dinosaur Park Formation in Alberta, Canada (Beavan and Russell, 1999; Brinkman et al., 2005). Other reports of *P. renae* from the Late Maastrichtian are from the New Egypt Formation of New Jersey (Case et al., 2001) and the Kemp Formation of Texas (Welton and Farish, 1993; Case and Cappetta, 1997b). Bourdon et al. (2011) recovered specimens of *Protoplatyrhina* from the Santonian Point Lookout Sandstone of New Mexico and suggested they have affinities to *P. renae*; however, they did not assign them to *P. renae*.

Genus **PSEUDOHYPOLOPHUS** Cappetta and Case, 1975b

Type Species.—? *Hypolophus mcnultyi* Thurmond, 1971.

Pseudohypolophus mcnultyi (Thurmond, 1971)
Text-figs. 9.3–9.8

“Hypolophid teeth” McNulty, 1964: pp. 537, 538, pl. 1–4.
? *Hypolophus mcnultyi* Thurmond, 1971: p. 220–222, fig. 12.
Pseudohypolophus mcnultyi (Thurmond). Cappetta and Case, 1975b: p. 306.
Hypolophus mcnultyi Thurmond. Thurmond and Jones, 1981: pp. 74, 75, text-fig. 35.

Pseudohypolophus mcnultyi (Thurmond). Schwimmer, 1986: p. 115.
Pseudohypolophus mcnultyi (Thurmond). Cappetta, 1987a: p. 141, figs. 119i–o.
Pseudohypolophus mcnultyi (Thurmond). Biddle and Landemaine, 1989: pp. 12, 13, Tf. 4, Abb. 2a–2c.
Pseudohypolophus mcnultyi (Thurmond). Kirkland, 1989: p. 52.
Pseudohypolophus mcnultyi (Thurmond). Landemaine, 1991: p. 30, pl. 15, figs. 1–7.
Pseudohypolophus mcnultyi (Thurmond). Stewart and Martin, 1993: p. 245, figs. 1c, d.
Pseudohypolophus mcnultyi (Thurmond). Welton and Farish, 1993: p. 134, figs. 1a–4c.
Pseudohypolophus mcnultyi (Thurmond). Williamson et al., 1993: p. 458, figs. 9.1–9.10.
Pseudohypolophus mcnultyi (Thurmond). Biddle, 1993: p. 50.
Pseudohypolophus mcnultyi (Thurmond). Hoganson et al., 1995: p. 60.
Pseudohypolophus mcnultyi (Thurmond). Hoganson et al., 1996: p. 41A.
Pseudohypolophus mcnultyi (Thurmond). Canudou et al., 1996: p. 46, Abb. 6.
Pseudohypolophus mcnultyi (Thurmond). Cicimurri, 1998: pp. 126, 127, pl. 16, figs. 8–10.
Pseudohypolophus mcnultyi (Thurmond). Cappetta and Case, 1999: p. 42, pl. 28, figs. 1–9, pl. 29, figs. 1–4.
Pseudohypolophus mcnultyi (Thurmond). Kriwet, 1999: pp. 126, 127, text fig. 3, fig. 6, text fig. 4, fig. 7.
Pseudohypolophus mcnultyi (Thurmond). Hartstein et al., 1999: p. 18, pl. 1, fig. 12.
Pseudohypolophus mcnultyi (Thurmond). Cicimurri, 2000: pp. 105, 106, fig. 2.6.
Pseudohypolophus mcnultyi (Thurmond). Johnson and Lucas, 2002: pp. 88–90, figs. 1, 2.
Pseudohypolophus mcnultyi (Thurmond). Becker et al., 2004: p. 786, figs. 4w–z.
Pseudohypolophus mcnultyi (Thurmond). Cook et al., 2008: p. 1193, fig. 5E.

Description.—Teeth small (range in size from H. 1.0 mm, W. 1.3 mm to H. 4.4 mm, W. 7.3 mm). Crown and root about equal in height. Teeth rhomboidal (small, younger specimens) to hexagonal (large specimens) on occlusal outline. Crown is high, smooth, and has rounded margins. Occlusal surface flat to slightly convex. Marginal edge of crown overhangs root around the entire tooth circumference. Thin collar separates crown from root. Lingual flange weakly developed. Bilobed root with triangular lobes. Lobes separated by a deep and wide nutritive groove. Nutritive groove contains one (smaller, younger teeth) to several (larger teeth) foramina. Basal attachment surfaces of root lobes are slightly convex. Numerous foramina pierce the root lobe faces just below the base of the crown. Some of these foramina expand to form vertical grooves on the root faces. Smaller specimens generally have fewer root lobe foramina. Many teeth exhibit wear facets on crown margins.

Material.—Sites NDGS L35 and NDGS L140 produced a majority of the 429 teeth of *P. mcnultyi* (Table 2). Site NDGS L35 yielded the largest (NDGS 4071, H. 4.4 mm, W. 7.3 mm) and smallest (NDGS 4072, H. 1.0 mm, W. 1.3 mm) specimens. The illustrated material includes: ND 07-74.2 (Text-fig. 9.3, a lingual view; H. 4.3 mm, W. 6.7 mm); ND 07-74.3 (Text-fig. 9.4, a lingual view; H. 3.5 mm, W. 4.2 mm); ND 94-38.19 (Text-figs. 9.5, 9.6, lingual and occlusal views; H. 3.2 mm, W. 2.5 mm); and ND 94-38.18 (Text-figs. 9.7, 9.8, lingual and basal views; H. 2.4 mm, W. 2.6 mm). All illustrated and measured specimens are from locality NDGS L35.

Remarks.—Cappetta and Case (1975b) named the genus *Pseudohypolophus* based on the type species from the Albian Paluxy Formation of north central Texas, ?*Hypolophus mcnultyi* reported by Thurmond (1971). Cappetta (1987a) assigned *Pseudohypolophus* to Rhinobatoidei without placing the genus in a family, and maintained that classification in 2006 (Cappetta, 2006). Thurmond and Jones (1981) apparently rejected that generic assignment when they reported *Hypolophus mcnultyi* from the Middle Paluxy of Texas. Manning and Dockery (1992) proposed that *Pseudohypolophus* should be placed in *Brachyrhizodus*, but this reclassification has been rejected by subsequent authors (Table 1). Case et al. (2001a) allocated a second species to this genus and named it *Pseudohypolophus ellipsis* based on a single specimen from the Santonian Eutaw Formation in Georgia. *Pseudohypolophus ellipsis* has an elliptical occlusal outline and is 1 cm wide. Many of the larger *P. mcnultyi* teeth from the Fox Hills Formation have occlusal outlines approaching elliptical, but none of them are 1 cm wide. The widest tooth in our Fox Hills Formation *P. mcnultyi* series is 7.3 mm wide. *Hypolophus sylvestris* was reported from the Paleocene Cannonball Formation in North Dakota and is morphologically somewhat similar to *P. mcnultyi* (Cvancara and Hoganson, 1993). The primary difference between the two is that the crown of *H. sylvestris* consists of osteodentine, whereas the crown of *P. mcnultyi* consists of orthodentine. *Pseudohypolophus mcnultyi* was durophagous. Wear facets on many *P. mcnultyi* crown margins indicate that adjacent teeth abraded each other and were more loosely arranged in the mouth compared to some other ray taxa, such as *Myledaphus*, whose adjacent teeth are immovable against one another.

Remarkably, *Pseudohypolophus mcnultyi* is a temporally and geographically far-ranging species. In Texas, Meyer (1974) reported the occurrence of this taxon from the Albian Travis Peak, Glen Rose, Paluxy, and Walnut formations; the Arlington Member (Cenomanian) of the Woodbine Group; Six Flags Member (Cenomanian) and Bell Member (Turonian) of the Eagle Ford Group; Tombigbee Sand (Santonian); and

the Wolfe City Formation (Campanian). He suggested an Aptian–Campanian age range for the species. Welton and Farish (1993) noted the abundant occurrence of *P. mcnultyi* in offshore marine and brackish bay sediments in several formations throughout Texas, including Glen Rose, Paluxy, Walnut, Weno, Pawpaw, Grayson, Pepper, Woodbine, and lower Eagle Ford and suggested an Aptian through Cenomanian age for the taxon. Cicimurri (1998, 2000) reported *P. mcnultyi* from the Albian Newcastle Sandstone in Wyoming and early late Turonian Turner Sandstone Member of the Carlisle Shale in South Dakota. Williamson et al. (1993) collected fossils of this species from nearshore deposits of the upper sandstone member of the Dakota Formation and the basal Mancos Shale (upper Cenomanian) at Black Mesa, Arizona. Kirkland (1989) recovered this taxon from the middle Turonian of Nebraska. Stewart and Martin (1993) found *P. mcnultyi* in the early middle Turonian deposits of eastern South Dakota. Schwimmer (1986) and Case and Schwimmer (1988) noted *Pseudohypolophus* sp. in the Campanian Blufftown Formation of Georgia. Cappetta and Case (1999) identified *P. mcnultyi* from the upper Cenomanian Woodbine Formation in Texas. *Pseudohypolophus mcnultyi* was reported from the Maastrichtian Severn Formation in Bowie, Maryland by Hartstein et al. (1999).

In the Western Interior Seaway, the northern-most record is one made by Cook et al. (2008) from the Middle Cenomanian Dunvegan Formation of northwestern Alberta. In the central portion of the WIS, the first report of *Pseudohypolophus mcnultyi* from the Fox Hills Formation was by Hoganson et al. (1996) from the Timber Lake Member in North Dakota. Becker et al. (2004) reported this species from the Fairpoint Member of the Fox Hills Formation in South Dakota. These reports indicate that *Pseudohypolophus mcnultyi* has a range of Aptian–Maastrichtian.

Pseudohypolophus mcnultyi is also known from the Cretaceous in Europe. Landemaine (1991) reported this species from the Cenomanian of southern France. Kriwet (1999) and Canudo et al. (1996) reported *P. mcnultyi* from Lower Cretaceous (lower Barremian) of Spain. Biddle and Landemaine (1989) and Biddle (1993) reported *P. mcnultyi* from the lower Cretaceous of the Paris Basin.

The geographic and stratigraphic ranges of *P. mcnultyi* are incongruously long and expansive when compared with those of other skate and ray taxa encountered in this study. This may suggest that the species was evolutionarily static throughout the Cretaceous and therefore was perhaps a eurytopic generalist, a condition supported by its rather uncomplicated tooth morphology and by fossil occurrences in offshore, shallower nearshore, and brackish deposits (Welton and Farish, 1993). Alternatively, it may suggest that dental morphologic differences among species of *Pseudohypolophus* are subtle and not

yet easily recognized among the global Cretaceous fauna. The solution lies beyond the scope of this research.

Indetermined Rhinobatoid Centrum

Species B

Text-figs. 12.50–12.53

Description.—Symmetrical vertebra with distinctive lateral, ventral, and dorsal aspects as illustrated in Text-figs. 12.50–12.53.

Material.—The illustrated specimen (UND-PC 15905) is the best preserved one of three from a collection of surface-gleaned material at NDGS L148 that may be from the same fish. It is 15.3 mm high, 15.5 mm wide, and 10.4 mm long. Another of the specimens (NDGS 4073) is smaller and concave ventrally; the third (NDGS 4074), badly broken, is larger in diameter and has a circular centrum, as does the specimen in Text-fig. 12.50.

Remarks.—These specimens seem morphologically similar, but the smaller is decidedly ovate. They have superficial similarities with amiid centra illustrated by Brinkman (2004, p. 23), but they are not comparable. Nor does the expression of neural arch and parapophyseal pits conform precisely to any of the morphogroups used by Brinkman and Neuman, 2002. Newbrey (personal communication, 2012) has examined the figured specimen and suggested that it belongs to a rhinobatoid, perhaps a species of *Pseudohypolophus*. We place these centra with the rhinobatoids, but leave them unassigned at present.

Suborder RAJOIDEI Garman, 1913

Family RAJIDAE Blainville, 1816

Genus *WALTERAJA* Siverson and Cappetta, 2001

Type species.—*Walteraja exigua* Siverson and Cappetta, 2001.

Walteraja exigua Siverson and Cappetta, 2001

Text-figs. 9.22, 9.23

Walteraja exigua Siverson and Cappetta, 2001: pp. 435–438, text-fig. 2, pl. 1, figs. 1–13, pl. 2, figs. 1–12.

Description.—Tooth extremely small, cuspidate, and asymmetrical. Cusp is very high, conical, slightly mesio-distally compressed and disto-lingually directed. A transverse cutting edge occurs on apical half of cusp. Collar broad and distinct. A distinct labial visor overhangs the root and the inside of this visor is flat. The median overhang, or uvula, is not prominent.

Bilobed root is incomplete. One margino-lingual foramina is preserved and a foramina is evident in the concave base of the root.

Material.—One male tooth, ND 94-38.23 (Text-figs. 9.22, 9.23; H. 1.0 mm, W. 0.7 mm), is from site NDGS L35.

Remarks.—Siverson and Cappetta (2001) described this species from the lowermost Maastrichtian of the Kristianstad Basin of southern Sweden. The present occurrence extends the geographic and stratigraphic range of the species into the Late Middle Maastrichtian of the midcontinent of North America. It is the first record from the Fox Hills Formation.

Suborder **SCLERORHYNCHOIDEI** Cappetta, 1980

Family **SCLERORHYNCHIDAE** Cappetta, 1974

Genus *ISCHYRHIZA* Leidy, 1856

Type species.—*Ischyrrhiza mira* Leidy, 1856.

Ischyrrhiza avoncola Estes, 1964

Text-figs. 9.17–9.21

Ischyrrhiza avoncola Estes, 1964: pp. 13–15, figs. 6a–d. (figured as *Onchosaurus avoncolus* n. sp.).

Ischyrrhiza avoncola Estes. Slaughter and Steiner, 1968: pp. 237, 238, text fig. 3L.

Ischyrrhiza avoncola Estes. Cappetta, 1974: pp. 510, 511, pl. 1, figs. 8–13.

Ischyrrhiza texana Cappetta and Case, 1975a: pp. 306, 307, figs. 6a–e.

Ischyrrhiza avoncola Estes. Williamson et al., 1993: p. 460, figs. 10.10–10.12.

Ischyrrhiza avoncola Estes. Wolberg, 1985: pp. 14–16, fig. 5.9.

Ischyrrhiza mira Hoganson et al., 1995: p. 60.

Ischyrrhiza texana Hoganson et al. 1995: p. 60.

Ischyrrhiza mira Hoganson et al., 1996: p. 41A.

Ischyrrhiza texana Hoganson et al., 1996: p. 41A.

Ischyrrhiza sp. Hoganson et al., 1997: p. 53A.

Ischyrrhiza monasterica Case and Cappetta, 1997: p. 148, pl. 11, fig. 5.

Ischyrrhiza avoncola Estes. Cicimurri, 1998: pp. 128, 129, pl. 17, nos. 5–7.

Ischyrrhiza cf. *avoncola* Hartstein et al., 1999: p. 18; p. 21, pl. 2, fig. 30.

Ischyrrhiza sp. Hoganson and Murphy, 2002: p. 263.

Ischyrrhiza avoncola Estes. Pearson et al., 2002: p. 154.

Ischyrrhiza avoncola Estes. Becker et al., 2004: p. 786, fig. 5, A–D.

Ischyrrhiza avoncola Estes. Becker et al., 2006: p. 707, figs. 4.1–4.3.

Ischyrrhiza avoncola Estes. Cook et al., 2014: p. 236, fig. 3D.

Description.—Teeth small, less than 4 mm in height. Crown $\frac{1}{3}$ the height of the root except in specimen ND94-38.25

(Text-figs. 9.18, 9.19), where crown height equals that of root. Conical crown is inclined posteriorly. Sharp, at times sinuous, cutting edge extends from base of crown to pointed apex on anterior face of crown. Specimen ND94-38.25 has two parallel cutting edges on anterior face of crown that extend $\frac{2}{3}$ the distance up the crown; posterior face of crown is smooth. Short oblique or longitudinal ridges occur on bulging crown foot and extend a short distance up the crown. Bilobate root, triangular in anterior view, is constricted at crown foot and widens rapidly to base. Margin of root lobes may be slightly crenulated or digitate and widely flared, as in specimen ND94-38.25 (Text-figs. 9.18, 9.19). In basal view root is rectangular; base is slightly concave. There is a single foramen at center of basal attachment surface.

Material.—Thirty-one rostral teeth. Illustrated specimens include: ND 94-38.24 (Text-figs. 9.17, 9.21; H 3.2 mm, W 2.3 mm), ND 94-38.25 (Text-figs. 9.18, 9.19; H 1.9 mm, W 1.5 mm), and ND 94-38.26 (Text-fig. 9.20; H 1.8 mm, W 1.5 mm), all from NDGS L35 (Table 2).

Remarks.—Rostral teeth of *Ischyrrhiza avoncola* are distinguishable from rostral teeth of other *Ischyrrhiza* species by their small size, conical crown shape, very short crown compared to root, ornament on the crown, and root shape. Specimen ND94-38.25 (Text-figs. 9.18, 9.19) is somewhat atypical because of its shorter crown relative to root height and flaring root margins. This is probably one of the posterior rostral teeth which are generally shorter, stubbier and have expanded attachment surfaces as Welton and Farish (1993, p. 142, fig. 2) illustrated for the similar species, *I. texana*.

Case and Cappetta (1997) described a new species, *I. monasterica*, from the Maastrichtian Kemp Formation in Texas based on a few rostral teeth. They suggested that it is similar to, but not conspecific with, *I. avoncola* in having a longer and more slender crown and a much less concave root. We believe these characters fall within the range of *I. avoncola* and that the Kemp material should be referred to this taxon. *Ischyrrhiza mira* and *I. texana* reported by Hoganson et al. (1995, 1996), and *Ischyrrhiza* sp. (Hoganson et al., 1997) are here assigned to *Ischyrrhiza avoncola*.

Turonian and Cenomanian rostral teeth have been attributed to *Ischyrrhiza avoncola* (e.g., Cappetta, 1974; Cappetta and Case, 1975b), but Meyer (1974) and Cicimurri (1998) reassigned them to *Ischyrrhiza schneideri*. We would also question the assignment to *I. avoncola* of material in the Greenhorn Formation, Arizona (Williamson et al., 1993). Welton and Farish (1993) suggest that *I. avoncola* is restricted to the Campanian and Maastrichtian. Meyer (1974) also synonymizes *Ischyrrhiza avoncola* of Slaughter and Steiner (1968) with *I. schneideri*.

Material from the Montian Kincaid Formation of Texas (Slaughter and Steiner, 1968) is probably reworked. Wolberg (1985) also noted it from the Turonian Atarque Sandstone Member of the Tres Hermanos Formation of New Mexico.

Ischyrrhiza avoncola of Maastrichtian age has been reported from the following formations: Fox Hills Formation of South Dakota (Bouchard, 1990; Cicimurri, 1998; Becker et al., 2004); Hell Creek Formation of North Dakota and Montana (Murphy et al., 1995; Pearson et al., 2002; Estes and Berberian, 1970; Estes et al., 1969; Bryant, 1989; Archibald, 1996; Cook et al., 2014); Lance Formation of Wyoming (Estes, 1964); Upper Maastrichtian Arkadelphia Formation of Arkansas (Becker et al., 2006); Maastrichtian, New Jersey (Case, 1995); Severn Formation of Maryland (Hartstein et al., 1999); Campanian Marshalltown Formation, Delaware (Lauginiger, 1984); and Campanian and Maastrichtian Taylor and Navarro groups throughout Texas (Welton and Farish, 1993).

Cited as *Ischyrrhiza* cf. *I. avoncola*, it is known from the Laramie Formation of Colorado (Carpenter, 1979), the Donoho Creek Formation of South Carolina (Cicimurri, 2007), and the Teapot Sandstone Member, Mesaverde Formation of Wyoming (Case, 1987). Case (1978) also reported *I. cf. I. avoncola* from the Campanian Judith River Formation of Montana. We have not seen these specimens, and a personal communication from Brinkman (2018) questions the species identification.

Hoganson and Murphy (2002) listed the species from the marine Breien Member of the Hell Creek Formation of North Dakota as *Ischyrrhiza* sp. This unit overlies the Fox Hills Formation in the Missouri Valley of North Dakota (Text-fig. 2) and is Late Maastrichtian. Cook et al. (2014) illustrated a single specimen of *I. avoncola* from the Bug Creek ant hills location in eastern Montana. They questioned an earlier report of *Ischyrrhiza* sp. from that site by Bryant (1989).

Family **PTYCHOTRYGONIDAE** Kriwet, Nunn, and Klug, 2009

Genus **PTYCHOTRYGON** Jaekel, 1894

Type species.—*Ptychodus triangularis* Reuss, 1845.

Ptychotrygon winni Case and Cappetta, 1997
Text-figs. 9.24–9.31

Ptychotrygon winni Case and Cappetta, 1997: p. 150, pl. 13, figs. 1–3.

Ptychotrygon species 2 Cicimurri, 1998: p. 138, pl. 17, fig. 19.

Ptychotrygon triangularis (Reuss). Hoganson et al., 1995: p. 60.

Ptychotrygon triangularis (Reuss). Hoganson et al., 1996: p. 41A.

Ptychotrygon cf. *P. texana* Hoganson and Murphy, 2002: p. 263, fig. 12V.

Description.—Teeth small (~3 mm wide and ~2 mm high). Teeth mesolingually elongate and bilaterally symmetrical in outline. Crown is high, pyramidal, and triangular in labial view. Prominent and sharp transverse ridge separates labial and lingual crown faces. Angle between labial and lingual crown faces is sharp. Apex of crown is pointed. Labial face of crown is concave or slightly convex, and bears sinuous, at times discontinuous low crests that can be transversely oriented or slightly anastomosing. Labial protuberance at crown foot is large, overhangs root, and is sometimes worn. Lingual face is truncated and smooth except for sinuous, transverse ridge that extends across lingual face and weakly concave hollow on lingual protuberance, which overhangs root.

Root is rhombic and holaulacorhizous. Root is as wide as crown, lobes triangular, and separated by a wide, deep nutritive groove. Nutritive groove contains a large foramina, and is flanked by a pair of large foramina on lingual face of root. Basal attachment surface of root is flat.

Material.—Ninety-six teeth of *P. winni* are present in the Fox Hills collection (Table 2). Illustrated specimens include: ND 94-38.27 (Text-fig. 9.24; H. 2.2 mm, W. 3.0 mm); ND 94-38.28 (Text-fig. 9.27; H. 2.3 mm, W. 3.2 mm); ND 99-6.7 (Text-fig. 9.29; H. 1.7 mm, W. 3.0 mm); and ND 95-1.77 (Text-fig. 9.30; H. 2.0 mm, W. 3.0 mm). The largest tooth (NDGS 4075) measures H. 2.8 mm, W. 4.9 mm, and the smallest (NDGS 4076) is H. 1.8 mm, W. 2.4 mm; both are from site L140.

Remarks.—The overall appearance of oral teeth of *Ptychotrygon* is similar and species are differentiated primarily based on ornamentation of the crown. Our specimens possess sinuous, at times discontinuous, low crests that are either transversely oriented or anastomosing on the labial face of the crown, as in *Ptychotrygon winni* from the Maastrichtian Kemp Clay of Texas, initially described by Case and Cappetta (1997). Our specimens differ from *Ptychotrygon triangularis* and *Ptychotrygon vermiculata* in having less distinct transverse ridges on the labial crown faces. We had originally referred these specimens to *Ptychotrygon triangularis* (Hoganson et al., 1995, 1996), but we found they conform more closely to *P. winni*.

Bouchard (1990) first reported a *Ptychotrygon* species from the Fox Hills Formation in South Dakota based on a single tooth. Cicimurri (1998) reexamined that tooth and reported one other tooth from the formation in South Dakota and designated them *Ptychotrygon* species 1 and 2 respectively. It is unlikely that species 1 is *P. winni* due to presence of a very concave lingual crown face. Cicimurri (1998) suggested that it may be *P. blainensis*. *Ptychotrygon* species 2 may belong to *P. winni* because it has short interconnected ridges and tubercles on its labial crown face.

Becker et al. (2004) identified a single tooth from the Fox Hills Formation in South Dakota as *Ptychotrygon* cf. *P. vermiculata*. Unlike in *P. winni*, two sinuous ridges occur across the labial crown face. They also referred teeth from the Maastrichtian Arkadelphia Formation of Arkansas to *P. cf. P. vermiculata*. Their figured specimen (Becker et al., 2006, fig. 4.20–4.24) may be a bit erosionally polished, thus making details of the enamel surface somewhat obscure. Therefore, we remain unsure of the correct trivial placement of the Arkadelphia specimens.

Ptychotrygon blainensis, a similar species, has been reported from the Campanian Judith River Formation of Montana (Case, 1978), Frontier Formation of Wyoming (Breithaupt, 1985), and the Dinosaur Park Formation, Alberta (Beavan and Russell, 1999). One broken specimen from the Maastrichtian Breien Member of the Hell Creek Formation, North Dakota, was called *Ptychotrygon* cf. *P. texana* by Hoganson and Murphy (2002). *Ptychotrygon texana* was synonymized with *P. vermiculata* by Case and Cappetta (1997); therefore, the Breien specimen should be referred to *P. cf. P. vermiculata*.

Species belonging to *Ptychotrygon* are widely recorded from the Western Interior Seaway and Atlantic Coastal Plain. Late Cretaceous occurrences seem to include an increasing number of species which may suggest that the coast paleogeography was becoming more complicated, leading to isolation and increased speciation during seaway regression (McNulty and Slaughter, 1972; Breithaupt, 1985; Williamson et al., 1989, 1993; Hartstein et al., 1999; Brinkman et al., 2005; Cook et al., 2008; Bourdon et al., 2011).

Ptychotrygon greybullensis Case, 1987

Text-figs. 9.32, 9.33

Ptychotrygon greybullensis Case, 1987: p. 28, pl. 14, figs. 4a–5b.

Description.—Tooth small, mesiodistally elongate, and bilaterally symmetrical in outline. Crown is high, pyramidal and triangular in labial view. Transverse ridge separates labial and lingual faces of crown. Angle between labial and lingual crown faces is sharp. Apex of crown is also sharp. Labial face is concave and essentially devoid of ornamentation; labial protuberance at crown foot is massive, worn and overhangs root. Lingual face is truncated and smooth except for sinuous transverse ridge that extends across lingual crown face and weakly concave hollow on crown protuberance. Lingual protuberance overhangs the root.

Root is rhombic, holaulacorhizous, and extends slightly beyond the margins of crown. Root lobes are triangular and are separated by a wide, deep nutritive groove which contains a very large foramen. On the lingual face of the root, one large

foramen is found on one side of the nutritive groove and two on the other. Basal attachment surface of the root is flat.

Material.—One tooth, ND 99-5.8 (Text-figs. 9.32, 9.33; H. 3.4 mm, W. 5.0 mm), originated from site NDGS L140. The entire collection includes seven teeth, six of which are from NDGS L140 and one from Bowman County, ND (NDGS L35).

Remarks.—Teeth of *Ptychotrygon* species are very similar to each other in appearance and, as discussed above, are identified primarily based on crown ornamentation. Only two species have crowns that are essentially or nearly devoid of ornamentation, *Ptychotrygon greybullensis* and *Texatrygon hooveri*. Our specimen is distinguishable from the Turonian–Cenomanian *T. hooveri* by presence of a distinct, sinuous transverse ridge that extends across the lingual crown face.

The only other occurrence of *P. greybullensis* is from the Campanian Mesaverde Formation of Wyoming (Case, 1987).

Order **MYLIOBATIFORMES** Compagno, 1973
 Superfamily **DASYATOIDEA** Whitley, 1940
 Family **DASYATIDAE** Jordan, 1888
 Genus **DASYATIS** Rafinesque, 1810

Type species.—*Raja pastinaca* Linnaeus, 1758 (by monotypy).

Dasyatis northdakotaensis n. sp.
 Text-figs. 9.34–9.36; 10.1–10.4

Diagnosis.—Teeth extremely small; crown of female tooth is bulbous with a subrectangular outline in occlusal view. Crown surfaces smooth; lingual face of crown is convex, producing a concavity extending around the lingual and labial margins of the crown. Crown overhangs root around the entire margin; labial visor of crown weakly crenulate. Root robust and bilobate; each lobe is subrectangular. Large nutritive groove that contains three basal foramina separates root lobes. Several nutritive foramina penetrate margins of tooth; basal attachment sutures of root lobes are slightly convex.

Crown of male tooth is subrectangular in occlusal outline, smooth, and possesses a distinct cusp. Lingual face of crown has indentation on either side of the central cusp. Cutting edge extends from tip of crown to nearly the lateral margins of the crown. Subtriangular root lobes are separated by nutritive groove containing one central foramen; tips of root lobes project beyond lingual face of crown. Root lobes are proportionately smaller than on female tooth.

Description.—Description same as diagnosis.

Types.—Holotype, probable female, ND 94-38.20 (Text-figs. 9.34, 9.35, 10.1, and 10.2). Allotype, probably male, ND 94-38.11 (Text-figs. 9.36, 10.3, and 10.4).

Material.—Two teeth, one male, one female. Male tooth (allotype) is ND 94-38.11 (Text-figs. 9.36, 10.3, and 10.4; H. 0.6 mm, W. 0.8 mm). Female tooth (holotype) is ND 94-38.20 (Text-figs. 9.34, 9.35, 10.1, 10.2; H. 1.5 mm, W. 1.2 mm).

Type locality.—NDGS L35, Timber Lake Member, Fox Hills Formation (Maastrichtian), Bowman Co., North Dakota.

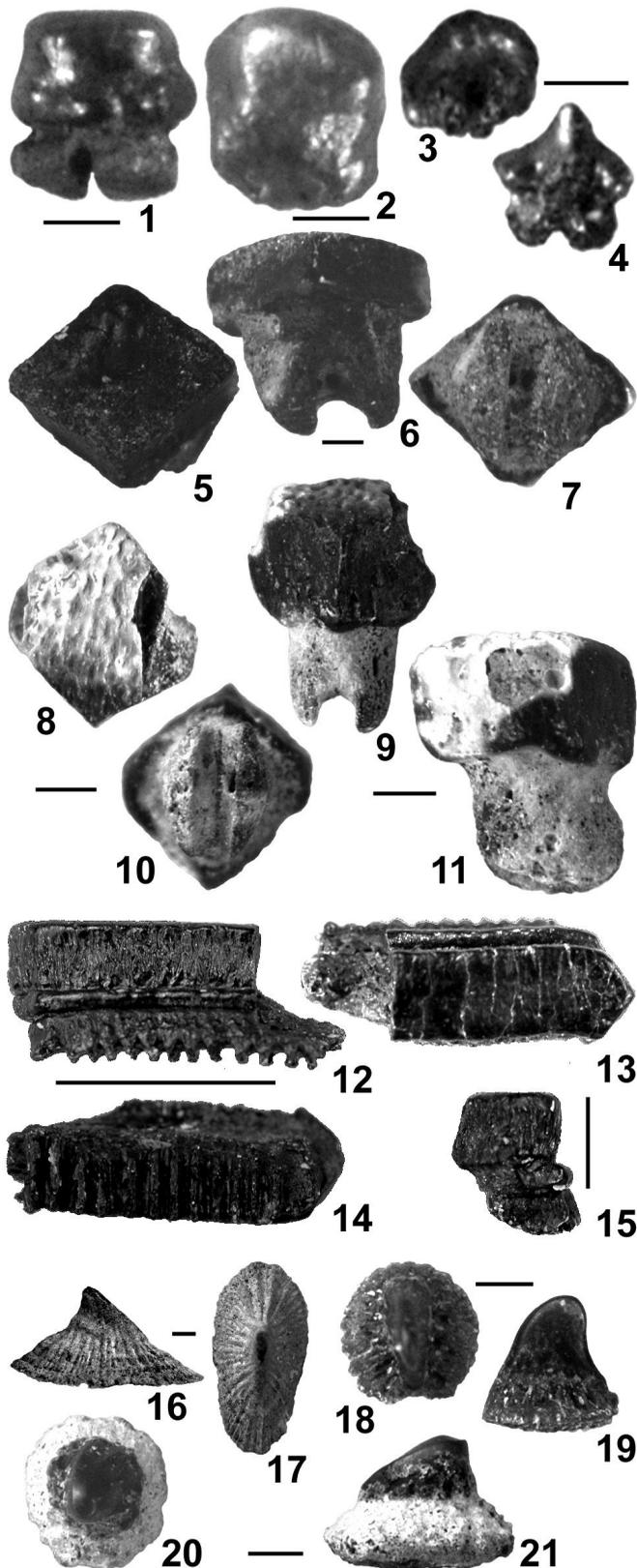
Etymology.—The name recognizes a species of *Dasyatis* first found in North Dakota.

Remarks.—*Dasyatis northdakotaensis* n. sp. is the first *Dasyatis* reported from the Fox Hills Formation. Case and Cappetta (1997) described *Dasyatis commercensis* from the Late Maastrichtian Kemp Clay of Texas, a species that does not have a bulbous crown. The labial face of *D. commercensis* is pitted compared to the smooth crown of *D. northdakotaensis* n. sp.

Welton and Farish (1993) noted species of *Dasyatis* from the Woodbine through the Navarro groups in Texas and ranging in age from Cenomanian to Maastrichtian. Their illustrated specimens are from the Maastrichtian Kemp Formation. These are specimens that have a flattened crown and pitted occlusal face. They also illustrated an undetermined specimen as ?Dasyatidae from strata of undetermined age (sometime between the Albian and Cenomanian) from Texas that does have a somewhat globose crown, but it, too, is highly pitted and scalloped.

Hartstein et al. (1999) illustrated a *Dasyatis* sp. from the Late Cretaceous Severn Formation of Maryland but did not describe it. Case et al. (2001b) described *Dasyatis newegyptiensis* from the Late Maastrichtian New Egypt Formation of New Jersey. The crown of *D. newegyptiensis* is pitted, unlike the smooth crown of *D. northdakotaensis* n. sp.

Three new species of *Dasyatis* from the Late Cretaceous of Bolivia were described by Cappetta (1975b). *Dasyatis branisai* does not have a well-developed nutritive groove and its root is not bilobed; thus, it differs from *D. northdakotaensis* n. sp., which has a well-developed nutritive groove and bilobed root. The crown of *D. branisai* is also flattened, not bulbous. *Dasyatis molinoensis* has a flattened labial face, an ornamented crown, and a poorly-defined nutritive groove. *Dasyatis schaefferi* has a globose and smooth crown similar to *D. northdakotaensis* n. sp., but is differentiated by having a carina on the margins of the crown and by having a less well-defined bilobate root.



Cvancara and Hoganson (1993) described *D. concavifoveus* from the Paleocene Cannonball Formation in North Dakota. *Dasyatis concavifoveus* cannot be confused with *D. northdakotaensis* n. sp. because the labial face of the crown is concave and pitted. A specimen of *Dasyatis* sp. recently illustrated by Cook et al. (2014, page 244, fig. A2) from the Paleocene Tullock Member of the Fort Union Formation of Montana has a pitted crown and is larger than *D. northdakotaensis* n. sp. Wroblewski (2004) mentioned the occurrence of a new species of *Dasyatis* in the lower Paleocene Ferris Formation in Wyoming; however, he did not describe it and provided inadequate illustrations that prohibit us from evaluating it in comparison with *D. northdakotaensis* n. sp.

Superfamily MYLIOBATOIDEA Compagno, 1973

Family MYLIOBATIDAE Bonaparte, 1838

Genus "MYLIOBATIS" Cuvier, 1816

Type species.—*Raja aquila* Linnaeus 1758.

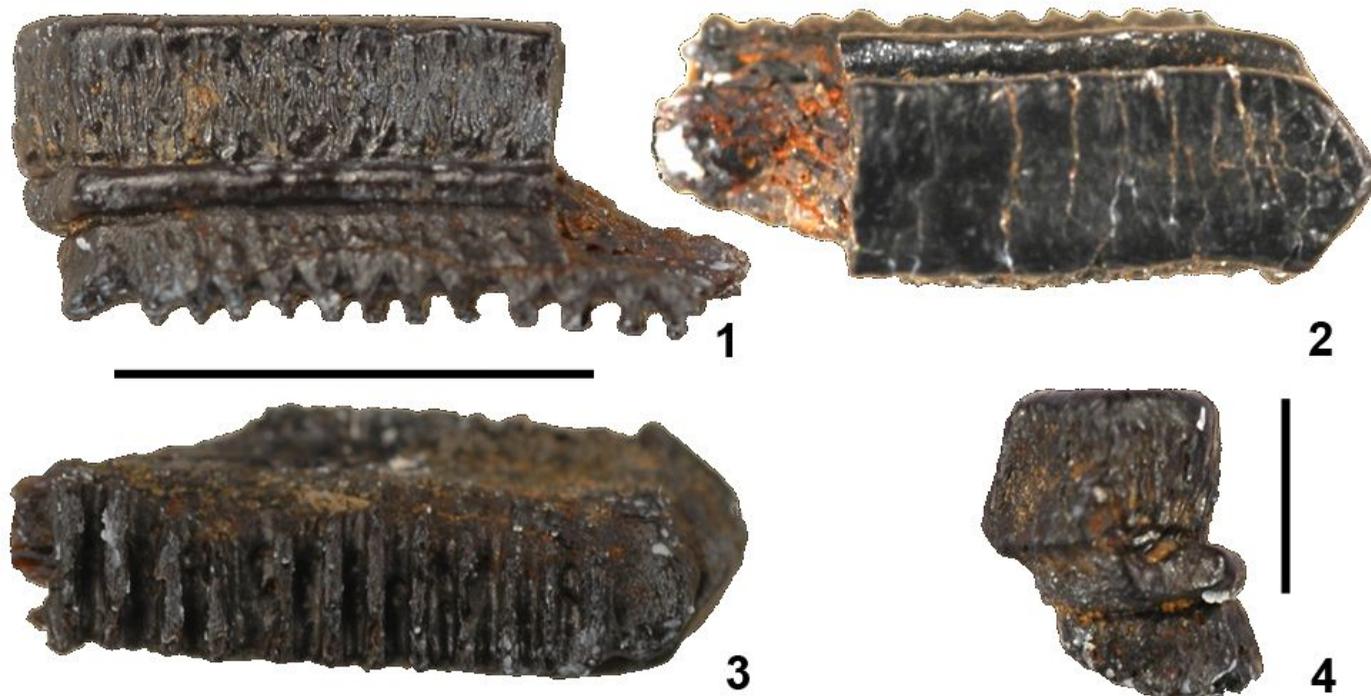
"*Myliobatis*" *foxhillsensis* n. sp.

Text-figs. 10.12–10.15; 11.1–11.4

Diagnosis.—A ray having median teeth with offset root, strong hemi-cylindrical, lingual apron interlocking with labial facet of next tooth in plate; finely polyaulacorhizous root (1.7 nutritive grooves per mm) with grooves less than half the depth of root, wrinkled (folded) margins surrounding crown, and crown with vermiculate enameloid on margins of upper surface. Adjacent teeth as yet unknown.

Description.—A single well preserved fragment of a median grinding tooth (Text-figs. 10.12–10.15, 11.1–11.4) having flat, smooth crown with strong v-shaped lateral margin, suggesting probability that tooth was hexagonal. Grinding surface smooth (Text-fig. 11.2), with very slight unevenness at margins; lingual and labial margins straight, distinctly wrinkled; a well-developed, ridge-like, hemi-cylindrical (in cross-section) lingual extension or apron extends beyond crown base on lingual side where it protrudes over offset portion of

←
Text-fig. 10.—Fox Hills Formation rays and miscellaneous denticle morphotypes. 10.1–10.4, *Dasyatis northdakotaensis* n. sp.; 10.1, 10.2, holotype, probable female (ND 94-38.20); 10.3, 10.4, allotype, probable male (ND 94-38.11). 10.5–10.7, *Rhombodus levis* Capetta and Case, 1975a (NDGS 1696). 10.8–10.11, *Rhombodus* sp. (NDGS 1700). 10.12–10.15, "*Myliobatis*" foxhillsensis n. sp., holotype (ND 95-13.78). 10.16, 10.17 *Elasmobranchii* dermal denticle morphotype 2 (NDGS 1702). 10.18, 10.19 *Elasmobranchii* dermal denticle morphotype 3 (NDGS 1703). 10.20, 10.21 *Elasmobranchii* dermal denticle morphotype 3 (NDGS 1704). Scale bar = 0.5 mm except 10.8–10.11, 10.12–10.14 = 5 mm; 10.15 = 2.5 mm; and 10.16–10.21 = 1 mm.



Text-fig. 11.—“*Myliobatis*” *foxhillsensis* *n. sp.*, holotype, broken tooth (ND 95-13.78); 11.1, lingual view showing wrinkled crown margin, apron, and root divisions; 11.2, occlusal view showing v-shaped lateral margin, smooth occlusal surface, and lingual apron; 11.3, root view showing polyaulacorhizal condition; 11.4, lateral end view showing apron overhang and shape of root displacement. Scale bar 11.1–11.3 = 5 mm; 11.4 = 2.5 mm.

the polyaulacorhizal root (Text-figs. 11.1, 11.4). Root finely divided, having 1.7 nutritive grooves per millimeter; grooves well defined but their depth is less than half of root thickness (Text-figs. 11.1, 11.4). Tooth appears uniform in height throughout length but the broken section suggests that the root is beginning to curve downward as if it was becoming arched; therefore, perhaps, a change of thickness should be anticipated in complete specimens. Root properties suggest a derived taxon.

Type.—A single specimen, ND 95-13.78 (Text-figs. 10.12–10.15, 11.1–11.4), is designated the holotype and is reposit in the North Dakota Geological Survey State Fossil Collection at the North Dakota Heritage Center, Bismarck, ND.

Material.—A single specimen (ND 95-13.78) is 3.5 mm high, 7.7 mm (broken) wide, and 3.2 mm long, with crown length of 2.3 mm, crown height of 1.4 mm above apron and 2.2 mm including apron; root is 1.3 mm high with 13 nutritive grooves in 7.74 mm of width. Tooth margins straight with lateral end forming symmetrical “V” shape. Specimen shows no wear.

Type locality.—The holotype was screened from fine sand attributed to the Timber Lake Member of the Fox Hills

Formation. It was deposited in a protected, inshore lagoonal or estuarine setting at NDGS L140 in Logan County, North Dakota.

Etymology.—This species is named for its occurrence in the upper Maastrichtian Fox Hills Formation of south-central North Dakota.

Remarks.—*Myliobatis*, the well-known eagle rays, has more than 150 assigned species (Cappetta, 1987a, 1992) based on the Holocene species *Myliobatis aquila* (Linnaeus), including a few suggested assignments of Cretaceous material (Hartstein et al., 1986, 1999). At present the taxon is both descriptive of modern ray species and serves as a form genus for fossil species of Cretaceous and Cenozoic ages. Two other genera of Myliobatidae are also known from Late Cretaceous strata, *Brachyrhizodus* Romer, 1942 and *Igdabatis* Cappetta, 1972. Of these, *Igdabatis* appears to be the more derived genus based on the advanced root design of the type species.

Brachyrhizodus wichitaensis was originally thought by Romer (1942) to have been from Permian rocks, but it has subsequently been recognized by others, including Cappetta (1987a) that the type specimen was float originating from Late Cretaceous strata. *Brachyrhizodus wichitaensis* is a basal form lacking interlocking median teeth and having a very coarse

nutritive groove pattern, if only a few grooves per tooth. It occurs in rocks of Santonian to lower Campanian age on the Atlantic and Gulf Coasts (Welton and Farish, 1993). This species cannot be confused with our material.

Myliobatis sp. has been discussed from two sites in the lower Middle Maastrichtian Severn Formation of Maryland (Hartstein and Decina, 1986; Harstein et al., 1999). They figure (Hartstein et al., 1999, pl. 1, fig. 6) an attached pair of median crusher teeth which are gently arcuate with lateral margins that form an asymmetrical V-shape rather than the symmetrical V-shape of the Fox Hills form. No cross-section is illustrated, but there seems to be more crown exposed on one end than the other of the two teeth suggesting some root offset. The crown has a fine pitting or roughness to it. The root is more coarsely divided (0.7 canals per mm) than is the Fox Hills species, which has 1.7 grooves per mm. These teeth are roughly four times wider than our specimen and not conspecific with the North Dakota material.

Two Campanian specimens from the Ozan and Wolfe City formations of Texas figured by Welton and Farish (1993) are narrow (11–12 mm), broad median teeth with approximately 0.8 canals per mm, again coarser than the Fox Hills species.

Igdabatis was first recognized by Cappetta (1972) from numerous isolated teeth in the Maastrichtian of Nigeria. *Igdabatis sigmodon* Cappetta has a finely divided root (1.06 grooves per mm), similar to that of "*Myliobatis*" *foxbillsensis* n. sp. with a crown that shows constant thickness on one half of the median teeth and tapering thickness on the other half beginning at the center on the most arcuate teeth of the nine teeth illustrated (Cappetta 1972, pl. 8, fig. 1–3).

Jain and Sahni (1983) recognized *Igdabatis sigmodon* from Maastrichtian age intertrappean sediments in Maripalli, India and reported it under the name *I. sigmoides*, a *lapsis calami* (Cappetta, 1987a, 1992). Prasad and Cappetta (1993) described a second species, *I. indicus* from intertrappean beds of peninsular India, and they reassigned to *Igdabatis* specimens they believed had been erroneously assigned to *Dasyatis* and *Rhinoptera*. The taxon was illustrated from the Maastrichtian red beds of the Trepmp Formation of the south-central Pyrenees by Soler-Gijón and López-Martínez (1998). Their median tooth was 17.5 mm wide with eight nutritive grooves (0.48 per mm) and lacked a lingual apron or ridge for interlocking with neighbors. The lateral tooth they illustrated (fig. 3) does show such an apron. Both teeth show a foveolate textured surface. *Igdabatis indicus* teeth have highly ornamented crowns and low roots. The number of grooves per millimeter is approximately 0.5 in these very small median teeth. In both cases, they are not similar to '*M.*' *foxbillsensis* n. sp. and in fact they seem to vary from the generic definition established for *I. sigmodon*.

There seems no entirely satisfactory genus to hold our specimen so we have taken the more conservative course and assigned the new species to the Cretaceous form genus "*Myliobatis*" until additional discoveries allow better definition of its generic affinities. The Fox Hills species is highly derived for Cretaceous myliobatids, but seems best placed in the form genus. Because the tooth crown maintains thickness to its edge, because the root is grooved at a rate greater than one groove per millimeter, and because the crown enameloid is slightly vermiculate on the margins, the tooth seems close to both *Igdabatis* and *Myliobatis*, but shape properties of a complete tooth are needed in order to make definitive assignment. Both the size and morphologic properties do serve to distinguish it from all other Late Cretaceous rays at the species level, hence designation of the new species herein.

The Paleocene (Thanetian) teeth from the Cannonball Formation of North Dakota, recorded with question as *Myliobatis* by Cvancara and Hoganson (1993), bear a strong resemblance to *Igdabatis sigmodon*, as illustrated by Cappetta (1972). Cvancara and Hoganson (1993) also noted their close resemblance to *Rhinoptera*. The specimens of median teeth from the Cannonball Formation do not show an offset root, nor a lingual bib or apron, characters that readily distinguish them from the Fox Hills specimen.

Family **RHOMBODONTIDAE** Cappetta, 1987a
Genus **RHOMBODUS** Dames, 1881

Type species.—*Rhombodus binkhorsti* Dames, 1881.

Rhombodus levis Cappetta and Case, 1975a
Text-figs. 10.5–10.7

Rhombodus levis Cappetta and Case, 1975a: pp. 36, 37, pl. 9, figs. 12–23.

Rhombodus levis Cappetta and Case. Lauginiger and Hartstein, 1983: pp. 16, 17, pl. 5, figs. 64–69.

?*Rhombodus levis* Cappetta and Case. Lauginiger, 1984: pp. 142, 143.

Rhombodus laevis [sic] Cappetta and Case. Gallagher et al., 1986: p. 31.

Rhombodus laevis [sic] Cappetta and Case. Cappetta, 1987a: p. 175.

Rhombodus laevis [sic] Cappetta and Case. Case and Schwimmer, 1988: p. 297, figs. 6.6–6.9.

Rhombodus levis Cappetta and Case. Robb, III, 1989: p. 81, figs. 11A–C.

Rhombodus levis Cappetta and Case. Soler-Gijón and Lopez-Martínez, 1998: p. 6.

Rhombodus laevis [sic] Cappetta and Case. Case et al., 2001b: p. 121, pl. 3, figs. 50–54.

Rhombodus levis Cappetta and Case. Becker et al., 2004: p. 788, figs. 5M–P.

Description.—Small, rhombic, pavement-crushing teeth having crown with sharply orthogonal edges and little to no rounding on any corners; enameloid of flat occlusal surface smooth, very slightly vermiculate or textured under magnification; simple holaulacorhizous root with nutritive groove crossing labio-lingually has two foramina located slightly off-center in the groove; root approximately same height as crown (Text-figs. 10.6, 10.7).

Material.—Four specimens, all from NDGS L140: NDGS 1696 (Text-figs. 10.5–10.7; H. 2.8 mm, W. 2.8 mm, L. 2.4 mm); unfigured material includes NDGS 1697 (H. 2.4 mm (crown H. 1.3 mm), W. 2.6 mm, L. 2.0 mm), NDGS 1698 (H. 2.8 mm, W. 2.05 mm, L. 2.2 mm), and NDGS 1699 (one-half specimen broken on nutritive groove; H. 2.10 mm, W. 1.39 mm (broken), L. 2.6 mm).

Remarks.—*Rhombodus levis* is reported with increasing frequency from locations beyond its type locality in the lower Maastrichtian Mount Laurel Formation of New Jersey (Cappetta, 1975a) as noted by the synonymy given above. Translated from its original description, *R. levis* is distinguishable from all other *Rhombodus* species by its smooth crown, lack of a basal “cushion”, and its tall root. The holotype, however, is given as 6.3 mm high, 6.8 mm wide, and 6.2 mm long, a size not duplicated by most of the material others have assigned to this species, including the Fox Hills specimens. In this consideration, we include those specimens discussed by authors under the name *R. “laevis”* as cited above which we assume to have originated as a slip of the pen, for it differs from the original spelling (Cappetta and Case, 1975a, p. 36).

Rhombodus binkhorsti Dames, 1881, the type species from the Chalk of Maastricht, has folded enameloid around entire margin of the crown and a smooth crown, although the fine SEM illustrations of Noubhani and Cappetta (1994) indicate one specimen (pl. 2, fig 5a,b) which has a finely foveolate crown. It occurs in the Maastrichtian of Texas (Welton and Farish, 1993; Case and Cappetta, 1997), in the Arkadelphia Formation of Arkansas (Becker et al., 2006) and also several records from the Atlantic Coastal Plain of North America (Hartstein et al., 1999; Becker et al., 2004).

Arambourg (1952) described three species of *Rhombodus* among the rays of Morocco in addition to the type. In their revision of the Rhombodontidae, Noubhani and Cappetta (1994) accepted *R. binkhorsti* (Dames, 1881) and the three species of Arambourg (1952). *Rhombodus microdon* has finely folded—almost in dendritic patterns—margins on pavement crushers. Fine pits also occur over the upper portions of the lateral margins and extend onto the occlusal surface. Short roots relative to crown height and is generally smaller (average crown width 2.6 mm vs 10.4 mm for *R. binkhorsti*) (Noubhani

and Cappetta, 1994, table 7). *Rhombodus meridionalis* was recognized by a more convex crown with rounded edges. This latter character places it nearer to the third of Arambourg’s species, *R. bondoni*, which Noubhani and Cappetta (1994) made the type species of their new genus *Dasyrhombodus*. *Dasyrhombodus bondoni* crusher teeth are quite convex, have a marginal rim or flare—all with a foveolate pattern—and rather smooth margins on the crown. Roots are short relative to crown height.

In addition, Noubhani and Cappetta (1994) recognized a new species, *Rhombodus andriesi*, from Upper Maastrichtian beds of Ould er-Rami in the Ganntour Basin, Morocco. This species has medium-sized crushing teeth with flat, finely pitted surfaces, folded lateral margins with a concavity on both lateral margins of the lingual corner, and a well-developed bib or apron around the base of the crown. None of these teeth resemble the Fox Hills specimens, although we note below some material with more ornamentation than any assignable to *R. levis*.

Rhombodus levis is mentioned as part of a large fauna including marine and deltaic taxa from a Late Campanian locality in the Doho Creek Formation, South Carolina by Cicimurri (2007, p. 59, 61). The species was not illustrated.

Vullo (2005), when describing *R. carentonensis* from the type Campanian of France, makes mention of the fact that it is the earliest *Rhombodus* and only true *Rhombodus* species from the Campanian. He noted that all other *Rhombodus* species are Early Maastrichtian, and he excludes the Campanian *R. levis* specimens from Georgia (Case and Schwimmer, 1988) as belonging close to *Hypsobatis*, a rhinobatoid genus (Vullo, 2005). If he is correct, the Fox Hills specimens from NDGS L140 (Table 2) extend the range of *R. levis* into the Late Maastrichtian.

Rhombodus sp.

Text-figs. 10.8–10.11

Description.—Two typically rhomboid teeth, having smooth crown margins but with flat, strongly wrinkled occlusal surfaces of crowns. Margins of crown are uneven but not striated or wrinkled. Root holaulachorizal with wide nutritive groove having two foramina, one on each side of the groove and both centrally located in the root.

Material.—Two teeth, both from NDGS L140, include NDGS 1700 (Text-figs. 10.8, 10.11; H. 3.9 mm, W. 3.14 mm (broken), L. 3.24 mm) and unfigured NDGS 1701 (H. 2.29 mm, W. 2.83 mm, L. 2.25 mm), somewhat damaged by microborers, but showing good morphology and enameloid, having typical rhombic crowns with angular margins and having occlusal surfaces strongly wrinkled.

Remarks.—These unusual teeth possess a set of characteristics that are unlike any other *Rhombodus* species. The wrinkled crown suggests *R. binkhorsti*, whereas the smooth lateral margins of the crown do not. Smooth margins are indicative of *R. levis*, but that species is noted for a smooth crown. The size is typical of some specimens assigned to *Rhombodus levis*, although the holotype of *R. levis* is more than 6 mm wide. More material is needed to properly define this species.

Elasmobranchii Placoid Scale Morphotype 1
Text-figs. 9.39, 9.40

Description.—Morphological terminology used in the following placoid scale and dermal denticle descriptions is based on those proposed by Thies (1995) and Johns et al. (2005). Placoid scales are very small: largest specimen is 1.34 mm in length. Crown and base are thin and of about equal thickness. Base margin extends beyond crown margin in apical view. Scales are symmetrical and oval to elliptical in apical view. Crown anterior margin is convex and crown posterior margin is pointed, creating a unicuspate, lanceolate shape. Two semi-parallel, longitudinal ridges extend from the anterior margin of the crown and converge at a point at the posterior margin, giving the scale a streamlined appearance. The bases of the Fox Hills Formation placoid scales are either not preserved or poorly preserved.

Material.—Four specimens from L35, Bowman County, North Dakota, including: ND 94-38.16 (Text-fig. 9.39; L. 0.97 mm, W. 0.92 mm), ND 94-38.15 (Text-fig. 9.40; L. 1.34 mm, W. 0.65 mm), ND 94-38 (L. 0.90 mm, W. 0.86 mm), and ND 94-38 (L. 0.91 mm, W. 0.86 mm).

Remarks.—Applegate (1967), Reif (1978, 1985), Cappetta (1987a), Welton and Farish (1993), and Shimada et al. (2006) have all pointed out that, because elasmobranch placoid scales vary within species—they are from different parts of an individual's body, and from different ontogenetic stages within a species—it is unlikely that isolated fossil placoid scales can be assignable to a genus or species. To show morphological variability in placoid scales, Welton and Farish (1993) provided an illustration demonstrating the numerous morphological placoid scale types of the extant Thresher shark *Alopias vulpinus*. Cappetta (1987a) noted that identification of fossil placoid scales to shark families may be possible after future study. Reif (1985) and Campbell (2003) speculated that fossil placoid scale 'form species' may have potential stratigraphic utility.

Minute lanceolate placoid scales have been reported from multiple stratigraphic units from several parts of the world (e.g., Cappetta, 1987a; Johns et al., 2005; Welton and

Farish, 1993; Reif, 1978; Thies, 1995; Shimada et al., 2006; Campbell, 2003; Williamson et al., 1993). But these reports have been of mostly tricuspidate or multicuspate forms. The Fox Hills Formation placoid scales are similar to a unicuspate placoid scale from the Cenomanian Woodbine Formation of Texas illustrated by Welton and Farish (1993, figure 19f). They did not speculate on the kind of shark that possessed the scale.

In general, unicuspate denticles that are very thin and have leaf-shaped cusps with an entire posterior margin occur in slow-moving sharks (such as the living triakid *Mustelus canis*) in nearshore environments where the scales appear to deter the attachments of parasites and to reduce abrasion (Cappetta, 1987a; Reif, 1988; Kent, 1994). Imbricated tricuspate and multicuspate placoid scales are found on fast-swimming pelagic and nektic sharks where they enhance water flow along the body.

Elasmobranchii Dermal Denticle Morphotype 1
Text-fig. 9.41

Description.—Elasmobranchii Dermal Denticle Morphotype 1 is small: largest specimen is 2.68 mm in greatest dimension. Base and crown semicircular to subtriangular in apical view. Base is twice as thick as crown. Crown is bulbous and smooth. Numerous well-defined ridges on the apical surface of the base radiate from the crown to the base margin.

Material.—Seven roughly circular specimens with maximum and minimum dimensions recorded (Table 2), including: ND 94-38.14 (Text-fig. 9.41; 1.77 mm x 1.75 mm), ND 99-5 (1.60 mm x 1.26 mm), ND 95-13 (2.58 mm x 2.02 mm), ND 99-5 (2.68 mm x 2.39 mm), and ND 99-5 (2.30 mm x 2.01 mm).

Remarks.—Dermal denticles are enlarged and bulbous to thorn-like placoid scales found along the midline of the back and tail in many rays (Welton and Farish, 1993). Case (1978, plate 6, fig. 8a, b) figured a dermal denticle similar to Dermal Denticle Morphotype 1 from the Campanian, Judith River Formation of Montana and referred to it as the rhinobatoid *Protolatyrhina renae*. The Judith River specimen has a semicircular base with radiating ridges like Morphotype 1, but its crown is much smaller than in our specimen. Thies (1995, fig. 6 O–L) illustrated a dermal denticle with radiating ridges on its base and a small crown from the Late Jurassic of Germany that he identified as *Asterodermus*, also a rhinobatoid. Williamson et al. (1993, fig. 14; 1, 2) figured a dermal denticle recovered from the Cenomanian–Turonian Greenhorn Cyclothem of Black Mesa, Arizona with a semicircular base containing radiating ridges similar to our Fox Hills specimen.

They referred to it as Type A dermal denticle and noted that it was similar to the denticle that Estes (1964, fig. 8d) identified as *Myledaphus bipartitus*. They suggested that the Type A dermal was more likely from one of the batoids that they had identified from teeth: *Ischyrrhiza schneideri*, *Onchoprists dunklei*, or *Pseudohypolophus mcnultyi*. Dermal Denticle Morphotype 1 is also similar to a specimen figured by Estes (1964, fig. 8d), but we also believe that Morphotype 1 is likely a batoid from one of the species that we have identified from teeth from the Fox Hills Formation, either *Protoplatyrhina renae* or *Pseudohypolophus mcnultyi*. Deynat (2000, fig. 1c) illustrated a dermal denticle with radiating ridges attributed to the modern ray *Atlantoraja castelnaui* that is similar to Dermal Denticle Morphotype 1.

In living rhinobatoids, dermal denticles are located along the back, surrounding the eyes and rostrum, and corners of the mouth; the more pointed denticles are concentrated in the most vulnerable areas (Case, 1978). Cappetta (1987a) observed that selachians that bear these kinds of strong dermal denticles with robust crowns are not fast swimmers and generally are bottom or near-bottom dwellers.

Elasmobranchii Dermal Denticle Morphotype 2

Text-figs. 10.16, 10.17

Description.—Dermal denticle large, largest specimen is 9.48 mm in length. Bilaterally symmetrical with elliptical (ovoid) outline in apical view. Limpet shaped. Ventral surface of base is concave. Numerous and distinct ridges on the base radiate from base of crown to margin of base. At least three concentric ridges or growth lines extend around perimeter of base. Laterally compressed, thorn-shaped crown is reclined and is directed posteriorly. Crown is short, about $\frac{1}{3}$ height of base. Crown is missing or broken on several specimens.

Material.—Nine specimens (Table 2), including: NDGS 1702 (Text-figs. 10.16, 10.17; H. 4.59 mm, W. 4.67 mm, L. 9.48 mm), ND 99-6 (H. 3.15 mm (broken crown), W. 3.89 mm, L. 6.35 mm), ND 99-5 (H. 2.92 mm (broken crown), W. 3.50 mm, L. 5.36 mm), ND 99-6 (H. 1.81 mm (broken crown), W. 3.88 mm, L. 3.90 mm), ND 99-6 (H. 2.21 mm, W. 1.87 mm, L. 2.24 mm), ND 99-5 (H. 2.00 mm (broken crown), W. 2.00 mm, L. 4.67 mm), ND 99-6 (H. 2.97 mm, W. 2.45 mm, L. 4.13 mm), ND 94-38 (H. 3.52 mm, W. 5.28 mm, L. 6.48 mm), and ND 95-13 (H. 3.47 mm, W. 5.31 mm, L. 7.26 mm).

Remarks.—Reif (1979) noted that only three families of living batoids, Rhinobatidae, Dasyatidae, and Rajidae, have large scales (dermal denticles). He illustrated two specimens that are very similar to one another and to Dermal Denticle

Morphotype 2, the rajid *Raja molassicus* from the Miocene Obere Meesmolasse, Switzerland, and the dasyatid *Dasyatis backler* from the Pliocene Bone Valley Formation, Florida (Reif, 1979, fig. 1, d, e; fig. 4). Case (1978, plate 6, fig. 5a, b) figured a dermal denticle that is very similar to ours from the Campanian Judith River Formation, Montana, and identified it as rhinobatoid *Myledaphus bipartitus*. Dermal Denticles A and B reported by Becker et al. (2002, fig. 5A–C; fig. 5D–H) are similar to our Fox Hills specimens, but have neither concentric growth rings nor radiating ridges on the base. The dorsal surface of Dermal Denticle A has distinct tuberculations which our specimen does not. They questionably assigned their Dermal Denticle A to the myliobatid *Brachyrhizodus wichitaensis* and their Dermal Denticle B to the rhombodontid *Rhombodus levis*. Robb (1989, fig. 17A, B and 17C, D) published schematic line drawings of two different dermal denticles from the Campanian Black Creek Formation, North Carolina. The denticle in his diagram (fig. 17A, B) is very similar to our Morphotype 2 because it is bilaterally symmetrical and appears to have radiating ridges on its base. He provisionally identified this denticle as ?*Rhombus* sp. His specimen, shown in fig. 17C, D, has tuberculations similar to Dermal Denticle A of Becker et al. (2002). Cappetta and Case (1975a, plate 9, fig. 21–23) illustrated a bilaterally symmetrical dermal denticle and questionably identified it as the myliobatid *Rhombodus levis* from the Campanian–Maastrichtian Monmouth Group from New Jersey. Although similar to our Morphotype 2, the apical surface of the base is tuberculate and is similar to Dermal Denticle A of Becker et al. (2002). Case (1987, fig. 12c) figured a large, symmetrical dermal denticle from the Campanian Mesaverde Formation from Wyoming, but this specimen—which he referred to as the myliobatid *Brachyrhizodus wichitaensis*—has distinct tuberculae similar to Dermal Denticle A of Becker et al. (2002) and is therefore different than Morphotype 2. Dermal Denticle Morphotype 2 is similar to the unidentified denticles illustrated by Bourdon et al. (2011, fig. 28K) from the Santonian Point Lookout Sandstone of central New Mexico.

Maisey and Denton (2016) described the patterning of dermal denticles in an Early Cretaceous hybodont shark, *Tribodus limae*, from Brazil. They noted that shagreen from *T. limae* possessed two distinct types and size classes of denticles that were shed, replaced, and added to during life. Fox Hills denticles of Morphotypes 2 and 3 in Text-figs. 10.16–10.21 include morphologies somewhat similar to the two denticle types illustrated by Maisey and Denton (2016, fig. 3 and fig. 7a) as hybodont denticles, and we acknowledge this general similarity. Elasmobranchii Dermal Denticle Morphotype 2 is similar to the specimen from the Montana Judith River Formation illustrated by Case (1978) as his Morphotype 3, which he referred to as the rhinobatoid *Myledaphus biparti-*

tus. Brinkman (personal communication, 2018) noted that dermal denticles of this kind do not occur in the Belly River Group in Canada where *Myledaphus* is abundant, and suggests that these denticles are from another elasmobranch.

Elasmobranchii Dermal Denticle Morphotype 3

Text-figs. 10.18–10.21

Description.—Dermal denticle with circular or subcircular outline in apical view. Largest specimen is 3.70 mm in length. Robust base with convex ventral surface. Base generally unornamented, but may have indistinct ridges radiating from the base of the crown to the margin. Margin of the base may appear serrated because of the ridge terminations. Numerous foramina occur in the base beneath crown in some specimens. Crown is variable, conical, bulbous, or thorn-shaped. The crown is erect or slightly directed posteriorly and may be flattened from wear. Most crowns are smooth, but some have folds in the enamel forming vertical ridges, primarily at the base of the crown. This dermal denticle exhibits variable morphology.

Material.—Thirteen specimens from NDGS L140 and one specimen from NDGS L148, including: NDGS 1703 (Text-figs. 10.18, 10.19; H. 2.51 mm, W. 2.43 mm, L. 2.48 mm), NDGS 1704 (Text-figs. 10.20, 10.21; H. 1.82 mm, W. 2.59 mm, L. length 2.80 mm), ND 99-5 (H. 1.02 mm, W. 2.15 mm, L. 2.2 mm), ND 99-5 (H. 3.11 mm, W. 3.16 mm, L. 3.70 mm), ND 95-7 (H. 1.45 mm, W. 1.59 mm, L. 2.10 mm), ND 99-6 (H. 1.95 mm, W. 2.15 mm, L. 2.84 mm), ND 99-6 (H. 1.39 mm, W. 1.74 mm, L. 2.0 mm), ND 99-6 (H. 1.39 mm, W. 1.88 mm, L. 1.91 mm), ND 99-6 (H. 1.32 mm, W. 1.72 mm (broken), L. 2.05 mm), ND 99-5 (H. 1.29 mm, W. 2.30, L. 2.42 mm), ND 99-5 (H. 1.26 mm, W. 1.89 mm, L. 2.11 mm), ND 95-5 (H. 1.25 mm, W. 2.17 mm, L. 2.27 mm), and ND 95-5 (H. 2.86 mm, W. 2.83 mm, L. 3.81 mm).

Remarks.—There have been several reports of dermal denticles that are similar to the Fox Hills Formation Elasmobranchii Dermal Denticle Morphotype 3. Estes (1964, fig. 8d, p. 17) illustrated a dermal denticle from the Late Cretaceous Lance Formation in Wyoming that is very similar to Morphotype 3, which he identified as the Rhinobatoid *Myledaphus bipartitus*. Similar denticles, also attributed to *Myledaphus bipartitus* by Brinkman (2004, fig. 3, pg. 7), were found with an articulated specimen of that species from the Campanian Dinosaur Park Formation, Alberta, Canada.

This type of dermal denticle has been attributed to other batoids from several localities and stratigraphic intervals, including: *Hypolophus sylvestris* from the Eocene London Clay,

England (White, 1931); *Hypolophus malembeernis* from the Miocene of the lower Congo Basin (Darteville and Casier, 1959); *Cretorectolobus olsoni* from the Campanian Judith River Formation of Montana (Case, 1978); *Rhinobatus latus* from the Late Campanian Mesaverde Formation, Wyoming (Case, 1987); rays that occur throughout the Cretaceous of Texas (Welton and Farish, 1993); a batoid from the Cenomanian–Turonian Greenhorn Cyclothem, Arizona (Williamson et al., 1993); a batoid from the Late Cretaceous Severn Formation, Maryland (Hartstein et al., 1999); unidentified chondrichthyan dermal denticles from the Campanian Dinosaur Park Formation, Alberta (Beavan and Russell, 1999); an unidentified Elasmobranchii from the Maastrichtian Breien Member of the Hell Creek Formation (Hoganson and Murphy, 2002); and a batoid from the Cenomanian Greenhorn Formation, Colorado (Shimada et al., 2006). Similar unidentified dermal denticles have been reported from the Santonian Point Lookout Sandstone, New Mexico (Bourdon et al., 2011, figs. 28A, B, F).

Elasmobranchii Dermal Denticle Morphotype 3 from the Fox Hills is from a batoid and is most likely from *Myledaphus bipartitus* based on its similarity to denticles associated with an articulated specimen reported from the Campanian Dinosaur Park Formation by Brinkman (2004). Although more highly ornamented, the *Myledaphus* sp. denticles illustrated by Cook et al. (2014, p. 239, figs. 4E, F) from the Hell Creek Formation of eastern Montana are reminiscent of denticles we have tentatively assigned here to *Myledaphus* sp. Dermal denticles that are robust and bear thorns are from taxa that live near or on the bottom of the ocean (Cappetta, 1987a).

Subclass **HOLOCEPHALI** Bonaparte, 1832
Order **CHIMAERIFORMES** Obruchev, 1953
Suborder **CHIMAEROIDEI** Patterson, 1965
Family **CALLORHYNCHIDAE** Garman, 1901
Genus **ISCHYODUS** Egerton, 1843

Type species.—*Chimaera townsendii* Buckland, 1835.

Ischyodus raybaasi Hoganson and Erickson, 2005
Text-figs. 9.37, 9.38

Mylognathus priscus (Leidy). Waage, 1968: pl.12, fig. M.

Mylognathus priscus (Leidy). Feldmann and Palubniak, 1975: p. 230, pl. 2, fig. 12.

Ischyodus sp. Hoganson et al., 1994: p. 95.

Ischyodus sp. Murphy et al., 1995: pp. 66, 73, appendix D, fig. S.

Ischyodus ?bifurcatus Popov and Ivanov, 1996: p. 55, fig. 2.

Ischyodus sp. Hoganson et al., 1996: p. 41A.

Ischyodus sp. Hoganson et al., 1997: p. 53A.

Ischyodus n. sp. Hoganson and Murphy, 2002: p. 263, fig. 12E.

Ischyodus rayhaasi Hoganson and Erickson, 2005: text-fig. 3, pl. 1, figs. 1–12.

Ischyodus rayhaasi Hoganson et al., 2015: pp. 30–34, figs. 5.1, 5.2, 5.6, 5.8.

Description.—Mandibular tooth plate (Text-figs. 9.37, 9.38) large, robust, and nearly complete except for absence of a small portion of basal margin between the median tritor and posterior outer tritor. Five tritors are present: symphyseal tritor, anterior inner tritor, median tritor, anterior outer tritor, and posterior outer tritor. An indistinct accessory median tritor is present. Median tritor is massive and unequally bifurcate. Tip of the outer branch of the median tritor is directly posterior to, and in line with, the anterior outer tritor; tip of the inner branch of the median tritor ends equal with, or extends slightly beyond, the anterior tip of the anterior outer tritor. Posterior outer tritor, anterior outer tritor, and anterior inner tritor distinct, straight, and subparallel to one another. Anterior inner tritor is on a raised, blade-like projection of the tooth plate (Hoganson and Erickson, 2005).

Palatine tooth plate triangular in shape from occlusal view, laterally compressed, and more gracile than the mandibular tooth plate (Hoganson and Erickson, 2005, p. 717, figs. 1–9). Four tritors are present: anterior inner tritor, posterior inner tritor, median tritor, and outer tritor. These vary in width, but are always closely spaced and lie in the same relative position. The anterior inner tritor is elongate; median tritor extends anterior of the posterior inner tritor; outer tritor elongate and distinctly curved (Hoganson and Erickson, 2005).

Morphology of the vomerine tooth plate is unknown due to absence of referable material.

Material.—Three tooth plates, one left mandibular, and two right palatines. The left mandibular tooth plate (ND 99-6.1; Text-figs. 9.37, 9.38) from NDGS L140 has a length of 64.39 mm, width of 29.38 mm, and thickness of 13.13 mm; the unfigured right palatine tooth plate (ND 95-13.32) from NDGS L140 has a length of 25.68 mm, width of 14.65 mm, and thickness of 7.61 mm (broken); and the unfigured right palatine tooth plate (ND 00-58.1) from NDGS L145 has a length of 30.02 mm, width of 15.38 mm, and thickness of 14.03 mm (broken). Five additional chimaeroid specimens were examined from the Fox Hills Formation, but they were too incomplete to identify further.

Remarks.—This species is present in the upper portion of the Fox Hills Formation in rocks of estuarine origin (Feldmann and Palubniak, 1975) as part of a widespread assemblage that Erickson (1974) referred to as the *Crassostrea-Pachymelania* Assemblage Zone. It represents a distinctive, geographically widespread ratfish that was present in the boreal region and

into the Volga region of Russia (Popov and Ivanov, 1996) during the latest Cretaceous.

Regionally, in South Dakota a specimen was figured by Waage (1968) from the Iron Lightning Member of the Fox Hills Formation later referred to *I. rayhaasi* (Hoganson and Erickson, 2005). In North Dakota, this species has also been identified in the Breien Member of the deltaic Hell Creek Formation (Hoganson and Murphy, 2002), a marine tongue representing a local readvance of the Fox Hills Sea probably due to distributary shifts and platform subsidence by dewatering on the Hell Creek Delta. Breien Member specimens are also associated with oyster-rich estuarine biofacies. The species is closely related to the Campanian–early Maastrichtian species *Ischyodus bifurcatus* (Case, 1978), but tritors of *I. rayhaasi* are quite distinctive. This relationship was discussed recently by Hoganson et al. (2015) regarding the occurrence of *I. rayhaasi* in the Fox Hills Formation in Colorado. Cvanca and Hoganson (1993) have shown that the *Ischyodus* present in the Paleocene marine Cannonball Formation in North Dakota is *I. dolloi*.

Class **OSTEICHTHYES** Huxley, 1880
Order **LEPISOSTEIFORMES** Hay, 1929
Family **LEPISOSTEIDAE** Cuvier, 1825
Genus Indetermined

Material.—Two unfigured, fragmentary, yet unmistakable ganoid scales (NDGS 4077 and NDGS 4078) with portions of a rhombid edge preserved from locality NDGS L140 (Table 2) are unassignable other than to family. No complete scales are present.

Remarks.—Ganoid scales of gar are a frequent component of coastal Late Cretaceous ecosystems and are to be expected from the Fox Hills Formation. They have been noted from similar settings in the Campanian Judith River Formation of Montana and from equivalent rocks in Canadian prairie provinces, where they are represented by the genus *Atractosteus* (Peng et al., 2001; Johnson and Storer, 1974), and from the Lance and Hell Creek formations of Montana and North Dakota (Estes, 1964; Bryant, 1989) where they are represented by *Lepisosteus* spp. Since these reports, Grande (2010) described differences between the scales of *Atractosteus* and *Lepisosteus*, requiring reevaluation of these reports.

In the Fox Hills Formation of South Dakota, Becker et al. (2009) have found gar scales in the Fairpoint Member.

Fossil lepisosteids are known from freshwater deposits (Wiley, 1976). Although living species occur primarily in freshwater habitats, some occupy brackish and even marine habitats (Suttkus, 1963).

Order **AMIIFORMES** Hay, 1929

Family **AMIIDAE** Bonaparte, 1838

Subfamily **VIDALAMIINAE** Grande and Bemis, 1998

Genus **MELVIUS** Bryant, 1988

Type species.—*Melvius thomasi* Bryant, 1988.

Melvius sp.

Text-figs. 12.26–12.29

Description.—Large vertebra of rather porous bone with impressed centra and laterally expanded margins, one of which is broken away, the other attenuating to a rounded point. Dorsal and ventral margins smoothly arcuate with very slight concavity in ventral profile. Ventral margin also slightly damaged on one side.

Material.—A single vertebra (UND PC-976; Text-figs. 12.26–12.29) 30.4 mm high, 38.5 mm wide, and 10.4 mm long was extracted from a concretion at site NDGS L155 (Table 2).

Remarks.—The amiid fish genus *Melvius* was described by Bryant (1988) for fish remains from the Hell Creek Formation of Montana that have a pronounced concavity of the ventrolateral surfaces of the major vertebrae (see Grande and Bemis, 1998, fig. 286). Those vertebrae show a flattened dorsal surface as well. Our specimen has a smoothly rounded dorsal surface and a very indistinct concavity conforming to that of the upper specimen of figure 288F of Grande and Bemis (1998), the type material of *M. chauliodus* from the Campanian Fruitland Formation of New Mexico.

Two nominal species are presently included in the genus *Melvius*. *Melvius thomasi* from the upper Hell Creek Formation of eastern Montana and adjacent North Dakota is the type species (Bryant, 1987 [1988]) and has been noted from freshwater deposits in both the Judith River and Hell Creek formations of the northern midcontinent of North America (Bryant, 1987 [1988], Brinkman et al., 2013, 2017). It is distinguished from *M. chauliodus* (Hall and Wolberg, 1989) by having a much more sharply defined ornamentation pattern on the postinfraorbital (Grande and Bemis, 1998). *Melvius chauliodus* is known from the Fruitland Formation of New Mexico and is thought to have been a subtropical or tropical species (Sullivan et al., 2011). The morphological differences between *M. thomasi* and *M. chauliodus* and their geographic separation may be unjustifiable based upon some recent discoveries. A nearly complete skull assigned to *M. chauliodus*—because it was taken from the same stratigraphic horizon as the type of *M. chauliodus* (Hall and Wolberg, 1989) and had the same morphological features as the type—

was found to have a more highly ornamented postinfraorbital than the *M. chauliodus* holotype. In this case, ornamentation was comparable to that of *M. thomasi* (Sullivan et al., 2011). It seems increasingly probable that discovery of more specimens may entirely erase the distinctions once drawn between the more northern *Melvius thomasi* and its southern congener *M. chauliodus*. Unassigned specimens of vidalamiine teeth and a large centrum from the Late Cretaceous Straight Cliffs Formation of Utah differ from *M. thomasi* according to Brinkman et al. (2013). Our incomplete centrum (Text-figs. 12.26–12.29) is sufficient to demonstrate the presence of *Melvius* sp. in the Fox Hills Formation, but it does not provide further illumination on the composition of the genus.

The modern related species *Amia calva* is a medium-sized ambush predator in North American temperate, lentic, and slow-moving lotic freshwater habitats (Grande and Bemis, 1998). It feeds virtually on anything that passes by, including fish, crayfish, amphibians, juvenile turtles, and other vertebrates. It breathes air from the surface and thus it tolerates poorly-oxygenated water conditions, a particularly useful trait in times of seasonal drought. Bayous and oxbow lakes today are frequented by *Amia calva*. *Melvius* sp. was an ambush predator which inhabited coastal freshwater systems, as well as marine and estuarine coastal settings. However, the Vidalamiinae were fundamentally a marine subfamily (Bryant 1987[1988], Grande and Bemis, 1998).

Subfamily **AMIINAE** Bonaparte, 1838

Genus **CYCLURUS** Agassiz, 1844

Type species.—*Cyclurus valenciennesi* Agassiz, 1844.

Cyclurus fragosus (Jordan, 1927)

Text-figs. 12.56–12.58

Kindleia fragosa Jordan, 1927: pp. 145–147, figs. 1–14.

Kindleia fragosa Jordan. Estes, 1964: pp. 29–37, figs. 15b, 16e, 17a, b, 18b.

Amia fragosa (Jordan). Estes and Berberian, 1969: pp. 1–10, figs. 1a–d, 2a, b, 3a.

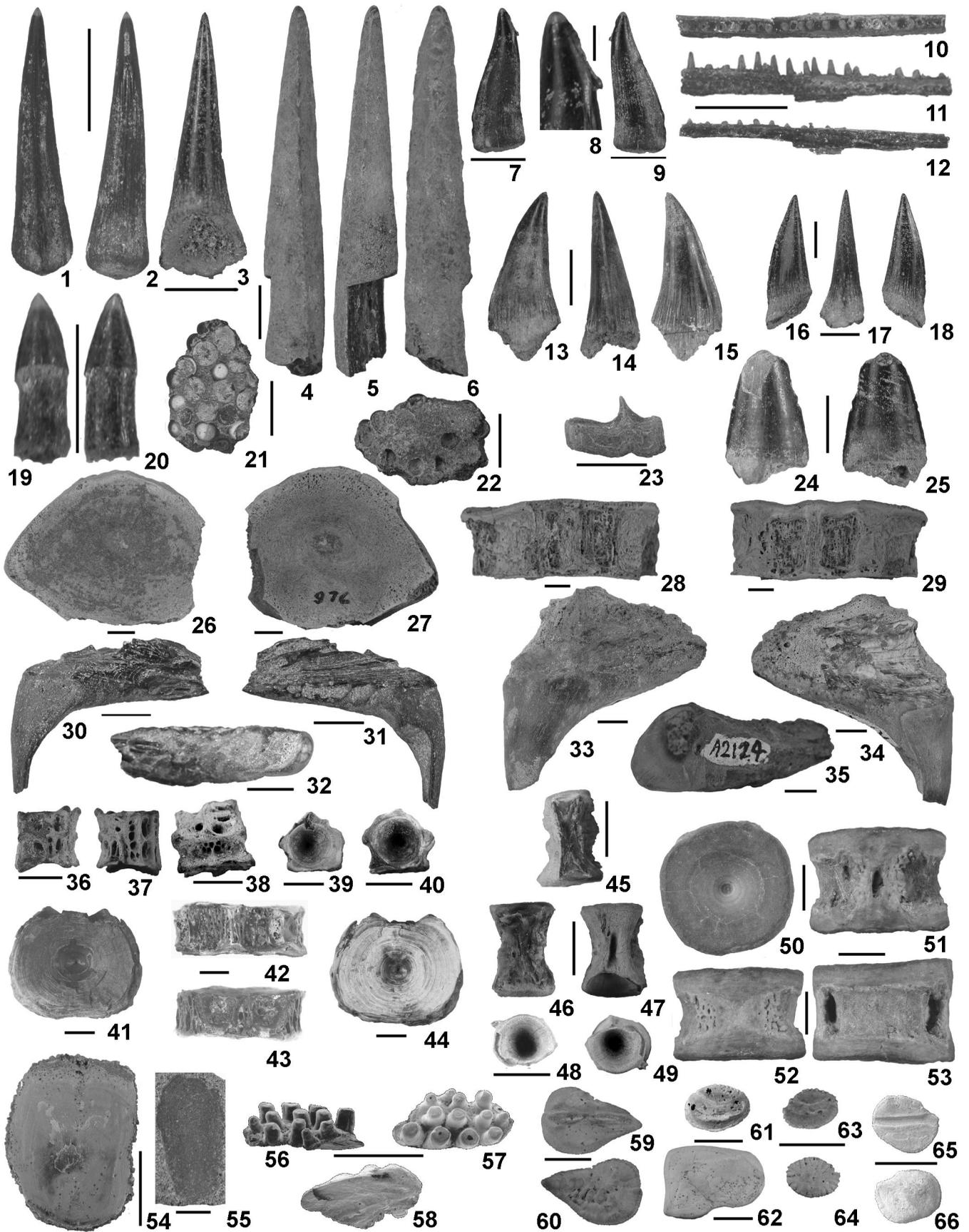
Amia fragosa (Jordan). Estes et al., 1969: p. 10.

Cyclurus fragosus (Jordan). Grande and Bemis, 1998: pp. 280–294, figs. 134A, pp. 179–188.

(Please see discussion of synonymy in Grande and Bemis 1998, p. 280.)

Description.—Thin, flat, incomplete tooth plate from an amiid coronoid complex. Teeth flat-tipped, styliform. Twelve teeth on plate, total number of teeth uncertain.

Material.—One specimen (ND 99-6.8; Text-figs. 12.56–12.58; H. 2.9 mm, W. 3.2 mm, L. 6.8 mm) screened from sediments at NDGS L140 (Table 2).



Remarks.—The modern bowfin *Amia calva* possesses several palatine and coronoid plates (Grande and Bemis, 1998) with pointed, styliform teeth for gripping prey. Estes (1964, fig. 17) illustrated the comparison of those modern *Amia calva* teeth with upper and lower batteries of teeth of *Kindleia fragosa*, an amiid from the Lance Formation of Wyoming. In 1969, Estes and Berberian suggested that *Kindleia* was a synonym of *Amia* based on numerous character comparisons. Grande and Bemis (1998) pointed out that *Kindleia* is a junior subjective synonym of *Cyclurus* (Agassiz, 1844) and that a key character separating species of *Amia* from *Cyclurus* is that individual coronoid teeth of *Cyclurus* species were flat or rounded crushing teeth, rather than pointed teeth. Our specimen is from a coronoid plate complex similar to that illustrated by Estes (1964, p. 37) for *Kindleia fragosa* (= *Cyclurus fragosus*).

Today *Amia calva* is a freshwater ambush predator that frequents shallow, warm waters of delta distributaries, lakes, and slow-flowing rivers, often with dense aquatic weed growth. We suggest, as did Grande and Bemis (1998), that the *Cyclurus fragosus* from the Fox Hills likely occupied those same habitats. However, the crushing dentition implies it was a molluscivore similar to, or conspecific with, *C. fragosus* from the Scollard Formation of Alberta (Jordan, 1927; Grande and Bemis, 1998) and the Lance Formation (Estes, 1964). The Fox Hills *C. fragosus* is Late Maastrichtian in age.

Indetermined Teleost Tooth

Species C

Text-figs. 12.19, 12.20

Description.—Crown thick, slightly compressed (both faces equally convex) with a sharp, continuous cutting edge reaching to crown foot. Both crown faces smooth, with no bulge at crown foot. Root cylindrical and simple. Crown is same length as root remnant. It is estimated that the crown length would have been not more than half the length of root. Root is hollow.

Material.—Two teeth, each with broken root (Table 2). Tooth ND 99-5.9 (Text-figs. 12.19, 12.20; H. 4.1 mm (broken), W. 1.3 mm) is from NDGS L140. Unfigured tooth ND 94-38.23 (H. 2.7 mm (broken), W. 0.7 mm) is from NDGS L35.

Remarks.—After comparison with teeth illustrated by (Grande and Bemis, 1998), these teeth seem best placed within the Amiidae, but are different than those of *Melvius*.

Order **PACHYCORMIFORMES** Berg, 1940

Family **PACHYCORMIDAE** Woodward, 1895

Genus **PROTOSPHYRAENA** Leidy, 1857

Type species.—*Protosphyraena nitida* (Cope, 1872).

Protosphyraena sp.

Text fig. 12.3, 12.13–12.18, 12.24, 12.25

Description.—Smooth, laterally compressed, heavily-enamelled, gently-curved lateral teeth with slightly flared base on which numerous fine ridges originate and pass toward the tip for approximately 5–8 mm. Lateral teeth wide at base, rapidly tapering to a point (Text-figs. 12.13–12.18). Cutting edge preserved on most, some showing breakage and wear (Text-figs. 12.24, 12.25). Teeth curve gently lingually and posteriorly. Anterior margin gently convex and formed into a sharp keel extending nearly to the tip. Anterior tooth (Text-fig. 12.3) long, very gently curved, somewhat laterally compressed with flared base possessing pattern of fine ridges similar to those noted above. Anterior margin possesses a sharp keel extending from base to tip. These teeth are commonly preserved with a high polish.

Material.—Seventy four lateral teeth and one anterior tooth (Table 2). These include: anterior tooth NDGS 1706 (presently missing from collections; Text-fig. 12.3; H. 49.0 mm, W. 16.5), lateral tooth ND 95-13.80 (Text-figs. 12.13–12.15; H. 14.67 mm, W. 6.10 mm (maximum)), lateral tooth ND 99-5.10 (Text-figs. 12.16–12.18; H. 18.66 mm, W. 7.28

← Text-fig. 12.—*Rhinobatoid and Teleosts of the Fox Hills Formation*. 12.1, 12.2, *Enchodus cf. E. ferox* Leidy, 1855 (missing from coll.). 12.3, 12.13–12.18, 12.24, 12.25, *Protosphyraena* sp.; 12.3, *mandibular? anterior tooth* (NDGS 1706); 12.13–12.15 (ND 95-13.80); 12.16–12.18 (ND 99-5.10); 12.24, 12.25 (ND 95-13.81) *lateral teeth*. 12.4–12.6, *Xiphactinus vetus* (Leidy, 1856) (ND 95-13.79). 12.7–12.9, *Enchodus dirus* Leidy, 1857 (ND 99-13.83). 12.30–12.35, *Enchodus cf. E. ferox* Leidy, 1855; 12.30–12.32 (ND 95-13.82); 12.33–12.35 (UND-PC 15907). 12.10–12.12, *Belonostomus longirostris* (Lambe, 1902) (ND 99-6.9). 12.19, 12.20, *Species C, indetermined teleost tooth* (ND 99-5.9). 12.21, 12.22, *Paralbula casei* Estes, 1969 (SLU #1804). 12.23, *Species D, indetermined bone fragment* (ND 99-6.10). 12.26–12.29, *Melvius* sp. (UND-PC 976). 12.36–12.40, *Species E vertebral morphoserries type IB-2* (Brinkman, 2004) (ND 07-78.1). 12.41–12.44, *Paratarpon? sp.* (ND 00-58.2). 12.45–12.49, *Species F vertebral morphoserries type IIIA-1 of Brinkman* (2004, p. 57, fig. 5) (ND 94-38.17). 12.50–12.53, *Species B, indetermined rhinobatid centrum* (UND-PC 15905). 12.54, *Species G, ?Amiidae scale* (ND 07-80.1). 12.55, *Species H, indetermined teleost scale* (NDGS 1707). 12.56–12.58, *Cyclurus fragosus* (Jordan, 1927) *tooth plate* (ND 99-6.8). 12.59, 12.60, *cf. Bathylagus* sp. (ND 99-6.12). 12.61, 12.63, 12.64, “*Apogonidarum*” *maastrichtiensis* Nolf and Stringer, 1996; 12.61, *right saccular otolith* (NDGS 1705); 12.63, 12.64, *left saccular otolith* (ND 99-6.11). 12.62, *Vorhisia vulpes* Frizzell, 1965, *left utricular otolith* (UND-PC 15906). 12.65, 12.66, *Pollerspoeckia siegsdorfensis* Schwarzahns, 2010 (ND 99-6.13). Scale bars are 5 mm except 12.1, 12.2 = 10 mm; 12.3 = 15 mm; 12.8 = 1 mm; and 12.19 = 3 mm.

mm (maximum)), and lateral tooth ND 95-13.81 (Text-figs. 12.24, 12.25; H. 11.57 mm (broken), W. 7.24 mm (maximum)).

Remarks.—Leidy (1857) described as *Protosphyraena ferox* teeth sent to him from the British Chalk where that species is commonly found. Cope (1872 [1873]) applied the generic name *Erisichthe* to specimens from the Niobrara Chalk of Kansas and described *E. nitida*. Subsequently, *Erisichthe* was determined to be a junior synonym of *Protosphyraena*.

The collection developed for our study contains numerous examples of the postero-lateral teeth of *Protosphyraena* (Text-figs. 12.13–12.18), but only one anterior tooth, suggesting their scarcity. The Fox Hills species was a form with gracile teeth compared to species from the Niobrara of Kansas, where there are perhaps three species of this large predator. The Fox Hills species is smaller and more gracile than *P. nitida* (Cope, 1892), *P. perniciosus* (Cope, 1874), or *P. tenuis* (Loomis, 1900).

Protosphyraena gladius has been assigned to *Protosphyraena* by several workers, most recently by Parris et al. (2007), whose specimen from the Pierre Shale is based on a pair of pectoral fins. These structures are frequently preserved in this genus. They noted that the pectoral fins of their specimen were ossified with a perpendicular fabric forming the leading edge, unlike any other *Protosphyraena* species. Interestingly, *P. gladius* has recently been removed from *Protosphyraena* and assigned to *Bonnerichthys* because, among other things, it has a different pectoral fin structure and lacks teeth of any kind (Friedman et al., 2007). It is believed to have been a large, edentulous, ram-feeding planktivore in Cretaceous seas based on a new specimen, the first preserved with a skull of '*P. gladius*' (Friedman et al., 2007).

Protosphyraena species were large Cretaceous billfish with a prolonged upper jaw similar to modern billfish, or marlin. However, unlike those, a battery of elongate, forwardly projecting anterior teeth in both jaws were significant predatory weapons that snatched prey, which were then passed back to the lateral teeth for slicing and gulping. The Fox Hills species was smaller than those of the Niobrara species complex and had unusually sharp teeth. The North Dakota material was found in estuarine sediments where smaller size may have been more effective.

This genus has not been reported from the Fox Hills Formation previously.

Order **ASPIDORHYNCHIFORMES** Bleeker, 1859

Family **ASPIDORHYNCHIDAE** Bleeker, 1859

Genus **BELONOSTOMUS** Agassiz, 1844

Type species.—*Belonostomus tenuirostris* Agassiz, 1833.

Belonostomus longirostris (Lambe, 1902)

Text-figs. 12.10–12.12

Diphyodus longirostris Lambe, 1902: p. 30.

Belonostomus longirostris (Lambe). Estes, 1964: p. 22, figs. 12–14.

Belonostomus sp. Johnson and Storer, 1974: p. 20, fig. 18.

Belonostomus longirostris (Lambe). Bryant, 1987: pp. 1–3, figs. 1A, B.

Belonostomus longirostris (Lambe). Peng et al., 2001, p. 13, pl. 3, figs. 11, 12, 17.

Belonostomus longirostris (Lambe). Forey et al., 2003: p. 244.

Belonostomus sp. Brinkman, 2004: pp. 10, 11, figs. 1, 2, 3.

?dentary fragment *Incertae sedis* Becker et al., 2009: p. 1036; p. 1014, figs. 2S, T.

Description.—Prementary (presymphyseal) with 12 teeth present and nine or ten missing aligned down the central axis of the bone. A row of much smaller teeth, lateral to the axial row, begins approximately 5 mm before the posterior break. Ventral margin of bone is incomplete.

Material.—A single jaw fragment (ND 99-6.9; Text-figs. 12.10–12.12; 14.7 mm long), from site NDGS L140 is intact and satisfactory for identification, though is broken at each end. Three additional fragments lacking teeth are present as well.

Remarks.—This delicate-toothed fish rostrum is readily recognizable as that of *Belonostomus longirostris* following the description by Estes (1964) and discussion by Bryant (1987). The lower jaw fragment illustrated herein (Text-figs. 12.10–12.12) is articulated with an upper jaw having a double row of teeth, the lower resting between the two upper rows to produce a formidable tool for predation of tiny aquatic organisms (e.g., fish larvae and insects). A section of dentary illustrated by Becker et al. (2009) has a single row of teeth similar to those of the lower jaw of *Belonostomus* and may be assignable to *B. longirostris*.

Belonostomus is one of three aspidiform genera, the other two being *Vinctifer* and *Aspidorhynchus*, distinguished by the relative lengths of upper and lower jaws and of the prementary, among other characters (Forey et al., 2003). Of these, *Belonostomus* has upper and lower jaws of the same length and a long prementary that joins the dentary at an oblique angle. The genus has a European and North American distribution from the Jurassic (Kimmeridgian) through the Cretaceous (Maastrichtian) in the northern hemisphere and includes two questionable taxa in the southern hemisphere (Brito, 1997). The genus ranged widely in North America and Europe during the Late Cretaceous.

Wilson and Chalifa (1989) illustrated a presymphyseal bone fragment from the Turonian Kaskapu Formation of

Alberta resembling that of *B. longirostris* to which they assigned it with caution. *Belonostomus longirostris* has been recognized from: the Lance Formation of Wyoming (Estes, 1964; Whitmore and Martin, 1986; Bryant, 1989); the Foremost and Oldman formations (Peng et al., 2001) and Dinosaur Park Formation (Brinkman, 2004) of Alberta; and the Judith River Formation of Montana (Stanton and Hatcher, 1905; Sahni, 1972) and Alberta (Brinkman, 1990). The genus is cosmopolitan and most species are marine. However, *B. longirostris* is a member of the estuarine and freshwater communities of the Hell Creek Delta margin in North Dakota and nearby states. It seems to have been able to traverse from marginal marine to freshwater settings in the Fox Hills Seaway (Pearson et al., 2002).

Holtzman (1978) reported a specimen of *Belonostomus* from the Paleocene Tongue River Formation in central North Dakota, thereby extending the range of the genus into the Paleogene. Bryant (1987) seems to have accepted that occurrence, remarking that Holtzman's specimen from the Hell Creek Formation in Montana resembles a 1 cm long fragment with a distinctly "pinched" dorsal margin that is not assignable to *B. longirostris*. A Paleocene range extension for the genus has not generally been accepted (Forey et al., 2003), but remains to be determined.

Order **ICHTHYODECTIFORMES** Bardack and
Sprinkle, 1969
Family **ICHTHYODECTIDAE** Crook, 1892
Genus *XIPHACTINUS* Leidy, 1870

Type species.—*Xiphactinus audax* Leidy, 1870.

Xiphactinus vetus (Leidy, 1856)
Text-figs. 12.4–12.6

- Polygonodon vetus* Leidy, 1856: p. 221.
Polygonodon rectus Emmons, 1858: pp. 218, 219.
Mossasaurus [sic] *rectus* (Emmons, 1858): p. 218.
Portheus angulatus Cope, 1872: pp. 337, 338.
Portheus angulatus Cope. Kerr, 1875: p. 32.
Polygonodon rectus Emmons. Miller, 1967: p. 229.
Xiphactinus audax Leidy, 1870. Schwimmer, 1981: p. 84, pl. 10, fig. 7.
Xiphactinus audax Leidy. Schwimmer, 1986: p. 115, pl. 1, figs. H, I.
Xiphactinus sp. Lauginiger, 1986: pp. 55, 56.
Xiphactinus sp. Gallagher et al., 1986 (partim): p. 31.
Xiphactinus sp. cf. *X. audax* Gallagher et al., 1986 (partim): p. 25.
Xiphactinus audax Leidy. Robb, 1989: pp. 77, 82, 83, fig. 20.
Xiphactinus audax Leidy. Case and Schwimmer, 1988: p. 300, fig. 6.29.
Xiphactinus audax Leidy. Manning and Dockery, 1992: pp. 12, 13, fig. 5.

Xiphactinus angulatus (Cope). Schwimmer et al., 1992: p. 51A.

Xiphactinus audax Leidy. Gallagher, 1993: p. 100, 111.

Xiphactinus vetus (Leidy). Schwimmer et al., 1997b: pp. 611, 612, figs. 2F–Y, 3G–L.

Description.—A single large tooth, broken at base, with a cutting edge (carina) forming the anterior and posterior margin around the entire tooth. A slight posteriorly-directed curvature begins approximately 1.5 mm before the tip. Tooth no longer strongly enameled, but retaining enamel along the cutting edges. If striated, it was very weakly so because no record of this remains.

Material.—One tooth, ND 95-13.79, from NDGS L140 (Text-figs. 12.4–12.6; H. 36.7 mm (broken), W. 7.0 mm at base (broken)). Though incomplete, this specimen is well preserved with lateral carina present.

Remarks.—This taxon was originally described by Leidy in 1856 as *Polygonodon vetus*. Schwimmer et al. (1997b) pointed out that *Polygonodon* was believed to have been a reptilian genus at the time and that the genus is a senior synonym of *Xiphactinus*. Those authors also recognized that *X. vetus* is a senior synonym of both *Portheus angulatus* (Cope, 1872) and *Polygonodon rectus* (Emmons, 1858), as recorded in the synonymy above, which largely follows Schwimmer et al. (1997b). They recommend retention of *Xiphactinus* as the generic name applied to this species pending an appeal to the ICZN, which is in progress. We have accepted that recommendation.

The genus *Xiphactinus*, primarily represented by *X. audax*, occurred widely throughout the Western Interior Seaway, although it is best known from well-preserved skeletons from the Smokey Hill Member of the Niobrara Formation of Kansas (Williston, 1900). It has been recorded from the top of the Mt. Laurel Formation at the Campanian-Maastrichtian boundary (Ross and Fastovsky, 2006), the Niobrara Shale (Martin et al., 1998), the Pierre Shale of South Dakota (Parris et al., 2005, 2007), and localities on the Gulf Coast (Schwimmer et al., 1997b).

Xiphactinus vetus was resurrected by Schwimmer et al. (1997b) for large, oval, carinate, lightly striated ichthyodectid fish teeth which the Fox Hills material closely resembles. Their 26 teeth were found in association with oval vertebrae distinctive from those of *X. audax*. Review of the *Xiphactinus* occurrences demonstrated that two species were present, the younger of which (middle Campanian to Maastrichtian) possessed laterally compressed teeth with anterior and sometimes posterior carinae. They note that the species has not been recognized from the Western Interior, thus making ours the first mention. Parris et al. (2007) pointed out this same relationship in a discussion of *Xiphactinus* from the Sharon Springs Member of the Pierre Formation in South Dakota.

Order **ELOPIFORMES** Greenwood, Rosen, Weitzman,
and Meyer, 1966
Family **ELOPIDAE** Bonaparte, 1846
Genus **PARATARPON** Bardack, 1970

Type Species.—*Paratarpon apogerontus* Bardack, 1970.

***Paratarpon?* sp.**
Text-figs. 12.41–12.44

Description.—A large, thin, flat centrum with dorsal convexity and slight ventral concavity exhibiting widely-spaced rib articular pits and fine antero-posteriorly oriented pits conforming to the description of Brinkman (2004, p. 24). In a previous work by Brinkman and Neuman (2002, figs. 1–13), the Judith River material was referred to as Morphoserries Group IA.

Material.—A single specimen, ND 00-58.2, represents this species of Fox Hills teleost occurring at locality NDGS L145 (W. 22.5 mm, H. 18 mm).

Remarks.—This specimen conforms well to the description of *Paratarpon* vertebrae given by Brinkman (2004) from the Judith River Group, where at least two complete skeletons are known. This was a large, freshwater, tarpon-like fish (Brinkman et al., 2013, Murray and Cook, 2016), and it is rare in the Fox Hills Formation, for which this is the first record.

Family **PHYLLODONTIDAE** Sauvage, 1875
Genus **PARALBULA** Blake, 1940

Type species.—*Paralbula casei* Estes, 1969.

***Paralbula casei* Estes, 1969**
Text-figs. 12.21, 12.22

Paralbula casei Estes, 1969: p. 323, figs. 3a–f, 6c–e.

Paralbula sp. Sahni, 1972: p. 345, figs. 7R, S.

Paralbula casei Estes. Case and Schwimmer, 1988: p. 299, figs. 6.21, 6.22.

Paralbula casei Estes cf. *Paralbula casei* Bryant, 1989: p. 26.

Paralbula casei Estes. Beavan and Russell, 1999: p. 499, fig. 17.

Paralbula casei Estes. Peng et al., 2001: p. 15, pl. 3, figs. 27–30.

Paralbula casei Estes. Becker et al., 2009: p. 1033, figs. 2E, F.

Description.—A flattened, ovoid toothplate made up of individual round domal teeth that are in irregular stacks. Each tooth has a basal rim of a slightly larger circumference than the dome, thus producing a shelf that likely marked the portion of tooth inset in cartilage. Each tooth, if unworn, possesses a set of fine ridges radiating from the center; worn teeth

in the array are larger, thinner, and smooth, often with a replacement of smaller diameter teeth exposed nearby, and with a stacked replacement enameloid crown beneath each.

Material.—Two specimens that may be part of the same toothplate are SLU #1804 collected from NDGS L159. The figured specimen (Text-figs. 12.21, 12.22; H. 3.3 mm, W. 8.8 mm, L. 12.4 mm). An unfigured specimen has dimensions H. 2.7 mm, W. 6.3 mm, and L. 6.3 mm. This fish is represented at numerous localities by individual crushing teeth, 138 of which are found in the collection (Table 2).

Remarks.—Each specimen is a cluster of teeth preserved in manganese-rich limonite-cemented sandstone, such that each individual tooth is surrounded by sand grains. It seems that the teeth were held in cartilage rather than bone and that the cartilage was replaced by cemented sand grains during preservation. There seems to be no order of ranks or placement of teeth in rows or files. Peng et al. (2001) contains a useful synonymy of *P. casei*. Formerly placed in the Albulidae, Bryant (1989, p. 74) recognized that *Paralbula* was a phylodont teleost.

We assign the specimens to *Paralbula casei* because they conform to the general diagnosis of the species, although the individual teeth are not as tightly packed as they appear in the type specimen (Estes, 1969, fig. 3a–f.), which was collected from the Harding Farm, Holmdel, Monmouth County, New Jersey in the Maastrichtian Navesink Formation. A similar tooth plate from the Fairpoint Member (Becker et al., 2009) was assigned to *P. casei* with certainty. *Paralbula casei* has also been recorded from: the Black Creek Formation (Campanian) of North Carolina (Robb, 1989); the Blufftown Formation (Campanian) of Georgia (Case and Schwimmer 1988); tentatively from the Bug Creek Ant Hills of the Hell Creek Formation, Montana (Estes, 1969); the Belly River Group (=Judith River Group) (Eberth, 2005) of Alberta (Peng et al., 2001); and from the London Clay (Eocene) of Great Britain (Estes and Berberian, 1969).

Order **ALBULIFORMES** Greenwood, Rosen, Weitzman,
and Myers, 1966

Family **PTEROTHRISSIDAE** Gill, 1893
Genus **POLLERSPOECKIA** Schwarzhans, 2010

Type Species.—*Pollerspoeckia siegsdorfensis* Schwarzhans, 2010.

***Pollerspoeckia siegsdorfensis* Schwarzhans, 2010**
Text-figs. 12.65, 12.66

“genus ? Pterothrissidarum” *bohmi* (Koeken, 1891). Nolf, 2003: p. 158.

Pollerspoeckia siegsdorfensis Schwarzhans, 2010: p. 20, figs. 6, 7a–c, 8, 9, 10; *non* Schwarzhans, 1996: p. 418, fig. 1.

Description.—Saccular otolith subrectangular with rounded margins. Lateral (external) face convex. Medial (internal) face flat or slightly convex. Lateral face smooth and uneven with weakly-crenulated margins. Thin, straight sulcus extends diagonally across entire width of medial face from corner of dorsal rim margin to corner of lower posterior rim margin. Sulcus expands abruptly into a bulb-shaped ostium. Bulb-shaped ostium is about $\frac{1}{4}$ length of sulcus. Superior crista and inferior crista are parallel until ostium expansion. Ostium opens at ostial rim.

Material.—Four otoliths from NDGS L140, including a left saccular otolith (ND 99-6.13; Text-figs. 12.65, 12.66; H. 4.4 mm, W. 5.3 mm, T. 1.4 mm) and a left saccular otolith (NDGS 4079; H. 4.9 mm, W. 5.9 mm, T. 1.5 mm).

Remarks.—*Pollerspoeckia siegsdorfensis* is reported here for the first time from the Fox Hills Formation. This taxon was initially described from the Maastrichtian of the Gerhartsreiter Grabens, Bavaria (Schwarzhans 1996, 2010). The 1996 publication illustrated this genus and species without diagnosis. Nolf (2003, p. 156) pointed out that the original use of the name provided by Schwarzhans (1996, p. 418, fig. 1) was a *nomen nudem* caused by the delayed publication of his 1993 submission to *Palaeo Ichthyologica* of a manuscript that documented many new taxa. These taxa were eventually published in 2010 with proper diagnoses (Schwarzhans, 2010), including the genus and species here discussed. We view this an unfortunate setback to the understanding of Late Cretaceous otolith taxonomy, and we advocate setting aside International Commission on Zoological Nomenclature Code 13.1.1 in this case, thereby making this name available.

Order **SILURIFORMES** Cuvier, 1816

Family **ARIIDAE** Günther, 1864

Genus **VORHISIA** Frizzell, 1965

Type Species.—*Vorhisia vulpes* Frizzell, 1965.

Vorhisia vulpes Frizzell, 1965

Text-fig. 12.62

Vorhisia vulpes Frizzell, 1965: p.180, fig. 2.

Vorhisia vulpes Frizzell. Waage, 1968: pp. 126, 127, 157, pl. 12, fig. D.

Vorhisia vulpes Frizzell. Frizzell and Koenig, 1973: p. 695, figs. 1, 3, 4.

Vorhisia vulpes Frizzell. Feldmann and Palubniak, 1975: pl. 2, fig. 18.

Vorhisia sp. Huddleston and Savoie, 1983: p. 662, figs. 2F, G.

Vorhisia vulpes Frizzell. Nolf, 1985: p. 32.

“genus Siluriformorum” *vulpes* (Frizzell). Nolf, 1985: p. 48, 133.

Vorhisia vulpes Frizzell. Hoganston et al., 1996: p. 41A

“genus Ariidarum” *vulpes* Nolf and Stringer, 1996: p. 442, pl. 2, figs. 11, 12.

Vorhisia vulpes Frizzell. Carpenter et al., 2003: pp. 71–73, figs. 2a–c.

Description.—Very large, robust utricular otolith, subrectangular in outline. Laterally and medially compressed and unequally biconvex. Lateral (outer) face more convex than medial (inner) face. Upper margin nearly straight and joining the sulcal margin at a right angle (more or less). Sulcal margin slightly concave. Antisulcal margin broadly rounded. Lower margin with distinct, broad notch near vertical midline. Sulcal margin joins the lower margin at a right angle (more or less). Medial face smooth and uneven. Lateral face is uneven and shows growth lines on most specimens. Sulcus, which is restricted to lateral face, is long, shallow, and parallels the upper and sulcal margins. Numerous closely-spaced incised radial lines accentuate the sulcus. A short, triangular pit, which becomes a faint groove, extends diagonally from the notch on the lower margin toward the upper margin, about $\frac{3}{4}$ length of otolith, on the lateral face. Internal otolith structure is radially fibrous.

Material.—Seventy-eight specimens, including right and left utricular otoliths (Table 2). UND-PC 15906 is a left utricular otolith from site NDGS L168 (Text-fig. 12.62). Size range of utricular otoliths: largest (NDGS 4080), H. 10.1 mm, W. 13.6 mm, T. 4.1 mm; smallest (NDGS 4081), H. 3.1 mm, W. 4.2 mm, T. 1.6 mm.

Remarks.—*Vorhisia vulpes*, a marine catfish (Nolf and Stringer, 1996, p. 442) and the only catfish known from the Cretaceous of North America, was first described from the Maastrichtian Fox Hills Formation of South Dakota by Frizzell (1965). Other reports of this taxon from the Fox Hills Formation in South Dakota were by Waage (1968), Frizzell and Koenig (1973), Nolf and Stringer (1996), and Carpenter et al. (2003). This taxon was initially reported from the Fox Hills Formation of North Dakota by Feldmann and Palubniak (1975) and later by Hoganston et al. (1996). It is surprising, because of its size and robustness, that the only other reported occurrence of *Vorhisia vulpes* is from the Late Maastrichtian Severn Formation of Maryland (Huddleston and Savoie, 1983; Nolf and Stringer, 1996).

Frizzell and Koenig (1973) suggested that *Vorhisia vulpes* occurred commonly in brackish water and marine benthic

communities primarily in estuarine-deltaic environments. They also speculated that this catfish may have migrated seasonally to inshore waters. Based upon carbon, oxygen, and strontium isotope studies of *V. vulpes* otoliths from the Fox Hills Formation of South Dakota, Carpenter et al. (2003) determined this fish spawned in brackish water and migrated to open marine waters in the Western Interior Seaway during their first year. After about three years they returned to the estuary, presumably to spawn and die. Their isotope studies of *V. vulpes* otoliths also indicated that the Fox Hills seawater was about 18°C, which is consistent with temperature estimates for the northern part of the Western Interior Seaway during the latest Maastrichtian. Today the giant marine catfish of the Mekong Delta, which reach lengths of three meters or more, migrate from the sea hundreds of kilometers up river; they are being fished to near extinction (Hogan et al., 2004).

Order **ARGENTINIFORMES** Johnson and Patterson, 1996

Family **MICROSTOMATIDAE** Bleeker, 1859

Genus **BATHYLAGUS** Günther, 1878

Type Species.—*Bathylagus antarcticus*, Günther, 1878.

cf. *Bathylagus* sp.

Text-figs. 12.59, 12.60

Description.—Saccular otolith is robust, strongly bi-convex, slightly asymmetrical, and tear-dropped shaped in outline. Otolith is laterally-medially curved. Margin of lateral face weakly crenulated and short, indistinct ridges radiate to margin. Interior part of lateral face pustulose. Long and narrow sulcus extends nearly the entire length of medial face and is 1/3 to 1/2 way down from dorsal rim. Constriction divides sulcus into cauda and ostium at about midpoint. Superior cristis is straight across entire sulcus. Inferior crista concave beneath cauda and ostium. Weak reticulate ornamentation occurs on medial face in well-preserved specimens.

Material.—One hundred seventy-seven otoliths including both right and left saccular forms, all from NDGS L140 (Table 2). The largest specimen, ND 99-6.12, is a left saccular otolith (Text-figs. 12.59, 12.60; H. 7.2 mm, W. 10.5 mm, T. 2.6 mm). The smallest specimen (NDGS 4082) is a right saccular otolith with dimensions H. 2.3 mm, W. 3.8 mm, and T. 0.8 mm.

Remarks.—The otoliths of cf. *Bathylagus* sp. are newly reported herein from the Fox Hills Formation. Schwarzahns (1996, 2010) described a new genus and species of bathylagid otolith, *Protobathylagus effusus*, from the Maastrichtian of the

Gerhartsreiter Grabens, Bavaria. Our specimens are more elongate than *Protobathylagus* and more closely resemble otoliths of the living *Bathylagus*.

Given the state of uncertainty in otolith systematics at present, we have assigned these specimens to the group most similar morphologically, although it seems probable that they represent a new genus. Ordinal assignment of the entire group of smelt and smelt-like fishes seems equally confusing among living representatives of these fish. Presently, the Bathylagidae are placed in the argentiniforms, or pencil smelts. A difficulty with placement of our fossils seems to be that they occurred in shallow-water settings, whereas the modern taxa of all such smelts are deep-water inhabitants (written communication, G. L. Stringer). We would point out that it is most unlikely that the WIS contained “deep water” in the same sense to which modern workers are accustomed, and thus these smelt-like fish were probably more at ease in shallow-water habitats than are their modern relatives. The present is not always a precise “key to the past” for ecological conditions or habitat preferences.

Bathylagids are small smelts which today live in deep waters throughout the oceans to depths of 1,500 meters. The Fox Hills specimens are large otoliths; compared with those of the Maastrichtian *Protobathylagus effusus* of Bavaria (Schwarzahns, 2010), they are approximately ten times larger. Therefore, it is likely that their owners were large, a rather unsmelt-like condition. The occurrence of otoliths of this family in the Fox Hills Formation may indicate a habitat shift of that family from Late Cretaceous shallow-water habitats to deep water areas of today.

Order **AULOPIIFORMES** Rosen, 1973

Suborder **ENCHODONTOIDEI** Berg, 1940

Family **ENCHODONTIDAE** Woodward, 1901

Genus **ENCHODUS** Agassiz, 1835

Type species.—*Enchodus lewisiensis* (Mantell, 1822).

Enchodus dirus Leidy, 1857

Text-figs. 12.7–12.9

Phasganodus dirus (Leidy, 1857): p. 167.

Enchodus dirus Leidy. Goody, 1976: pp. 105, 106.

Enchodus dirus Leidy. Parris et al., 2007: pp. 105–107, fig. 7.

Description.—Sigmoid, strongly striated, laterally compressed dentary teeth with complete anterior cutting edge rounding the tip and terminating 2.3 mm below the tip on posterior edge at a barb that is well developed on pristine specimens, but may be absent on some. The tooth is symmetrical ovate in cross section with striae best developed on the posterior half toward the base.

Material.—Numerous teeth assignable to *Enchodus* are present, but many are not well enough preserved to allow species assignment. The collection includes 1,155 specimens assigned to the genus (Table 2). Measurements of several specimens here assigned to *E. dirus* are given as maximum length, maximum width in anterior posterior direction, and thickness at base; largest two lack barbs. These include: ND 99-13.83 (Text-figs. 12.7–12.9; H. 13.0 mm, W. 4.8 mm, T. 3.0 mm), ND 94-38 (H. 5.9 mm, W. 1.8 mm, T. 1.2 mm), ND 94-38 (H. 8.9 mm, 3.6 mm, 2.2 mm), SLU #1815 (H. 22.6 mm, W. 5.4 mm, T. 3.5 mm), and ND 99-6 (H. 34.3 mm, W. 9.4 mm, T. 5.5 mm).

Remarks.—*Enchodus* includes several species that are found with regularity as solitary teeth in strandline deposits similar to those of the Fox Hills Formation. Our samples have many small teeth and fragmentary specimens that we have not assigned. Following the revision of Goody (1976) and the usage of subsequent workers including Grandstaff and Parris (1990), Martin et al. (1998), Shimada and Cicimurri (2006), and Parris et al. (2007), we have recognized two *Enchodus* species, *E. dirus* and *E. cf. E. ferox* in the Fox Hills material. This discussion should be applied to both species.

Those assigned herein, with reservation to *E. ferox*, are based on the characters of two incomplete palatine bones with bases of the fang-like teeth in place but the apices missing. These possess most of the properties of the palatines of *E. ferox* as defined in Goody (1976) such as straightness, asymmetrical cross section, lack of striations, and robust palatines. It is not possible to know the presence or absence of carinae on cutting edges nor of barbs. *Enchodus ferox* teeth are not barbed, thus they are readily separated from teeth of *E. dirus*, which are barbed and heavily striated. Originally defined from New Jersey, *E. ferox* is thought to be confined to the Maastrichtian (Grandstaff and Parris, 1990) and to the Atlantic Coastal Plain. Therefore, this uncertain assignment represents a potential range extension for the species into the central Western Interior. However, a single large, straight *Enchodus* “fang” illustrated by Brinkman et al. (2005, fig. 26.3A) from the Lethbridge Coal at the top of the Dinosaur Park Formation is carinate on both anterior and posterior margins throughout its length and may be an example of *E. ferox* (see also discussion of *Xiphactinus vetus* herein).

The holotype of *Enchodus dirus* is a specimen of dentary described by Leidy in 1857 from the Cannonball River of North Dakota. Nearly the entire thickness of the Fox Hills Formation was exposed along the Cannonball River at the time of the early explorations, including its lower contact with the Pierre Shale presently covered by the waters of the Oahe Reservoir. Strandline sandstone of the Timber Lake Member is presently being eroded near the river mouth and these rocks

may well have produced the type specimen. Goody (1976) noted this type locality for the specimen and cited the specimens location as at the USNM. Martin et al. (1998, p. 48) mention their re-study of the holotype, confirming the accuracy of the locality data but noting that the specimen is ANSP 5347. We have not seen the specimen, but assume it to be housed at the Academy of Natural Sciences in Philadelphia as Martin et al. (1998) suggested.

We have assigned solitary teeth in a wide range of sizes to *E. dirus*, the one illustrated (Text-figs. 12.7–12.9) being a well-preserved specimen in the middle of the range noted above. The pristine teeth are barbed, sigmoid, and strongly striated, a combination which serves to distinguish them from teeth of *E. gladiolus*, which are finely striated, long and slender, and only slightly sigmoid, and from *E. ferox*, which is also unbarbed, finely striated, but not slender (Goody, 1976; Parris et al., 2007). Becker et al. (2009) recorded two specimens of *Enchodus*, a palatine tooth and a dentary fragment, from the Fairpoint Member in South Dakota. They noted that the jaw fragment included a marginal tooth that was blunt, a morphology often diagnostic of *E. ferox*; however, Becker et al. (2009) assigned the material to *E. gladiolus*, a somewhat more variable species that occurs most widely in Cenomanian through Campanian rocks. In addition to the Fairpoint record, *E. gladiolus* is known from the Greenhorn Limestone (Shimada et al., 2006), Niobrara Shale (Martin et al., 1998), and Pierre Shale (Parris et al., 2007) in the Western Interior.

Enchodus dirus is believed to range from the top of the Santonian into the lower Maastrichtian. Its presence in North Dakota brings it at least into the *Jeletzkytes nebrascensis* Range Zone of the Western Interior. Goody (1976), Sahni (1984), and Arambourg (1952) discussed the distribution of Late Cretaceous *Enchodus* species beyond North America.

The occurrences of most complete specimens of this salmon-like genus in offshore deposits provide evidence that these fish were pelagic predators as suggested by Goody (1976). Fishman et al. (1995) also suggested that members of the genus were open water predators. Hargrave (2007) noted that two specimens of *Pteranodon* sp. from the Sharon Springs Member of the Pierre Shale contained associated vertebrae of *Enchodus* as possible stomach contents. This led her to suggest the fish were at times found near the ocean surface such that they could be captured by low-flying piscivorous reptiles. Their preservation in strandline deposits of the Fox Hills Formation implies that drifting carcasses occasionally made landfall on beaches of the Dakota Isthmus during the Maastrichtian. The genus does not seem to be found commonly in marine strand or estuarine deposits to the north and west, such as the Campanian Judith River Group of southern Alberta, Canada (Peng et al., 2001; Brinkman, 2004; Brinkman et al., 2004, 2005), with the single exception of the

palatine tooth mentioned above. Brinkman (personal communication, 2018) noted, however, that palatines and isolated teeth of *Enchodus* are relatively common in the marine shales at the top of the Dinosaur Park Formation.

Shein and Lewis (2007) recently quantified the frequency of vertebrate remains in the collections of various Alabama institutions, resulting in verification of *Enchodus* as the most frequently occurring fossil vertebrate. Apparently the Fox Hills Formation fauna is similar to those they sampled because *Enchodus* dominates numerically in this formation as well (Table 2). Data presented by Lauginiger (1986, p. 55) also verified this type of relationship in the Campanian of New Jersey. Interestingly, in Sweden, the Kristianstad Basin study by Bazzi (2014), which quantitatively assessed bulk samples, found that enchodontids were not dominant, but were considered extremely rare. Fielitz (1996) used teleost occurrences, particularly *Enchodus* spp., to generate statistical similarities of Turonian faunas within the WIS from above the Arctic Circle to Texas in an effort to develop paleobiogeographic distribution models. For the Turonian, he demonstrated both north-south differences, posited to result from currents, and east-west differences believed to result from water depth gradients being deeper in the west to shallower on the eastern side of the seaway. Further applications of *Enchodus* spp. to such studies of Campanian and Maastrichtian distributions should be pursued.

The genus ranges from the Santonian through the Maastrichtian, with the possibility of an occurrence in the Paleocene (Arambourg, 1952) which Forey et al. (2003), following Cappetta (1987b), suggest refers to reworked material from the underlying Maastrichtian Ouled Abouan phosphates in Morocco. Forey et al. (2003) recognized a new *Enchodus*, *E. mecoanalis*, from a full skeleton in the Sannine Limestone, but there are not illustrated teeth of the specimen. Distribution of *Enchodus* during the Late Cretaceous was likely global.

Enchodus cf. *E. ferox* Leidy, 1855
Text-figs. 12.1, 12.2, 12.30–12.35

Description.—Two palatine bones from different individuals, each with attached, non-striated, broken palatine fang appearing to be straight and asymmetrical at base. Surface of palatine is covered in layered enameloid, producing distinct laminations. Position of the maxillary groove is obscure and appears to be more parallel to the long axis of the palatine than oblique to it as in *E. ferox*, but incompleteness may play a role in this. In both specimens the enameloid margin of the groove distal from the tooth base is ornamented with five or six beads separated by pits. During examination, the smaller specimen separated into two pieces, further revealing the laminated condition of the enameloid. Condition of the teeth is unknown with regard to cutting edges and barbs.

Material.—*Enchodus* is represented in the Fox Hills collection by numerous complete and fragmented teeth and two palatine bones with fangs (both incomplete) having the base of the palatine tooth intact. Only the palatine fangs are here being assigned to *E. cf. E. ferox*. The larger, more massive specimen (UND-PC 15907; Text-figs. 12.33–12.35) from site NDGS L179 is 36.6 mm high, including incomplete bone and remaining tooth, and 34.9 mm long, whereas the smaller, more gracile specimen (ND 95-13.82; Text-figs. 12.30–12.32) from NDGS L140 is 16.5 mm high and 19.4 mm long. The specimen (NDGS 4083) in Text-figs. 12.1, 12.2 is missing from the collection at this time.

Remarks.—The two palatine bones with broken fangs, though different in size, are similar in morphology and are here assigned to *Enchodus* cf. *E. ferox* which represents a widespread Maastrichtian species first recognized from the No. 5 Greensand (Merchantville Fm.?) of New Jersey (Leidy, 1855; Fowler, 1911; Goody, 1976; Robb, 2004). Recently, workers have suggested that *E. ferox* was restricted to the Maastrichtian Stage (Parris et al., 2007). (See discussion under *E. dirus* above for further comparisons.) Mention of *E. ferox* from the Cenomanian Namoura chalk deposits of the Sannine Limestone of Lebanon (Forey et al., 2003) is an uncertain assignment at present.

The ordinal assignment of *Enchodus* herein follows that used by Parris et al. (2007) for Pierre Shale material from South Dakota. We recognize that some workers (e.g., Case and Schwimmer, 1988) have assigned these teleosts to the Salmoniformes, but Fox Hills specimens do not offer any information supporting this assignment.

Order **PERCIFORMES** Bleeker, 1859
Family **APOGONIDAE** Günther, 1859
Genus “**APOGONIDARUM**” Nolf and Stringer, 1996

Type Species.—“form genus Apogonidarum” *maastrichtiensis* Nolf and Stringer, 1996.

“*Apogonidarum*” *maastrichtiensis* (Nolf and Stringer, 1996)
Text-figs. 12.61, 12.63, 12.64

Apogonidae-B Huddleston and Savoie, 1983: p. 662, fig. 3C.
Apogonidae sp. 2 Stringer, 1991: p. 14, pl. 2, fig. 8.
“genus Apogonidarum” *maastrichtiensis* Nolf and Stinger, 1996:
p. 449, pl. 5, figs. 9, 10.

Description.—Saccular otolith oval to circular in outline. Lateral (outer) face smooth, uneven, and slightly convex. In smaller, younger specimens the rim of lateral face is crenulated with radiating grooves. In larger specimens the rim of the lat-

eral face is essentially smooth. Medial (inner) face is flat to slightly concave. Very wide ($\frac{1}{3}$ of medial face surface), vertically curved sulcus on inner face. Superior and inferior crista are essentially parallel in small specimens, but ostium widens in larger specimens. Ostium and cauda are about equal in length. Colliculum nearly fills ostium. In cauda, colliculum is triangular or tear-drop shape and only fills upper part.

Material.—Eight saccular otoliths all from NDGS L40 (Table 2), including: a right saccular otolith (NDGS 1705; Text-fig. 12.61; H. 4.8 mm, W. 6.7 mm, T. 1.8 mm) and a left saccular otolith (ND 99-6.11; Text-fig. 12.63, 12.64; H. 3.2 mm, W. 4.3 mm, T. 1.1 mm). The largest saccular otolith (left) (NDGS 4084) has dimensions H. 4.9 mm and W. 6.5 mm; the smallest (left) (NDGS 4085) has dimensions H. 2.5 mm, W. 3.3 mm, and T. 0.9 mm).

Remarks.—“*Apogonidarum*” *maastrichtiensis* is here newly reported from the Fox Hills Formation. This taxon has also been reported from the Maastrichtian Ripley Formation, Mississippi (Stringer, 1991) and the Maastrichtian Severn Formation, Maryland (Huddleston and Savoie, 1983; Nolf and Stringer, 1996).

Apogonidae, or cardinal fishes, are found today in the Atlantic, Indian, and Pacific oceans. They are primarily marine, but some species are found in brackish and even freshwater habitats. Today they live in tropical to subtropical environments (Huddleston and Savoie, 1983).

Teleost Incertae Sedis

Indetermined Teleost? Bone Fragment Species D Text-fig. 12.23

Description.—This is a uniquely shaped, smooth, dense bone fragment which is thin and flat in one dimension, elongate and projecting a spine-like apophysis in the other dimension.

Material.—One of three specimens is ND 99-6.10 from locality NDGS L140. It is 4.9 mm high and 7.1 mm long (Text-fig. 12.23).

Remarks.—This specimen seems stereotypical and is illustrated for completeness for future reference. It is likely a portion of the gular or gill plate structure of a teleost.

Vertebral Morphoserries Type IB-2

Species E Text-fig. 12.36–12.40

Vertebral morphoserries type IB-2 of Brinkman and Neuman (2002, p. 150, fig. 2); Brinkman (2004, p. 55, figs. 15–28).

Description.—A mid-region vertebra with deep centrum with distinctive arches.

Material.—One specimen, ND 07-78.1, with H. 7.5 mm, W. 7.7 mm, and L. 7.5 mm from locality SLU A929 (=NDGS L160).

Remarks.—A few specimens suggest presence of an esocoid fish in the Fox Hills coastal region or its fluvial tributaries, and this specimen is from that group. It seems similar to material illustrated as centra of type 1B-2 by Brinkman (2004, p. 55; see also Brinkman and Neuman, 2002). No identification is possible at this time.

Vertebral Morphoserries Type IIIa-1

Species F Text-fig. 12.45–12.49

Vertebral morphoserries type IIIA-1 of Brinkman and Neuman (2002, p. 150, fig. 8); Brinkman (2004, p. 57, fig. 5).

Description.—A group of small (caudal?) vertebrae, of which the one illustrated is nearly the largest and best preserved, that have deep circular to slightly ovoid centra with apophyses missing or badly damaged, thus making orientation difficult.

Material.—Several specimens from a sieved assortment may belong to this morphospecies, including ND 94-38.17 (Text-figs. 12.45–12.49; H. 6.2 mm, W. 5.9 mm, L. 8.3 mm) from locality NDGS L35.

Remarks.—This material most closely resembles that included in morphoserries IIIA of Brinkman and Neuman (2002), but the vertebra lack a mid-dorsal ridge between the bases of the neural arch (See also Brinkman, 2004, p. 57, fig. 5). They are included in this study as a matter of record.

Indetermined Teleost Scales

Species G Text-fig. 12.54

Description.—Teleost scale with a minimum of six major concentric growth lines evident under magnification. Scale preserved as bluish phosphatic mineral in concretionary sandstone.

Material.—One specimen (ND 07-80.1; Text-fig. 12.54; L. 11.22 mm, W. 9.01 mm) preserved in concretionary medium sandstone from locality NDGS L144.

Remarks.—The specimen somewhat resembles amiid scales.

Species H
Text-fig. 12.55

Description.—Teleost scale in friable sandstone preserved in limonite is narrowest (7.2 mm) at anterior end and expands to a width of 10.3 mm at the widest, which was coincident with the end of the overlap zone of scales anterior to it. Four mm of the scale was curved to a tip, representing the exposed posterior portion of the scale. Scale is smooth, with a very indistinct concentric growth pattern suggested.

Material.—One complete scale (NDGS 1707; Text-fig. 12.55; L. 17.54 mm, W. 10.70 mm) from a series of 15 that were mostly partials from NDGS L140.

Remarks.—This scale is distinct from the previous species and represents a different fish from the formation, one of unknown identity.

PALEOECOLOGY

Paleoecological Setting

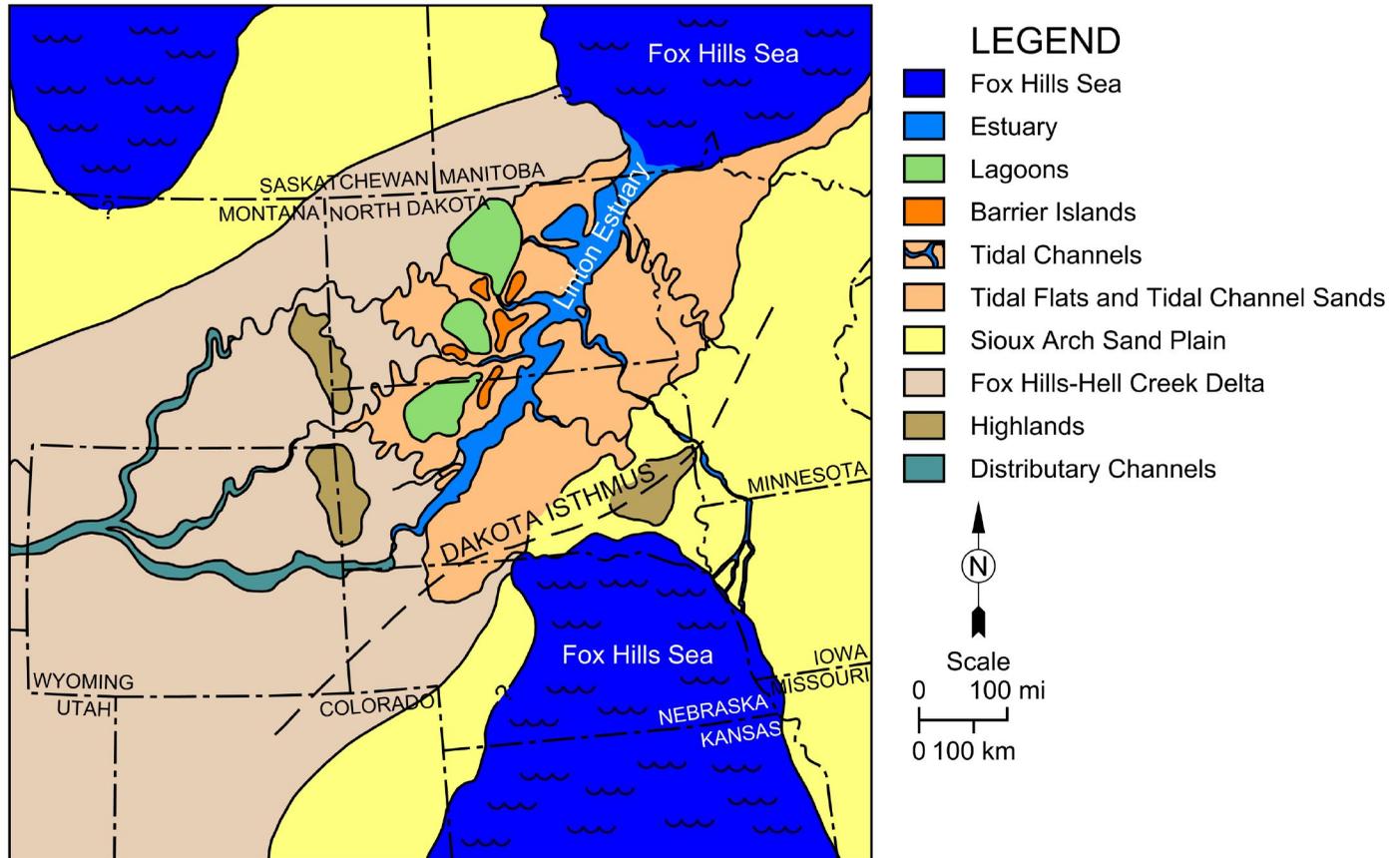
This investigation is an assessment of the youngest Late Maastrichtian coastal aquatic faunas of the North American midcontinent (Erickson et al., 2010) and also documents the eastern-most assemblage of the marginal marine vertebrate fauna of the Western Interior Seaway. Elements of this group of faunal associations (freshwater, brackish, and shallow marine) have been widely reported from Campanian and Lower or Middle Maastrichtian rocks of marginal marine strata including the Judith River, Dinosaur Park, Mesaverde, Lance, and Hell Creek formations (Brinkman, 1990, 2008; Peng et al., 1995; Brinkman et al., 2013, 2014; Cook et al., 2014). As Brinkman et al. (2004) have shown, the faunal elements of the Judith River Group and Dinosaur Park Formation (Brinkman, 2004) are loosely clustered in particular facies, allowing workers to prepare lists of taxa representative of each of their three defined habitat groups. This allowed quantitative comparison of taxon occurrences and definition of a “coastal” paleocommunity and an “inland” paleocommunity. This is less easily done in the North Dakota Fox Hills strata, where similar taxa are found, but the paleocommunity members of Brinkman (2002, 2004, 2008) are sometimes thoroughly mixed in the same bed. At Logan County site L140 (Table 2) for example, the same type of sediments contained a rich paleofauna of



Text-fig. 13.—Paleogeography of the Early Late Maastrichtian Fox Hills Sea presenting conditions as the Hell Creek Delta began to encroach upon the eastern shore of the seaway, a process which created a complex shoreline and began to isolate northern and southern portions of the former WIS (Erickson 1978, 1999), and formed the Dakota Isthmus upon closure (see Fig. 14). Map is modified from various workers including Williams and Stelck (1975), Feldmann (1972a), Erickson (1978, 1999).

tidal-flat marine invertebrates, estuarine invertebrates such as oysters, an occasional freshwater snail (*Physa* sp.), as well as a mix of vertebrates from multiple habitats (Hoganson and Erickson, 2005; Hoganson et al., 2007).

We suggest that the unusual physiographic conditions produced by the Hell Creek Delta encroaching on the near shore sand plains surrounding the Sioux Uplift (Text-figs. 13, 14) created a deposystem very sensitive to storm activity (Erickson, 1974), flooding, and related sea level fluctuations from tidal surges. The elongate arm of the Western Interior Seaway that developed along the western side of the Sioux Uplift and into which the margin of the Hell Creek Delta prograded served to connect faunas to the north with those of the Gulf Coast until the WIS withdrew sufficiently to restrict flow, producing a large estuary (Text-fig. 14). This marine-estuarine water body was tidally influenced; it fed numerous bays and lagoons that occupied the delta margin landward of the barrier islands and sand bars represented by sandstone of the Timber Lake Member of the Fox Hills Formation.



Text-fig. 14.—Paleogeomorphic details of the Dakota Isthmus including the Linton Estuary (Connett and Erickson, 1996), various bayous, lagoons, barrier bars, and tidal channels which were occupied by large populations of oysters. Deltaic setting lies to the west and tidal sand flat setting lies to the east. Image approximates time of deposition (*Wodehousia spinata* pollen zone) of the Linton Member of the Fox Hills Formation (Klett and Erickson, 1976). Barrier island morphologies and positions are based on data from Erickson (1992).

Enormous volumes of freshwater periodically inundated the lagoons and the estuary, creating notable fluctuations in salinity and sediment influx. These events occasionally produced extensive tempestite beds (Erickson, 1974). Such a setting propagated unstable habitats and mixed fossil assemblages as a result. The stratigraphic record of this interval of major environmental change was complicated further by the fluctuations of Late Maastrichtian sea level that occurred beginning with Fox Hills deposition. Because of this, the habitat and niche information of each taxon is blurred in the upper Fox Hills rocks.

The complex and dynamic deltaic setting of the Fox Hills Formation—where so many physically, chemically, and biologically varied habitats were in close proximity—provided habitats for diverse communities of animals (Tables 1, 2). This was determined by Hoganson et al. (2007) during study of the amphibian, reptilian, and avian fauna of the Fox Hills Formation, which included a mix of freshwater, marine, and terrestrial taxa. The diversity of fish taxa recovered from this formation allows detailed paleoecological analysis

and includes marine, lagoonal/estuarine, and freshwater species. This occurrence of an ecologically diverse fish fauna is attributed to the physical process of mixing skeletal parts in the dynamic depositional system. Inferences about ecological preferences of the Fox Hills Formation fish taxa can be made by comparison of these extinct taxa with living requirements of extant relatives and by comparison to other paleofaunas. Tooth morphologies of fossil material had a strong influence on these ecological decisions (Brinkman, 2008).

The marginal marine and brackish, near-shore depositional setting is indicated by the lithology of the formation and the occurrence of the mud shrimp (*Callianassa*) trace fossil *Ophiomorpha* and many mollusks, including gastropods (e.g., *Pachymelania*, *Neritina*, and *Neritoptyx*) and bivalves (e.g., *Crassostrea subtrigonalis* and *Corbicula*). The association of invertebrates, termed the *Crassostrea-Pachymelania* estuarine Biozone faunule by Erickson (1974), is further defined by the fish fauna.

Habitat Preferences

Few of the Fox Hills fish seem to have been restricted to freshwater conditions. A possible exception to that generality is the amiid *Cyclurus fragosus*, which is believed to have preferred fluvial habitats, such as rivers and oxbow lakes.

Examples of nearshore dwellers that preferred brackish to estuarine conditions are the sawfish *Ischyryhiza avoncola* and the rajiform *Myledaphus* sp. Sawfish today are nearshore dwellers and prefer brackish to estuarine conditions (Estes, 1964; Estes and Berberian, 1970), although they will enter river systems and even breed in completely freshwater habitats (Cook et al., 2014). *Myledaphus bipartitus* was probably mostly a freshwater taxon (Estes, 1964), however the occurrence of *Myledaphus* sp. in the Fox Hills Formation implies that these rays could tolerate brackish water conditions as well. Both *Myledaphus bipartitus* and *Ischyryhiza avoncola* have also been reported from fluvial deposits of the Hell Creek Formation near the shoreline of the Western Interior Seaway in south-central North Dakota (Hoganson et al., 1994) and from Hell Creek deposits further to the west in southwestern North Dakota (Pearson et al., 2002) and eastern Montana (Archibald, 1996; Cook et al., 2014). These species are also known from the Lance Formation in Wyoming (Estes, 1964).

An articulated specimen of *Myledaphus bipartitus* was described from fluvial deposits in the Dinosaur Park Formation, Alberta by Brinkman et al. (2005). They suggested that this taxon is related to extant guitarfish, which are shallow water, bottom-feeding rays often found in bays and estuaries. *Myledaphus bipartitus* was apparently euryhaline, residing in both marine and freshwater environments. As discussed earlier, this group of rhinobatoids is complicated by the addition of new generic and specific taxa, but their ecological requirements probably were similar. “*Myledaphus*” has commonly been found in Campanian and Maastrichtian deposits in the northern latitudes of the North American midcontinent.

Belonostomus longirostris is also a consistent member of the estuarine and freshwater communities of the Hell Creek Delta in North Dakota and nearby states and was likely able to traverse from marginal marine to freshwater habitats. A long, thin jaw filled with numerous simple peg-like teeth (Text-figs. 12.10–12.12) suggests this fish, perhaps 40 to 80 cm in length, was a predator of small fish and aquatic insects.

The vidalamiine *Melvius* was a taxon that could live in both freshwater and marine habitats (Grande and Bemis, 1998). It is mostly found in nonmarine Hell Creek Formation deposits (Bryant, 1987; Pearson et al., 2002). Bryant (1987, 1989) suggested that the type species, *Melvius thomasi*, probably entered marine water occasionally, but preferred residing in rivers along the margin of the Western Interior Seaway. Brinkman et al. (2013, 2017) and Sullivan et al. (2011) postulated that *Melvius* was an amiid with a more southerly distri-

bution during the Late Cretaceous. The occurrence of *Melvius* in the Fox Hills Formation in North Dakota implies that this taxon was near the northern limits of its range. In contrast, the amiinine *Cyclurus fragosus* apparently was stenotopic in freshwater (Grande and Bemis, 1998) and had a more northerly distribution than *Melvius* (Murray and Cook, 2016).

The catfish, *Vorbisia vulpes*, is another euryhaline taxon found in the Fox Hills Formation. Frizzell and Koenig (1973) noted that this species occurred commonly in brackish water and marine benthic communities, primarily in estuarine-deltaic environments and may have migrated seasonally to inshore waters. Based upon carbon, oxygen, and strontium isotope studies of *V. vulpes* otoliths from the Fox Hills Formation of South Dakota, Carpenter et al. (2003) determined that these catfish spawned in brackish water and migrated to open marine waters in the Western Interior Seaway during their first year. They probably did not migrate far upstream because the robust otoliths of *Vorbisia* have not been reported from the Hell Creek Formation, although they are common in the Iron Lightning Member near the top of the Fox Hills Formation (Waage, 1968). Alternatively, it may be that otoliths do not preserve in the Hell Creek Formation (personal communication, Newbrey, 2018).

A shallow marine and estuarine taxon recovered from the Fox Hills is the chimaeroid *Ischyodus rayhaasi*. Stahl (1999) pointed out that chimaeroids today inhabit, and did in the past, mostly nearshore marine waters. *Ischyodus rayhaasi* is found in the Fox Hills strata associated with oyster-rich estuarine biofacies (Feldmann and Palubniak, 1975) and other nearshore marine rocks in North Dakota (Hoganson and Erickson, 2005). It has also been reported from shallow marine deposits in the Fox Hills Formation in eastern Colorado (Hoganson et al., 2015) and the Breien Member of the Hell Creek Formation in south-central North Dakota (Hoganson and Murphy, 2002).

Estuaries and fresh to brackish habitats were preferred by phylloodontids (Estes, 1969; Estes and Hiatt, 1978) such as *Paralbula casei*. *Paratarpon*, a large, freshwater, tarpon-like fish and the lepisosteid gar, also mostly a freshwater fish, could tolerate brackish water (Brinkman et al., 2013; Murray and Cook, 2016). The pencil smelt, cf. *Bathylagus* sp., schooled in Fox Hills estuaries. Numerous otoliths of this smelt were recovered at site L140, indicating this life habit (Text-figs. 1, 13; Tables 2, 3). The hybodontid *Hybodus* sp. was also a nearshore to brackish water taxon (Welton and Farish, 1993; Cappetta and Case, 1999). “*Apogonidarum*” *maastrichtiensis*, a cardinal fish, seems to have preferred shallow marine conditions but ventured into brackish waters perhaps to feed or spawn.

The more obligate marine component of the Fox Hills fish fauna consisted of taxa that either inhabited shallow coastal waters or would venture into nearshore areas from

Table 3.—Habitat preferences of chondrichthyan and osteichthyan taxa from the Fox Hills Formation, North Dakota. Horizontal shading defines five habitat groupings. Vertical lines define subjective boundaries between habitats.

TAXON	MARINE WATER CONDITIONS				
	Marine	Nearshore	Open	BRACKISH WATER/ESTUARINE Strong tidal influence	RIVERINE/ LAGOONAL Weak tidal influence-strong freshwater influence
<i>Cyclurus fragosus</i>					
<i>Melvius</i> sp.					
Lepisosteidae					
<i>Paratarpon?</i> sp.					
<i>Myledaphus</i> sp.					
<i>Belonostomus longirostris</i>					
<i>Ischyrrhiza avonicola</i>					
<i>Parabula casei</i>					
cf. <i>Bethylagus</i> sp.					
" <i>Apogonidarum</i> " <i>maastrichtiensis</i>					
<i>Dasyatis northdakotaensis</i> n. sp.					
<i>Rhombodus levis</i>					
<i>Walteraja exigua</i>					
" <i>Myliobatis</i> " <i>foxhillsensis</i> n. sp.					
? <i>Hybodus</i> sp.					
<i>Squatina hassei</i>					
<i>Pollerspoeckia siegsdorfensis</i>					
<i>Ptychotrygon winni</i>					
<i>Synechodus turneri</i>					
<i>Palaeogaleus navarroensis</i>					
<i>Galeorhinus girardoti</i>					
<i>Archaeotriakis rochelleae</i>					
<i>Ptychotrygon greybullensis</i>					
<i>Ischyodus rayhaasi</i>					
<i>Cretorectolobus olsoni</i>					
<i>Ginglymostoma</i> sp.					
<i>Plicatoscyllium derameei</i>					
<i>Protoplatyrhina renae</i>					
<i>Pseudohypolophus mcultyi</i>					
<i>Squalus</i> sp.					
<i>Squalus ballingsloevensis</i>					
<i>Vorhisia vulpes</i>					
<i>Xiphactinus vetus</i>					
<i>Enchodus dirus</i>					
<i>Paraorthacodus andersoni</i>					
<i>Carcharias</i> cf. <i>C. tenuiplicatus</i>					
<i>Carcharias samhammeri</i>					
<i>Odontaspis aculeatus</i>					
<i>Protospinax</i> sp.					
<i>Cretalamna feldmanni</i> n. sp.					
<i>Serratolamna serrata</i>					
<i>Paranomotodon toddi</i>					
<i>Squalicorax pristodontus</i>					
<i>Enchodus</i> cf. <i>E. ferox</i>					

the open ocean. Triakids (or, soupfin sharks) live in warm to temperate nearshore habitats today, generally in depths of less than 2 m (Bigelow and Schroeder, 1948). The Fox Hills triakids *Palaeogaleus navarroensis*, *Galeorhinus girardoti*, and *Archaeotriakis rochelleae* occupied a similar habitat. *Squatina hassei* was also a marine coastal bottom dweller that would enter Fox Hills estuaries occasionally. *Synechodus turneri* inhabited waters of the coast and estuary. Today dasyatid rays inhabit shallow, coastal, tropical to temperate waters; it is assumed that *Dasyatis northdakotaensis* n. sp. and the rhombodontids *Rhombodus levis* and "*Myliobatis*" *foxhillsensis* n. sp. also inhabited marginal marine habitats transitional to the open ocean.

Two sclerorhynchids, *Ptychotrygon winni* and *Ptychotrygon greybullensis*, had overlapping habitat ranges and lived in both nearshore marine and estuarine settings. However, *P. greybullensis* was present at site L35 (Text-fig. 1, Table 2) which we believe to have been somewhat deeper open marine water than site L140, where they occurred together in a marginal marine habitat (Table 3).

Two squalids, *Squalus ballingsloevensis* and *Squalus* sp., were recovered from the Fox Hills Formation. Squalids today live in temperate to tropical waters to considerable depths. Siverson (1993) noted that *Squalus ballingsloevensis* inhabited shallow, temperate, coastal waters of the Kristianstad Basin during the earliest Maastrichtian. The Fox Hills *S. ballingsloevensis* also lived in shallow, near shore waters. Other near-

shore coastal taxa found in the Fox Hills include the bottom-dwelling wobbegong shark *Cretorectolobus olsoni*, the nurse sharks *Ginglymostoma* sp. and *Plicatoscyllium derameei*, the rajiforms *Protoplatyrhina renae* and *Pseudohypolophus mcultyi*, and possibly the bone fish *Pollerspoeckia siegsdorfensis*.

Related species were found to be part of a Hell Creek Formation fish fauna reported by Gates et al. (2019). They described chondrichthyan teeth removed from sediment associated with the specimen of *Tyrannosaurus rex* known as "Sue" that resides at the Field Museum of Natural History. Taxa reported are an unidentified carchariniform, a hybodontid, *Lonchidion selachos*, a new orectolobiform (*Galagodon nordquistae*), and the rhinobatoid *Myledaphus pustulosus*. Gates et al. (2019) point out the complexity of Hell Creek ecosystems represented by this association of sharks with *T. rex* and other terrestrial vertebrates. Proximity of marine and brackish habitats has been demonstrated as well by the Fox Hills vertebrates found in west-central South Dakota along the axis of the Linton Estuary (Text-fig. 14).

Several species in the Fox Hills fish assemblage are believed to have been open, deep-water taxa that would enter near shore areas primarily to feed. These include lamniforms *Carcharias* cf. *C. tenuiplicatus*, *Carcharias samhammeri*, *Odontaspis aculeatus*, *Cretalamna feldmanni* n. sp., *Serratolamna serrata*, *Paranomotodon toddi*, *Squalicorax pristodontus*, the palaeospinacid *Paraorthacodus andersoni*, the ich-

thyodectiform *Xiphactinus vetus*, the enchodontids *Enchodus dirus* and *Enchodus* cf. *E. ferox*, and the large pachycormid billfish *Protosphyraena* sp. An unusual ray, *Walteraja exigua*, generally lived in deeper nearshore areas.

Table 3 is a qualitative arrangement of the members of the Fox Hills fish assemblage according to interpretations of their habitat preferences and behaviors. Taxa are distributed by inferred depth and water conditions, ranging from open ocean to freshwater. Tidal influence was also interpreted based on sedimentological and stratigraphic relationships recognized in the field. Visual examination suggests five habitat groupings of the taxa (Table 3), riverine and lagoonal, estuarine, near-shore marine/estuarine, coastal marine, and open ocean. Table 3 illustrates the fluid nature of these associations because some species have eurytopic behavior patterns, including those that moved from marine to estuarine habitats when spawning (Carpenter et al., 2003).

Trophic Preferences

Inferences about the fish trophic community structure in the dynamic delta and shallow-marine ecological setting of the Fox Hills Sea can be made based on the fossil assemblage. This setting provided habitats for diverse freshwater, brackish water, and marine communities. Many of the fish taxa occupied the top of the food chain in nearshore habitats, although—as pointed out by Hoganson et al. (2007)—mosasaurs, marine birds, and non-marine reptiles including crocodiles, champsosaurs, and dinosaurs likely preyed on fish in this shallow marine habitat complex. The Fox Hills fish taxa can be grouped by food preference, feeding behavior, and life habit, including those that were bottom feeders and those that were pelagic (Table 4). Although most of these fish were predators, they undoubtedly scavenged to one degree or another; a few were obligatory scavengers.

Fish possessing teeth or tooth plates adapted for crushing shellfish include *Protoplatyrhina renae*, *Pseudohypolophus mc-nultyi*, *Myledaphus* sp., *Ptychotrygon winni*, *Ptychotrygon greybullensis*, *Walteraja exigua*, *Rhombodus levis*, *Dasyatis northdakotaensis* n. sp., “*Myliobatis*” *foxbillsensis* n. sp., *Ischyodus rayhaasi*, and *Cyclurus fragosus*. Phyllostodontids cruised the bottom feeding on the abundant invertebrates such as gastropods, bivalves, crustaceans, and soft-bodied animals that lived in nearshore areas (Welton and Farish, 1993; Stahl, 1999; Estes, 1969; Hoganson and Erickson, 2005; Hoganson et al., 2015). The sawfish *Ischyrrhiza* was a bottom dweller that preyed primarily on other fish, but it has been proposed that *Ischyrrhiza* would also dig into the ocean floor with its snout searching for shellfish (Welton and Farish, 1993). Triakids also fed on invertebrates, but likely preferred bony fish (Cvancara and Hoganson, 1993) (Table 4).

The apex fish predators were large ambush hunters, such as the lamniform sharks. This group included *Carcharias* cf. *C. tenuiplicatus*, *Carcharias samhammeri*, *Odontaspis aculeatus*, *Cretalamna feldmanni* n. sp., *Serratolamna serrata*, and *Paranomodon toddi*. These taxa possessed sleek, streamlined bodies, were fast swimmers, and exhibited sharp, pointed, flesh-ripping teeth. Another of the large lamniform predators was *Squalicorax pristodontus*. Based on skeletal analysis and the morphology of their placoid scales, Shimada and Cicimurri (2005) determined that species of *Squalicorax* were fast swimmers and similar to the living tiger shark, *Galeocerdo*, in their feeding habits. It possessed serrated teeth with posteriorly directed cusps similar to *Galeocerdo*. *Squalicorax* spp. have also been documented as scavengers. Schwimmer et al. (1997a) determined that *Squalicorax* scavenged carcasses of large marine animals during the Late Cretaceous based on gnaw marks on plesiosaur bones and even embedded teeth in a juvenile hadrosaur metatarsal and a plesiosaur rib. Other important apex predators in the Fox Hills Sea were *Protosphyraena* sp. and *Xiphactinus vetus*. *Protosphyraena* sp. may have used its bill to slash and disable prey in the same manner as billfish do today.

Other smaller predaceous sharks include the dogfish sharks *Squalus ballingsloevensis* and *Squalus* sp. Squalids today primarily feed on bony fish, but also eat other sharks, invertebrates, and even mammals (Compagno et al., 2005). They are also scavengers, a trophic style which has been recorded in the fossil record. *Squalus* teeth have been found in great numbers associated with skeletons of marine reptiles. Hoganson et al. (1999) reported that *Squalus* teeth were found with a skeleton of *Plioplatecarpus* from the Pierre Formation in North Dakota, and gnaw marks attributed to *Squalus* were found on the *Plioplatecarpus* bones. Other reports of fossil *Squalus* scavengers were by Martin and Fox (2007) and Bardet et al. (1998). Another of the small shark predators was the angel shark *Squatina hassei*. Angel sharks are coastal bottom-dwelling ambush predators (Stelbrink et al., 2010). The nurse shark *Plicatoscyllium derameei* probably occupied a similar niche as modern ginglymostomatids living in the littoral zone, feeding on bottom-dwelling invertebrates and small fish (Compagno et al., 2005). *Cretorectolobus olsoni*, similar to modern wobbegong sharks, was also a bottom dwelling predator.

Table 4 was constructed by inferring trophic behavior for each taxon and by arranging the resulting groupings into six guild-like categories. These are: omnivores, general invertebrate feeders, molluscivores, pelagic piscivores, benthic piscivores, and obligatory scavengers. We arranged these based on dental characteristics, systematic relationships with modern sharks, fossil evidence, reference to published reports, and personal communications. As with habitat interpretations (Table 3), trophic behaviors of some taxa were surely broad-

Table 4.—Trophic preferences of chondrichthyan and osteichthyan taxa from the Fox Hills Formation, North Dakota. Habitat groupings, as indicated in Table 3, separated by horizontal shading from top down, include riverine/lagoonal-strong freshwater influence, brackish water/estuarine-weak tidal influence, brackish water/estuarine-strong tidal influence, nearshore marine, and open ocean.

TAXON	OMNIVORES	GENERAL INVERTEBRATE	MOLLUSCIVORES	PELAGIC PISCIVORES	BENTHIC PISCIVORES	SCAVENGERS
<i>Cyclurus fragosus</i>						
<i>Melvius</i> sp.						
Lepisosteidae						
<i>Paratarpon</i> ? sp.						
<i>Myledaphus</i> sp.						
<i>Belonostomus longirostris</i>						
<i>Ischyrhiza avonicola</i>						
<i>Parabula casei</i>						
? <i>Bathylagus</i> sp.						
" <i>Apogonidarum</i> " <i>maastrichtiensis</i>						
<i>Dasyatis northdakotaensis</i> n. sp.						
<i>Rhombodus levis</i>						
<i>Walteraja exigua</i>						
" <i>Myliobatis</i> " <i>foxhillsensis</i> n. sp.						
? <i>Hybodus</i> sp.						
<i>Squatina hassei</i>						
<i>Pollerspoeckia siegsdorfensis</i>						
<i>Ptychotrygon winni</i>						
<i>Synechodus turneri</i>						
<i>Palaeogaleus navarroensis</i>						
<i>Galeorhinus girardoti</i>						
<i>Archaeotriakis rochelleae</i>						
<i>Ptychotrygon greybullensis</i>						
<i>Ischiodus rayhaasi</i>						
<i>Cretorectolobus olsoni</i>						
<i>Ginglymostoma</i> sp.						
<i>Plicatoscyllium derameei</i>						
<i>Protoplatyrhina renae</i>						
<i>Pseudohypolophus mcultyi</i>						
<i>Squalus</i> sp.						
<i>Squalus balingsloevensis</i>				???		
<i>Vorhisia vulpes</i>						
<i>Xiphactinus vetus</i>						
<i>Enchodus dirus</i>						
<i>Paraorthacodus andersoni</i>						
<i>Carcharias</i> cf. <i>C. tenuiplicatus</i>						
<i>Carcharias samhammeri</i>						
<i>Odontaspis aculeatus</i>						
<i>Protosphyraena</i> sp.						
<i>Cretalamna feldmanni</i> n. sp.						
<i>Serratolamna serrata</i>						
<i>Paranomotodon toddi</i>						
<i>Squalicorax pristodontus</i>						
<i>Enchodus</i> cf. <i>E. ferox</i>						

er than we have indicated in Table 4. Even so, the resulting guild-like groupings are useful when interpreting the complexity of the Fox Hills fish paleofauna. By using the habitat groupings derived from Table 3, it can be recognized that each habitat grouping contains species from most guilds as might be expected (Table 4).

The most impressive of the bony fish predators was the ichthyodectiform *Xiphactinus vetus*. This colossal fish could grow to lengths of five meters or more and possessed long, spike-like fangs (Text-figs. 12.4–12.6) that were used to prey on other large fish, and in turn it was preyed upon by sharks. Other open-water, salmon-like pelagic predators below the apex were the enchodontids *Enchodus dirus* and *Enchodus* cf. *E. ferox* (Goody, 1976; Fishman et al., 1995). Both of these species had palatine fangs for stabbing and holding prey as shown by Bishop (1972), who demonstrated predation by an

enchodontid upon crabs from the Pierre Formation. Their teeth are often abundant, suggesting that they were present in high numbers, probably as shoaling fish in the Late Cretaceous oceans worldwide.

Table 4 lists several smaller “bait fish” that served as prey, including the pencil smelt cf. *Bathylagus* sp., the bone fish *Pollerspoeckia siegsdorfensis*, and the cardinal fish “*Apogonidarum*” *maastrichtiensis*, represented by otoliths in the Fox Hills sediments. They were likely eaten by both apex and lower tier predators. Numerous small fish vertebrae, rib, other bone fragments, and scales are included in our collections, but remain unidentified (Text-figs. 12.36–12.40, 12.45–12.49, 12.54, 12.55, and 12.59–12.66). They represent additional species that belong to the cohort of “bait fish” upon which middle tier predators fed.

Although primarily freshwater fish, the lepisosteids also inhabited brackish and marine habitats (Suttkus, 1963). Living longnose gars are ambush predators that suspend among dense aquatic vegetation where they await small fish, which they strike using a lateral movement of their elongated, tooth-filled jaws (Becker, 1983, p. 247). *Melvius* sp. probably had similar life habits to the living *Amia*. It was a medium-to-large-sized, freshwater ambush predator that fed as a gulper on anything that passed by, including fish, crayfish, amphibians, juvenile turtles, and other vertebrates (Grande and Bemis, 1998). Modern *Amia calva* also scavenges dead fish and invertebrates (Becker, 1983, p. 253). We infer that *Melvius* sp. behaved similarly. It would have inhabited distributary channels, lagoons, and bays along the coastline of the Fox Hills Sea.

Important as it is to note from Table 4 how habitats were filled by various guilds, we find it important also to recognize where some guilds were unrepresented. The brackish water/estuarine–weak tidal habitat was missing omnivores, scavengers, and benthic piscivores (Table 4). Of course, fossils of these guild members may remain to be discovered, but we suggest that this habitat, as well as the guild of scavengers in the adjacent estuarine–strong tidally influenced habitat was likely populated by transitory hunters entering coastal bays and estuaries on a rising tide to feed and then departing as the tide changed. This feeding scenario is commonplace today and numerous species are involved in such transitory hunts.

The prevalence of molluscivores in estuarine and near-shore habitats is expected given the rich bivalve (Speden, 1970; Feldmann, 1972a) and gastropod (Erickson, 1974) faunas of the coast and estuaries (Feldman and Palubniak, 1975). Cephalopods were also very numerous at times and they were surely part of the diets of shell crushers in this habitat (Landman and Waage, 1993). These invertebrates represented a very substantial food resource for many of the WIS fish.

Weaker representation by the scavenger guild throughout the Fox Hills fauna (Table 4) may suggest that invertebrates such as crabs, lobsters, and ammonites—or alternatively larger vertebrates such as birds or turtles known to have been in the fauna (Hoganson, et al., 2007)—were filling that function close to shore.

The nearshore marine habitat had the most even distribution of feeding types. Seaward we find a sharp decrease in molluscivores and benthic piscivores where benthic invertebrate populations likely declined, but a commensurate increase in the number of pelagic piscivores is demonstrated (Table 4). This increase is driven largely by sharks.

We believe the Fox Hills Sea supported a balanced distribution of chondrichthyan and osteichthyan feeding guilds within the context of the larger marine and estuarine vertebrate communities of the WIS.

PALEOGEOGRAPHY

Physical Geography

Perhaps the most significant factor influencing conditions of marine climate, chemistry, current directions, oceanic temperature and, as a result, continental temperatures and climate in the central portion of the North American paleocontinent (roughly 43 to 47 degrees of north paleolatitude) was the sequence of paleogeographic events leading to the closing of the Western Interior Seaway during the Late Maastrichtian. The development of the Dakota Isthmus (Erickson, 1978, 1999) profoundly influenced both terrestrial and marine habitats because it became not only a barrier to fish migrations and marine currents (Wright, 1987; Kauffman, 1975, 1985; Marinovich, 1993; Roberts and Kirschbaum, 1995) between the Gulf Coast and the Arctic Ocean, but also a land bridge between the paleocontinents of Laramidia and Appalachia (Archibald, 1996), the first such crossing point in 70 million years (Text-fig. 13). It thus had both regional and global impacts upon faunal distributions.

Reconstructions of the Western Interior Seaway, in fact the early uses of the term as a paleogeographic feature, were stimulated by the publication of a map (schematic by today's standards) of the Cretaceous Seaway by Reeside (1944) in support of early work on the stratigraphy and biostratigraphy of Cretaceous deposits of the Western Interior. Reiterations of the map appeared for many decades before more detailed research began to add nuances to the coastline suggesting additional pathways for the marine waters (Williams and Stelck, 1975). The growing importance of marine geochemistry (Turtletot and Rye, 1969) has led in turn to the need for a better understanding of seaway morphology, depth, and current and tidal flow. Gill and Cobban (1973) recognized the geologic and paleogeographic significance of the Sheridan Delta (Hell Creek Delta), which prograded rapidly eastward from the rising Rocky Mountains of western Wyoming and Montana and was the source of a vast amount of sediment comprising alluvial–coastal plain and deltaic deposits (Judith River, Lance, and Hell Creek formations) in Campanian and Maastrichtian time.

Progradation of the Hell Creek Delta resulted in rapid migration of marine shorelines across the seaway. These were documented by Gill and Cobban (1973) using first occurrences of baculite range zones, as they were found at the top of shale deposits in contact with overlying shoreface sandstone units eastward to the type area of the Fox Hills Formation. The northeast-southwest strike of shoreline features (Bailey and Erickson, 1973) and sediment transport directions on barrier islands of the Timber Lake Member (Chayes and Erickson, 1973) document wave and current directions, as well as the orientation of the prograding delta front in the Missouri River

Valley region. From that position in the Missouri River Valley of South Dakota, the Late Maastrichtian rocks are absent due to glacial erosion or are covered by glacial debris, a result of control by the presence of the Transcontinental Arch, the Sioux Arch, or its surficial expression termed Sioux Ridge, a feature of the eastern shoreline of the WIS (Shurr et al., 1994). An outcrop of the Elk Butte Member of the Pierre Formation containing Late Maastrichtian ammonite zones was reexamined and its fauna discussed by Kennedy et al. (1998). This outcrop, located on the southeastern flank of the Sioux Arch, provides evidence that the closing of the Dakota Isthmus was imminent. Kennedy et al. (1998) noted that previous workers assigned these interbedded sandy silt and silty clay strata to the basal Fox Hills Formation. The Late Maastrichtian scaphite *Hoploscaphites nebrascensis* was reported from this fauna, indicating that foreset beds of the Hell Creek Delta had reached the southeastern edge of South Dakota by the time the Timber Lake Member beaches and barrier islands were formed in south-central North Dakota, as noted in the discussion of biostratigraphy herein.

The discussion regarding erosional intervals within the Fox Hills Formation 333 km to the west (Stoffer et al., 1998; Hartman et al., 2014) becomes significant because it suggests the sensitivity of Fox Hills deposition to either structural uplift, sea level fluctuation, or both as coastal progradation was occurring. The Iron Lightning Member lagoonal and estuarine facies (Waage, 1968; Feldmann, 1972a) in the Fox Hills Formation advanced rapidly over the type area in South Dakota and North Dakota to prograde against the Sioux Arch. The Linton Member of the Fox Hills Formation represents the earliest of multiple estuarine sandstone and siltstone deposits containing fragmented ammonite remains of the *Hoploscaphites nebrascensis* Zone (Klett and Erickson, 1976; Frye, 1964). At this point, the Dakota Isthmus was effectively closed. The paleogeographic configuration of the region appeared much as shown in Text-fig. 14.

The importance of paleogeography to the distribution of vertebrate faunas found in the Fox Hills Formation lies in the increasing abundance of lagoonal and estuarine sediments encountered in the eastern portion of the research area (Text-figs. 1, 14). It is also important to recognize that slight fluctuations of Late Maastrichtian sea level resulted in marine inundation of at least portions of the Dakota Isthmus, thus re-connecting the northern and southern arms of the WIS for varying periods of time. The Breien Member and Cantapeta Tongue of the Hell Creek Formation provide evidence for these events (Frye, 1964; Hoganson and Murphy, 2002; Murphy et al., 2002). The prominent feature of the seaway in both North Dakota and South Dakota during the latest Maastrichtian was a large estuary elongated parallel to the axis of the Sioux Arch (Text-fig. 14). This was termed the Bullhead Estuary by Connert

and Erickson (1996), but it is more appropriately described as the Linton Estuary for reasons of chronology, depositional conditions, and geographic extent of the Linton Member estuarine sandstone (Klett and Erickson, 1976). Local plant and animal distributions, such as mammals (Lillegraven and Ostresh, 1990), were controlled by the presence or absence of this estuary system as the Cretaceous sea receded from the midcontinent. The mixing of faunas of marine and estuarine origin was a result of this configuration.

An effect noted several times (Erickson, 1974; Kennedy and Cobban, 1976; Kauffman, 1977; Bouchard et al., 2002; Carpenter et al., 2002; Harries et al., 2008; Petersen et al., 2016) was the presence of freshwater influx into the Fox Hills Sea and Linton Estuary as the upper portion of the Fox Hills Formation was being deposited. For 150 years (Meek and Hayden, 1856), composition of invertebrate faunas has demonstrated the brackish water quality. Chemical and physical parameters of the Fox Hills Sea by applications of isotope geochemistry were originally studied by Turtelot and Rye (1969). As the paleogeographic complexity of the WIS in the Late Maastrichtian is increasingly understood, isotope studies of marine and estuarine water chemistry have likewise become more numerous and more sophisticated (Bouchard et al., 2002; Carpenter et al., 2002; Cochran et al., 2003; Dennis et al., 2013). Clumped isotope techniques have now demonstrated the freshwater, brackish water, and marine salinity values of the Fox Hills Sea using the pristine molluscan fossils of the formation (Petersen et al., 2016). Brackish waters were 11–26 psu (practical salinity units) (Fofonoff, 1985), whereas open marine, shallow waters were 20–32 psu and deep waters were 29–35 psu. These compare with marine values of 28–35 psu in the Maastrichtian Gulf of Mexico (Peterson et al., 2016).

Although this discussion has focused on the local effects of paleogeography, the more profound implications are those that altered marine and terrestrial paleoclimate for the entire midcontinent region. Most workers have agreed that the WIS was flushed by both a south-flowing, cool, boreal Arctic current and a north-flowing, warm, Tethyan or Gulf Coastal current (Kauffman, 1973; Wright, 1987; Slingerland et al., 1996). Interruption of those currents resulted in a cooler marine basin north of the Dakota Isthmus and a warmer basin to the south. Presence in Emmons County of the boreal marine bivalve *Arctica* sp. (Erickson, 1978) as well as distributions of Fox Hills gastropods (Sohl, 1971; Erickson, 1973) support the strengthening of a boreal influence during the middle Late Maastrichtian. This is the southern most occurrence of *Arctica* during the Late Cretaceous. However, the genus was a prominent member of the Bearpaw Shale fauna in southern Alberta, along with ammonites *Hoploscaphites* spp. and *Jeletzkytes* spp. (Birkelund, 1965; Riccardi, 1983). Jeletzky (1971) thorough-

Table 5.—Maastrichtian geographic ranges and correlation of Fox Hills chondrichthyan and osteichthyan taxa from North Dakota. Occurrences are noted by "FW" (Freshwater), "S" (Shallow Marine), and "D" (Deep Marine). Correlations to other North American Maastrichtian fish faunas, indicated on right columns in bold, and are denoted by "X".

TAXON	ALBERTA, SASK., CA	NORTH DAKOTA	WESTERN INTERIOR SEAWAY	TEXAS GULF COAST	MISSISSIPPI EMBAYMENT	ATLANTIC COAST	EUROPE	SWEDEN	NORTH AFRICA	KEMP FM.	ARKADELPHIA FM.	SEVERN FM.	NAVESINK, NEW EGYPT
<i>Melivius</i> sp.	FW	FW	FW										
<i>Cyclurus fragosus</i>	FW	FW	FW										
<i>Paratarpon?</i> sp.	FW												
<i>Myledaphus</i> sp.	FW	S, FW	S, FW										
<i>Belonostomus longirostris</i>	FW	S, FW	S, FW										
<i>Paralbula casei</i>		S,FW	S,FW			S,FW							X
<i>Ischyrhiza avonicola</i>		S,FW	S,FW	S,FW	S,FW	S,FW				X	X	X	X
<i>Enchodus dirus</i>	S	S											
" <i>Myliobatis</i> " <i>foxhillsensis</i> n.sp.		S											
<i>Dasyatis northdakotaensis</i> n.sp.		S											
<i>Archaeotriakis rochelleae</i>		S											
<i>Synechodus tumeri</i>		S											
<i>Ptychotrygon greybullensis</i>		S	S										
<i>Ptychotrygon winni</i>		S		S						X			
<i>Cretorectolobus olsoni</i>		S	S	S						X			
<i>Palaeogaleus navarroensis</i>		S	S	S						X			
? <i>Hybodus</i> sp.	S	S	S		S								
<i>Squatina hassei</i>		S	S	S	S	S	S			X	X		X
<i>Plicatoscyllium derameei</i>		S		S	S	S			S	X	X	X	
<i>Galeorhinus girardoti</i>		S	S		S	S				X	X	X	
" <i>Apogonidarum</i> " <i>maastrichtiensis</i>		S			S	S					X	X	
<i>Protoplatyrhina renae</i>		S	S	S		S				X			X
<i>Pseudohypolophus mcultyi</i>		S	S			S					X		
<i>Rhombodus levis</i>		S				S							
<i>Ischyodus rayhassi</i>		S	S				S						
<i>Vorhisia vulpes</i>		S				S					X		
<i>Enchodus</i> cf. <i>E. ferox</i>		S				S							X
<i>Walteraja exigua</i>		S						S					
<i>Pollerspoeckia siegsdorfensis</i>		S					S						
<i>Paraorthacodus andersoni</i>		S					S	?S					
<i>Xiphactinus vetus</i>		D											
<i>Carcharias</i> cf. <i>C. tenuiplicatus</i>		D											
<i>Cretalamna feldmanni</i> n.sp.		D											
<i>Paranomotodon toddi</i>		D			D					X			
<i>Carcharias samhammeri</i>		D			D	D				X			X
<i>Odontaspis aculeatus</i>		D	D		D	D					X	X	X
<i>Serratolamna serrata</i>		D	D		D	D	D		D	X	X	X	X
<i>Squalicorax pristodontus</i>		D			D	D	D		D	X		X	X
<i>Squalus ballingslovensis</i>		D						D					

ly documented a boreal province in Canada during the Late Cretaceous by mapping ammonite distributions. This fauna also supports geographic connections of the seaway with western Greenland during the Late Maastrichtian (Rosenkrantz, 1970; Birkelund, 1965). A connection remained there into, or recurred during, the Paleocene with invasion into North Dakota of the Cannonball Sea (Rosenkrantz, 1970; Feldmann, 1972b; Erickson, 1978). Presence of this boreal, cool water mass created more complicated continental climates. The same marine connections provided potential mi-

gratory pathways for members of the Fox Hills fish fauna as discussed below.

Fox Hills freshwater and estuarine osteichthyan and chondrichthyan taxa were dominantly a part of the Western Interior coastal and deltaic community equivalent to the central WIS subprovince of Nichols and Russell (1990). Gulf Coast/Atlantic Coast shark and ray communities (Table 5) indicate persistent influences of warm water of Tethyan affinity on shallow marine species. Few of these crossed to or from Europe. Deep water, or open ocean species, demonstrate

global geographic distributions through the Tethyan low latitude ocean. Importantly, a minor portion of the fauna including *Walteraja exigua*, *Paraorthacodus andersoni*, *Squalus ballingsloevensis*, and perhaps *Ischyodus rayhaasi* are present only in Scandinavia or the circumpolar region of Europe (Siverson, 1993; Siverson and Cappetta, 2001; Hoganson and Erickson, 2005).

This distribution is better reflected by Maastrichtian cool water invertebrate faunas of West Greenland (Birkelund, 1965; Rosenkrantz, 1970). Species of *Hoploscaphites* are part of the Western Interior endemic ammonite fauna (Birkelund, 1965; Kennedy, 1986) but few sharks have been collected from the Greenland Maastrichtian. *Lamna* (= *Cretalamna*) *appendiculata* (Rosenkrantz, 1970) is present and also found in the Breien Member of the Hell Creek Formation (Hoganson and Murphy, 2002). By the Danian, this boreal connection was strongly established among both vertebrate and invertebrate faunas (Rosenkrantz, 1970; Bendix-Almgreen, 1969; Feldmann, 1972b; Marinovich, 1993). Shark species held in common between the Paleocene Cannonball Formation of North Dakota and the Danian of West Greenland include *Paraorthacodus eocaenus* (Leriche), *Megasqualus orpiensis* (Winkler), *Squalus minor* Daimeries, *Palaeogaleus vincenti* (Daimeries), and *Palaeohypotodus rutoti* (Winkler). These represent nearly half of the post-extinction Danian chondrichthyan fauna of North Dakota (Bendix-Almgreen, 1969; Cvanara and Hoganson, 1993). This increase reflects long duration establishment of the boreal connection of the Cannonball Seaway through cold water regions, likely using the Hudson Bay channel (Text-fig. 13).

Paleobiogeography

The geographic distribution of Maastrichtian Fox Hills fish taxa includes species that are endemic to the northern WIS and only found in the Fox Hills Formation of North Dakota, taxa that range throughout the WIS, those that also occur in the Texas-Gulf Coast, Mississippi Embayment and Atlantic Coast Plain, species found in Alberta and Saskatchewan, south-central Canada, and those reported from Europe and north Africa (Table 5). The majority of Fox Hills taxa occur only in the United States and south-central Canada; however, a few are wide-ranging. This fauna includes several species that represent new geographic occurrences for North Dakota or for the WIS. New WIS occurrences include *Cretalamna feldmanni* n. sp., *Dasyatis northdakotaensis* n. sp., “*Myliobatis*” *foxbillsensis* n. sp., *Paranomotodon toddi*, *Rhombodus levis*, *Walteraja exigua*, *Xiphactinus vetus*, *Enchodus* cf. *E. ferox*, “*Apogonidarum*” *maastrichtiensis*, and *Pollerspoekia siegsdorfensis*. Origins of these WIS neophytes are evenly divided between boreal (Sweden, Bavaria) and Tethyan (Texas Gulf Coast, Mississippi Embayment) source areas. This emphasizes

that both biotic provinces were contributing new faunal elements to the Fox Hills Sea as the Dakota Isthmus was in the process of closing. Distribution of the three new species has not been tested.

The majority of Fox Hills fish that occurred in freshwater and brackish water habitats also commonly occurred in Canadian portions of the WIS in the Dinosaur Park Formation and in the Campanian Judith River Formation adjacent to the western margin of the Fox Hills Sea, with the exception of *Ischyrbiza avonicola* which is also recovered from Maastrichtian strata from the Texas Gulf Coast to the Atlantic Coast of New Jersey (Table 5). None of these freshwater taxa occurred outside of North America. Freshwater species *Melvius* sp. and *Cyclurus fragosus* may be limited to the WIS, whereas brackish tolerant species ranged more widely along the coasts of Laramidia and Appalachia. *Ischyrbiza avonicola* belonged to that more euryhaline group. We include this sawfish in the freshwater/brackish water assemblage (Table 3) because it occurs in rocks deposited well upstream from the sea in the Lance and Hell Creek formations (Estes, 1964) as well as in the Fox Hills Formation.

Myledaphus is frequently discovered in both Campanian and Maastrichtian freshwater deposits in northern latitudes (Case, 1978; Brinkman, 1990). *Cyclurus fragosus* is similarly restricted to freshwater deposits. *Melvius*, the other amiid in this fauna, ranged from New Mexico as far north as the Hell Creek Formation of eastern Montana (Bryant, 1989; Sullivan et al., 2011). It seems that the freshwater communities also show effects of latitudinal thermal gradients, with mixing of faunas at the latitude of the Dakota Isthmus (Brinkman et al., 2013, 2017).

Several of the Fox Hills species that dwelt in shallow marine waters and tidally-influenced brackish waters were restricted to the WIS where they were either endemic (Table 5) or, like *Walteraja exigua* and *Squalus ballingsloevensis*, had paleogeographic distributions in more boreal faunas such as in the Kristianstad Basin of Sweden (Siverson and Cappetta, 2001). A second subset of those species with shallow marine affinities occupied these habitats throughout the midcontinent and the Atlantic Coast (Tables 3 and 5). *Plicatoscyllium derameei* ranged into North Africa during the Maastrichtian.

Inspection of Tables 3 and 5 indicates that several shallow water species such as “*Myliobatis*” *foxbillsensis* n. sp., *Archaeotriakis rochelleae*, *Ptychotrygon greybullensis*, *P. winni*, *Cretorectolobus olsoni*, and *Palaeogaleus navarroensis* had narrower geographic distributions than did others, such as *Squatina hassei*, *Plicatoscyllium derameei*, or *Galeorhinus girardoti*. This may be an artifact of paleontologic studies or it may reflect real limitations of taxa based on habitat preferences, water temperature, or salt tolerances. Compagno (2005) presented distribution information for the modern, global shark

fauna, suggesting the importance of temperature as a significant controlling factor of shark distributions. Many of today's small and medium-sized sharks that favor neritic habitats are depicted with rather narrow geographic distributions, whereas larger, oceanic species have global distributions, particularly throughout the tropics (Compagno, 2005). Fox Hills taxa are distributed similarly, with oceanic species showing global geographic ranges.

Several of the lamniform, pelagic, open-marine species were cosmopolitan in North America and ranged widely into Europe, North Africa, and beyond. *Squalicorax pristodontus*, *Carcharias samhammeri*, *Paranomotodon toddi*, and *Serratolamna serrata* belong to this group of predators. Retzler et al. (2013) reported that these taxa were present in Israel: *S. pristodontus* in the Campanian, and *C. samhammeri* and *S. serrata* in the Maastrichtian. The Campanian occurrence is the oldest record of *S. pristodontus* (Retzler and Wilson, 2013), suggesting it may have originated in the Tethyan of the eastern Mediterranean or the Middle East.

We suggest that some members of the shallow Fox Hills fish assemblage may have required conditions associated with large river deltas that had high discharges of both water and sediment such as the Hell Creek Delta. Absence of those large river delta habitats may have limited species distributions and thus created disjunct distributions. Late Maastrichtian fish faunas may have been geographically limited, in part, by the number of such deltas available for colonization. Brinkman (1990) recognized similar deltaic faunas in the Campanian Judith River Formation. A taxon such as the big marine catfish *Vorhisia vulpes* may be an example of such a large distributary species.

Bony fish distributions are more difficult to track at the species level. *Enchodus* cf. *E. ferox* has perhaps a global range, including the Antarctic (Kriwet et al., 2006) and the Tethys of Morocco and Israel (Chalifa, 1996). At the generic level, the larger fish such as *Xiphactinus* sp. and *Protosphyraena* sp. were widely distributed in the Campanian and Maastrichtian of Antarctica, Africa, and the eastern Tethys (Kriwet et al., 2006).

The composition of the Fox Hills fish fauna is most similar to those of the middle Atlantic Coast, particularly the Severn Formation of Maryland, the Late Maastrichtian faunas of New Jersey, the Kemp Formation of Texas, and the Arkadelphia Formation of Arkansas (Table 5). Ten Fox Hills species are in common with the Severn Formation fauna, 10 with the Kemp fauna, six with the Arkadelphia fauna, and nine with the fauna of New Jersey (upper Navesink, Hornerstown, and New Egypt formations).

FOX HILLS FISH EXTINCTIONS

One of Earth's greatest biological crises occurred at the end of the Cretaceous Period about 66 Ma. Approximately 75% of species, 45% of genera, and 15% of families disappeared during this K-Pg extinction event (Jablonski, 1991; Sepkoski, 1991; Wilson, 2014). Although this mass extinction has been recognized world-wide, much of what we know about its biotic effects has been determined by studies in the upper North American midcontinent. It is there where the K-Pg boundary layer is exposed within the fluvial, coastal plain deposits of the Upper Cretaceous Hell Creek Formation, where it has been studied in several places in North Dakota and Montana (Johnson et al., 1989; Murphy et al., 1995; Nichols and Johnson, 2002; Moore et al., 2014). The conformable contact between the Hell Creek Formation and the fluvial, lacustrine, and paludal strata of the earliest Paleocene Fort Union Formation is also observable in numerous badlands outcrops. Both formations are fossiliferous and have yielded abundant plant, invertebrate, and vertebrate remains, allowing comparison of terrestrial faunas and floras before and after the extinction.

Fastovsky and Bercovici (2016) provided an excellent review (spanning several decades) of the numerous Hell Creek and Fort Union stratigraphic and paleontological investigations from this area pertinent to the K-Pg extinction. They summarized results of these studies by noting that at the K-Pg boundary: ~30 % of the palynoflora became extinct in southwestern North Dakota (Nichols, 2002); 78% of Hell Creek Formation macroflora species became extinct (Johnson, 1992, 2002); insect extinctions were similar to plant extinctions (Labandeira et al., 2002a,b); total extinction of non-avian dinosaurs (Sheehan et al., 1991; Pearson et al., 2002; Fastovsky and Sheehan, 2005); birds suffered a 41% extinction (Longrich et al., 2011); 75% extinction of mammals (although some became extinct before the boundary) (Wilson et al., 2014); no significant extinction in chelonians (Hutchison and Archibald, 1986; Lyson and Joyce, 2009; Lyson et al., 2011; Holroyd et al. 2014); 83% extinction of lizards and snakes (Longrich et al., 2013—a long ranging geographic study that included data from the Hell Creek Formation); 22% species-level extinction in salamanders and salamander-like lissamphibians (Wilson et al., 2014). Fastovsky and Bercovici (2016) also noted that Cvancara and Hoganson (1993) and Hoganson and Murphy (2002) identified Late Cretaceous extinctions of marine fish from the northern Western Interior Seaway in North Dakota. As a result of these studies, a debate has ensued as to whether Late Cretaceous extinctions were multi-caused and gradual during the Late Cretaceous, or abrupt at the end of the Cretaceous and caused by one or several catastrophic events (i.e., an asteroid impact).

Table 7.—Temporal ranges of osteichthyans of the Fox Hills, Hell Creek (Maastrichtian) and Cannonball (Paleocene) (shaded in tan) formations relative to the K-Pg boundary. Taxa grouped by order.

AGE		Lepisosteidae	Melurus sp.	Cyclurus fragosus	Protosphyraena sp.	Belonostomus longirostris	Xiphacanthus vetus	Paraterpon ? sp.	Pterothrissus sp.	Parabulita casei	Egertonia isodontia	Pollerspoecia siegsdorfensis	Vornisia vulpesc	Arius ? danicus	cf. Bathylagus sp.	Enchodus affinis	Enchodus cf. E. ferrox	*Apogonidarium" maastrichtiensis	Eutrichthyrus erpentinus	
Holocene	PALEOGENE / NEOGENE																			
Pleistocene																				
Pliocene																				
Miocene																				
Oligocene																				
Eocene																				
Paleocene																				
65.7 Ma																				
L. Maastrichtian	LATE CRETACEOUS																			
E. Maastrichtian																				
L. Campanian																				
E. Campanian																				
Santonian																				
Turonian																				
Cenomanian																				
Albian																				
CRET.																				

ception of *Otodus obliquus*, are only known from Paleocene or younger strata (Tables 6). None of the five osteichthyan species recovered from the Cannonball are found in the Cretaceous, except perhaps for the indetermined lepisosteid (Table 7), and none of the five osteichthyan genera, except perhaps for the indeterminate lepisosteid, extended beyond the Cretaceous. Cvancara and Hoganson (1993) suggested that these findings were consistent with discussions that marine fishes suffered a major extinction at the end of the Cretaceous and Paleocene fish recovery followed that event.

The Fox Hills and Cannonball formations are usually not found juxtaposed in outcrop except for isolated exposures in the Souris River area of McHenry County, North Dakota (Lemke, 1960). The duration of the temporal gap between the two formations is not precisely known. A Danian age for the Cannonball Formation is indicated by Foraminifera (Fox and Olson, 1969; Fenner, 1976) and mammalian remains from interfingering, nonmarine strata indirectly suggest the lower Cannonball is Danian in age and the upper Cannonball is Thanetian in age (Holtzman, 1978; Sloan, 1987). Meager mammalian remains directly from the Cannonball Formation tentatively indicate a Puercan/Torrejonian North American Land Mammal Age (NALMA). Cvancara and Hoganson (1993) suggested that it is likely the Danian-Thanetian boundary occurs within the formation. It should be noted that Lemke (1960, p. 24) reported that it appears the Cannonball Formation rests conformably on the Fox Hills Formation in the subsurface of McHenry County in central North

Dakota. None of the fish species found in the Cannonball Formation occurred during the Cretaceous worldwide except possibly *Otodus obliquus* (Cvancara and Hoganson, 1993). Undetermined species of Lepisosteidae do occur in both formations.

The Western Interior Seaway persisted in North Dakota after the Fox Hills Sea as documented by marine tongues, the lower Breien Member and upper Cantapeta Tongue, and perhaps others in the Hell Creek Formation which occur stratigraphically between the Fox Hills Formation and the Cannonball Formation in south-central North Dakota (Murphy et al., 2002, Hoganson and Murphy, 2002) (Text-fig. 2). Scholz and Hartman (2007) also noted that the Western Interior Seaway occupied North America's midcontinent well into the early Paleocene. This persistence is also indicated by Paleocene marine deposits in the Hanna Basin, Wyoming (Boyd and Lillegraven, 2011). The Breien Member was deposited within the *Jeletzkytes nebrascensis* Zone and is Lancian in age (Hoganson and Murphy, 2002). The Breien fish fauna is similar to the underlying Fox Hills fish fauna and has no species in common with those found in the overlying Cannonball Formation (Hoganson, 2000; Hoganson and Murphy, 2002). Hoganson (2000) and Hoganson and Murphy (2002) suggested that this Breien fauna lends support for an end-Cretaceous fish extinction. No fish fossils have yet been found in the Cantapeta Tongue.

Comparison of the Fox Hills and Cannonball fish faunas at the species and generic levels indicates that marine fish faunas were dramatically affected by the Late Cretaceous extinction in the northern Western Interior Seaway. All of the chondrichthyan species and 58% of the genera in the Fox Hills did not survive into the Paleocene, although 80% of the chondrichthyan families did survive. Kriwet and Benton (2004) suggested that K-Pg boundary global extinction rates for chondrichthyan families was 17%, whereas the Fox Hills extinction rate for chondrichthyan families was a bit higher at 20%.

All of the osteichthyan species, 77% of genera, and 33% of families in the Fox Hills Formation became extinct. Schwarzhans (1996) also noted a significant change in fish otolith taxa at the K-Pg boundary in Bavaria where only 25% of the Maastrichtian taxa extended into the Paleocene, similar to our findings. Fox Hills osteichthyan family extinction rates were slightly lower than chondrichthyans. Lower osteichthyan familial extinction rates were also noted by MacLeod et al. (1997), who reported that 90% of osteichthyan families survived the K-Pg boundary event globally. Friedman and Sallan (2012) proposed that family-level extinction rates for osteichthyans was probably closer to 20%.

Cavin (2002) noted that osteichthyan K-Pg boundary extinction rates were moderate and primarily specialized, epipelagic taxa were affected. Chondrichthyans generally have a

higher extinction risk than osteichthyans because of their usually larger size and lower fecundity (Field et al., 2009). Large-bodied teleostean apex predators had high extinction rates at the K-Pg boundary (e.g., *Xiphactinus* and *Protosphaena*) (Friedman, 2009). Even though bony fish extinction rates were generally low at the boundary, there was a major radiation of spiny-finned teleost fishes during the Paleogene (Friedman, 2010). A radiation of Actinopterygii after the K-Pg extinction was also noted by Sibert and Norris (2015) through study of ichthyolith (shark denticles and ray-finned fish teeth) assemblages from deep sea cores spanning the K-Pg boundary. This is not, however, reflected in the Cannonball fauna, probably because of the scarcity of osteichthyan remains in that formation.

Very few other comprehensive investigations have compared fish faunas before and after the K-Pg extinction. Our results, indicating a major extinction of chondrichthyan species in the Late Maastrichtian, compare well with faunas from open marine and nearshore deposits in Morocco studied by Noubhani and Cappetta (1997). They found 97% of species became extinct at the end of the Cretaceous. Two of these species—*Serratolamna serrata* and *Squalicorax pristodontus*, also found in the Fox Hills Formation—did not survive in the Western Interior Seaway. Far different results were reported by Adolfsson and Ward (2014) after study of K-Pg boundary chondrichthyan faunas from Denmark. They proposed that the majority of the chondrichthyan species, all but 33% (23% generic extinction rate), persisted across the K-Pg boundary. However, most of the species recovered in their study were boreal and deep water taxa (Adolfsson and Ward, 2014). Of the 27 chondrichthyan species reported from the Maastrichtian Danish Basin strata only one, *Squalicorax pristodontus*, is found in the shallow marine Fox Hills deposits. It was one of the Danish species that did become extinct. The discrepancy between the extinction rates of the deep water Danish species and shallow water Fox Hills species is consistent with Kriwet and Benton's (2004) observation that globally, deep water faunas were less affected by the K-Pg boundary event than shallow marine faunas. Global chondrichthyan diversity changes across the K-Pg boundary were determined by Kriwet and Benton (2004) to be $56 \pm 10\%$ loss of genera and $84 \pm 5\%$ loss of species, which is somewhat consistent with our results. Cappetta (1987b) noted that about 45% of chondrichthyan genera became extinct at the end of the Cretaceous worldwide, but he did not give an estimate for species.

Five species of elasmobranchs (*Myledaphus bipartitus*, *Ischyrhiza avoncola*, "*Squatirhina*" (= *Restesia*) *americana*, "*Brachaelurus*" (= *Protoginglymostoma*) *estesi*, and *Lissodius* (= *Lonchidion*) *selachos*) found in non-marine Hell Creek Formation deposits in Montana became extinct at the end of the Cretaceous (Bryant, 1989; Archibald and Bryant 1990;

Archibald, 1996; Freidman and Sallan, 2012). Freshwater teleosts in the formation were apparently little affected (Archibald, 1996).

Chondrichthyan pelagic piscivorous apex predators with broad feeding preferences and duraphagous benthic taxa were particularly susceptible to extinction pressures in global K-Pg chondrichthyan faunas (Gallagher, 2002; Kriwet and Benton, 2004). This is corroborated by the Fox Hills chondrichthyan fauna, as many of the Fox Hill predators that disappeared at the end of the Cretaceous were replaced by Cannonball species with similar trophic adaptations. Examples are the Fox Hills apex pelagic predators *Carcharias sambhammeri*, *Serratolamna serrata*, and *Cretalamna feldmanni* n. sp. being replaced by the Cannonball ecological analogue species *Palaeohypotodus rutoti*, *Paraorthacodus eoceanus*, and *Otodus obliquus*.

Bazzi et al. (2018) developed interesting comparative data relating to the evolution of tooth morphology of lamniform and carchariform sharks across the K-Pg boundary. Paleogene carchariform species in the replacement fauna of open ocean predators evolved forms similar to those of the extinct Cretaceous lamniform species. We have not yet tested this with the Fox Hills and Cannonball data, but we anticipate the results could have both ecologic and paleogeographic implications.

The Cannonball benthic duraphagous *Dasyatis concavifoveus* and *Ischyodus dolloi* are likely ecological replacements for the Fox Hills *Dasyatis northdakotaensis* n. sp. and *Ischyodus rayhassi*. Interestingly, no osteichthyan species found in the Cannonball Formation can be considered an ecological analogue to the large, predatory Fox Hills species, e.g., *Protosphaera* sp., *Enchodus dirus*, and *Xiphactinus vetus*, which became extinct at the end of the Cretaceous. There was a major radiation of acanthomorph pelagic predators in the Paleogene (Friedman, 2010; Near et al., 2013) that perhaps expanded later to fill those niches.

Chondrichthyan species richness was highest during the Late Maastrichtian as indicated by 35 species found in the Fox Hills Formation, compared with the low diversity of only 13 species recovered from the Paleocene Cannonball Formation. This Fox Hills–Cannonball chondrichthyan faunal transition of abrupt extinction and slow recovery has been noted globally by Kriwet and Benton (2004). D'Hodnt (2005) suggested this slow recovery of marine ecosystems after the K-Pg extinction can be explained by slow recovery of biogeochemical processes, primarily organic flux to the deep sea and production of calcium carbonate by marine plankton that radically declined after the extinction, thus affecting the food chain. The level of resolution of how abrupt the extinction was and how rapidly the renewal occurred awaits refinement of aging the Fox Hills, Hell Creek, and Cannonball formations. Diversification of the North Dakota fish fauna after the K-Pg

boundary extinction, probably through both evolutionary radiation and immigration, created a fauna of more modern aspect, where eight of the ten chondrichthyan and four out of the five osteichthyan families found in the Cannonball Formation still exist today.

CONCLUSIONS

Thirty-six species of chondrichthyan (19 sharks, 16 skates and rays, including four morphotype species, and one chimaeroid), from 32 genera (17 sharks, 14 skates and rays, including four morphotype genera, and one chimaeroid) and 20 (not including *incertae familiae*) families are described from 48 Late Maastrichtian Fox Hills Formation sites in south-central and southwestern North Dakota. Three of these taxa are new species: the otodontid *Cretalamna feldmanni* n. sp., the dasyatid *Dasyatis northdakotaensis* n. sp., and the rhombodontid "*Myliobatis*" *foxhillsensis* n. sp. Twelve other chondrichthyan species that are new occurrences for the Fox Hills Formation are: *Squalus ballingsloevensis*, *Plicatoscyllium derameei*, *Cretorectolobus olsoni*, *Carcharias* cf. *C. tenuiplicatus*, *Paranomotodon toddi*, *Squalicorax pristodontus*, *Palaeogaleus navarroensis*, *Archaeotriakis rochelleae*, *Paraorthacodus andersoni*, *Synechodus turneri*, *Walteraja exigua*, and *Rhombodus levis*.

Twenty species of osteichthyan (including five *incertae sedis*), from 18 genera (including five *incertae sedis*), and 12 families (possibly 17 families if each *incertae sedis* taxon represents a different family) are also identified from the Fox Hills Formation. The bony fish species reported for the first time from this formation are: a Lepisosteidae indet., *Melvius* sp., *Cyclurus fragosus*, *Protosphyraena* sp., *Belonostomus longirostris*, *Xiphactinus vetus*, *Paratarpon?* sp., *Pollerspoeckia siegsdorfensis*, cf. *Bathylagus* sp., *Enchodus* cf. *E. ferox*, and "*Apogonidarum*" *maastrichtiensis*. This is one of the youngest Cretaceous fish faunas reported from the central Western Interior Seaway. The similar fish fauna of the Breien Member of the overlying Hell Creek Formation is found in a younger marine tongue of the Fox Hills Sea.

The Fox Hills fish fossils, consisting of mostly teeth and disarticulated skeletal parts, were recovered from sediments laid down in a marginal marine, nearshore depositional setting and represent the following habitat groupings based on qualitative assessment of fish habitat preferences. These groupings are: "offshore marine," "nearshore marine," "brackish water estuarine—strong tidal influence," "brackish water estuarine—weak tidal influence," and "riverine/lagoonal—strong freshwater influence." Few of the Fox Hills taxa seem to be restricted to freshwater conditions except perhaps the amiid *Cyclurus fragosus*. The sawfish *Ischyrrhiza avonicola*, the rajiform *Myledaphus* sp., the aspidorhynchid *Belonomostus longirostris*, the amiid *Melvius* sp., the elopid *Paratarpon?*, and lepisosteid gars are examples of species that resided in freshwater

habitats, but regularly visited brackish or estuarine habitats. Shallow marine and brackish to estuarine taxa include: catfish *Vorbisia vulpes*, chimaeroid *Ischyodus rayhaasi*, phylloodontid *Paralbula casei*, pencil smelt cf. *Bathylagus* sp., hybodontid ?*Hybodus* sp., and the cardinal fish "*Apogonidarum*" *maastrichtiensis*. Marine species recovered from the Fox Hills Formation consist of those that either inhabited shallow coastal waters or those that ventured into the nearshore areas from open water. The shallow water taxa include: triakids *Palaeogaleus navarroensis*, *Galeorhinus girardoti*, and *Archaeotriakis rochelleae*; *Squatina hassei*; *Synechodus turneri*; *Dasyatis northdakotaensis* n. sp.; *Rhombodus levis*; "*Myliobatis*" *foxhillsensis* n. sp.; sclerorhynchids *Ptychotrygon winni* and *Ptychotrygon greybullensis*; squalids *Squalus ballingsloevensis* and *Squalus* sp.; wobbegong *Cretorectolobus olsoni*; nurse sharks *Ginglymostoma* sp. and *Plicatoscyllium derameei*; rajiforms *Protoplatyrhina renae* and *Pseudohypolophus mcnultyi*; and the bone fish *Pollerspoeckia siegsdorfensis*.

Open marine, deep water taxa that entered shallow water to feed are: the lamniforms *Carcharias* cf. *C. tenuiplicatus*, *Carcharias samhammeri*, *Odontaspis aculeatus*, *Cretalamna feldmanni* n. sp., *Serratolamna serrata*, *Paranomotodon toddi*, *Squalicorax pristodontus*; the palaeospinacid *Paraorthacodus andersoni*; the ichthyodectiform *Xiphactinus vetus*; the enchodontids *Enchodus dirus* and *Enchodus* cf. *E. ferox*; the pachycormid *Protosphyraena* sp.; and the rajid *Walteraja exigua*.

Inferences about feeding preferences were determined by tooth morphology and comparison to modern relatives and include omnivore, general invertebrate, molluscivore, pelagic piscivore, benthic piscivore, and scavenger. Durophagous species recovered are: *Protoplatyrhina renae*, *Pseudohypolophus mcnultyi*, *Myledaphus* sp., *Ptychotrygon winni*, *Ptychotrygon greybullensis*, *Walteraja exigua*, *Rhombodus levis*, *Dasyatis northdakotaensis* n. sp., "*Myliobatis*" *foxhillsensis* n. sp., *Ischyodus rayhaasi*, *Cyclurus fragosus*, *Paralbula casei*, and possibly *Ischyrrhiza avonicola*. Apex predators found are: *Carcharias* cf. *C. tenuiplicatus*, *Carcharias samhammeri*, *Odontaspis aculeatus*, *Cretalamna feldmanni* n. sp., *Serratolamna serrata*, *Paranomotodon toddi*, *Squalicorax pristodontus*, *Xiphactinus vetus*, *Protosphyraena* sp., *Enchodus dirus*, and *Enchodus* cf. *E. ferox*. Other smaller predaceous sharks in the fauna are: *Squalus ballingsloevensis*, *Squalus* sp., *Squatina hassei*, *Plicatoscyllium derameei*, and *Cretorectolobus olsoni*. Lepisosteid gars and *Melvius* sp. were ambush predators.

Most of the Fox Hills fish species were endemic to the central Western Interior Seaway. Other taxa within the fauna also occurred in the Texas Gulf Coast, Mississippi Embayment, and Atlantic Coastal Plain. The Fox Hills fish fauna is most similar to those of the Maastrichtian Kemp Formation in Texas, the Maastrichtian Severn Formation in Maryland, and the

Maastrichtian Navesink Formation in New Jersey. A few taxa were cosmopolitan in nature and inhabited Europe during the Maastrichtian, including: *Squatina hassei*, *Ischyodus rayhassi*, *Paraorthacodus andersoni*, *Walteraja exigua*, *Pollerspoeckia siegsdorfensis*, and *Squalus ballingsloevensis*. The presence of *Walteraja exigua* and *Squalus ballingsloevensis* suggests biogeographic connections to Greenland and Scandinavia. Some of the large lamniform open-marine pelagic predators, e.g., *Serratolamna serrata*, *Squalicorax pristodontus*, and *Carcharias samhammeri* also ranged to Europe, North Africa, and the eastern Mediterranean.

The Fox Hills fish fauna suggests both tethyan and boreal oceanic connections to the central WIS. Some members of the shallow water Fox Hills fish assemblage may have required conditions associated with large river deltas having high discharges of both water and sediment, such as were characteristic of the Hell Creek Delta.

The Fox Hills paleofauna documents a major extinction of fish in the Late Maastrichtian. None of the 36 chondrichthyan species recovered from the Fox Hills Formation range into the Paleocene worldwide. Thirteen of the 31 chondrichthyan genera ranged into the Paleocene, including: *Squatina*, *Squalus*, *Ginglymostoma*, *Carcharias*, *Odontaspis*, *Cretalamna*, *Palaeogaleus*, *Galeorhinus*, *Paraorthacodus*, *Synechodus*, *Myliobatis*, *Dasyatis*, and *Ischyodus*. None of the 20 osteichthyan species found in the Fox Hills Formation ranged into the Paleocene worldwide. Three of the 13 osteichthyan genera, *Cyclurus*, *Bathylagus*, and “*Apogonidarum*”, are believed to have survived into the Paleocene. Support for this being a major extinction is through comparison of the Late Maastrichtian Fox Hills fish fauna with the fish fauna of the Paleocene Cannonball Formation, which documents the last incursion of the Western Interior Sea into the upper midcontinent. None of the Fox Hills chondrichthyan or osteichthyan species occurs in the Cannonball Formation.

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INDEX

- Africa 2, 20, 27, 30, 68–70, 75
 Alberta 10, 14, 20, 22, 32, 35, 36, 39, 47, 51, 53, 54, 57, 62, 67–69
Alopias vulpinus 45
 ambush predators 20, 64, 66, 74
Amia calva 49, 51, 66
 Amiidae 13, 49, 51
 Amiiiformes 13, 49
 amphibian 2, 16
 Anacoracidae 12, 28, 71
 Angle shark 19
 Angola 27
Anomotodon toddi 27, 28
 Antarctica 70
 Apogonidae 14, 58, 59
 “*Apogonidarum*” 1, 14, 15, 51, 58, 62, 65, 68, 69, 72, 74
 “*Apogonidarum*” *maastrichtiensis* 1, 14, 15, 51, 58, 62, 65, 68, 69, 72, 74
 Appalachia 66, 69
Archaeotriakis 1, 12, 15, 16, 30, 31, 63, 65, 68, 69, 71, 74
Archaeotriakis ornatus 31
Archaeotriakis rochelleae 1, 12, 15, 16, 30, 31, 63, 65, 68, 69, 71, 74
 Argentiniformes 13, 56
 Ariidae 13, 55
Arctica 67
 Arkadelphia Formation 19, 21, 25, 27, 30, 38, 39, 44, 68–70
 Arlington Member 36
 Arlington Sandstone Member 23, 36
 Aspidorhynchidae 13, 52, 71
 Aspidorhynchiformes 13, 52
Aspidorhynchus 52
Asterodermus 45
 asteroid impact 70
 Atarque Sandstone Member 38
 Atlantic Coastal Plain 1, 39, 44, 57, 74
Atlantoraja castelnaui 46
 Aulopiformes 14, 56
 Badlands National Park 9
 “bait fish” 65
 barrier islands 60, 66, 67
Bathylagus 1, 13, 15, 51, 56, 62, 63, 65, 71, 72, 74, 75
 cf. *Bathylagus* sp. 13, 15, 51, 56, 63, 72
 Bavaria 55, 45, 69, 72
 Bearpaw Formation 10, 14, 20, 67
 Belgium 20, 26, 27, 30
 Bell Member 36
Belonostomus 1, 13, 15, 51–53, 62, 63, 65, 58, 72, 74
Belonostomus longirostris 1, 13, 15, 51, 52, 62, 63, 65, 68, 72, 74
 benthic 1, 55, 62, 64–66, 73, 74
 Billfish 52, 64
 biostratigraphy 5, 9, 66, 67
 birds 64, 66, 70
 Bivalvia 2
 Black Creek Formation 10, 20, 29, 46, 54
 Blufftown Formation 10, 36, 54
 Bone fish 63, 65, 74
 Bone Valley Formation 46
 bony fish 6, 64, 65, 70, 73, 74
 boreal 18, 48, 67–69, 73, 75
 bottom feeding 34, 62, 64
 Bowman County 1, 6–8, 28, 30, 40, 45
 “*Brachaelurus*” *estesi* 73
Brachyrhizodus 36, 42, 46
Brachyrhizodus wichitaensis 42, 46
 brackish 1, 2, 10, 34, 36, 48, 55, 56, 59–63, 65–67, 69, 74
 Breien Member 2, 4, 5, 8, 9, 24, 26, 27, 34, 38, 39, 47, 48, 62, 67, 69, 71, 72, 74
 British Chalk 52
 Bryozoa 2
 Bug Creek Ant Hills 38, 54
 Bulgaria 29
 Bullhead Estuary 67
 Bullhead Lithofacies 8
 Callorhynchidae 13, 47
 Cannonball Formation 2, 16, 18, 25, 30, 36, 41, 43, 48, 69, 71–75
 Cannonball River 2, 5, 57
 Cannonball Sea 68
 Cantapeta Tongue 2, 4, 8, 67, 71, 72
 Carcharhiniformes 12, 29
Carcharias 1, 2, 10, 12, 15, 22–24, 26, 29, 63–65, 68, 70, 71, 73–75
Carcharias cf. *C. tenuiplicatus* 1, 10, 12, 15, 22, 23, 63–65, 68, 71, 74
Carcharias heathi 23
Carcharias holmdelensis 23
Carcharias samhammeri 12, 15, 23, 24, 63–65, 68, 70, 71, 73–75
Carcharias sp. B 24
 Cardinal fish 62, 65, 74
 Carlisle Shale 36
 Catfish 14, 55, 56, 62, 70, 74
 Cedar Creek Anticline 6–8
Cederstroemia 19, 20, 22
 Cephalopoda 2
 chelonians 71
 Chesapeake Bay 24, 29
 Chimaeriformes 13, 15, 47
 Chimaeroid 2, 14, 48, 62, 74
 circumpolar 69
 coastal deposits 2, 34
 coastal paleocommunity 60
 coastal waters 18, 62, 63, 74
 Colgate Lithofacies 5, 8
 Colorado 2, 23, 34, 38, 47, 48, 62
 Congo Basin 27, 47
 cosmopolitan 1, 27, 53, 70, 75
 crabs 2, 65, 66
Crassostrea—*Pachymelania* Assemblage Zone 48, 61
Crassostrea subtrigonalis 8, 61
Cretalamna 1, 2, 12, 15, 16, 25, 26, 63–65, 68, 69, 71, 73–75
Cretalamna appendiculata 29, 69
Cretalamna catoxodon 26
Cretalamna feldmanni n. sp. 1, 12, 15, 25, 63, 65, 68, 71, 73
Cretalamna hattini 26
Cretascyllium 19
Cretodus sp. 25
Cretorectolobus 15, 19–22, 47, 63–65, 68, 69, 71, 74
Cretorectolobus olsoni 1, 10, 12, 15, 19, 21, 22, 47, 63–65, 68, 69, 71, 74
 crocodile 2
Cyclurus 1, 13, 15, 49, 51, 62–65, 68, 69, 71, 72, 74, 75
Cyclurus fragosus 1, 13, 15, 49, 51, 62–65, 68, 69, 72, 74
 Dakota Isthmus 1, 2, 20, 57, 60, 61, 66, 67, 69
 Dasyatidae 13, 40, 46
Dasyatis 1, 2, 13, 15, 32, 40, 41, 43, 46, 63–65, 68, 69, 71, 73–75
Dasyatis branisai 40

- Dasyatis commercensis* 40
Dasyatis concavifoveus 41, 71, 73
Dasyatis molinoensis 40
Dasyatis newegyptiensis 40
Dasyatis northdakotaensis n. sp. 1, 13, 15, 40, 63, 65, 68, 71, 73, 74
Dasyatis schaefferi 40
Dasyrhombodus 44
 deep marine 1, 68
 deep water 18, 56, 63, 68, 73, 74
 DeGrey Member 18
 delta 1, 2, 7, 8, 48, 51, 53, 56, 60, 62, 64, 66, 67, 70, 75
 delta-platform facies 2
 Demopolis Formation 20, 29
 Denmark 16, 29, 73
 dinosaur 10, 14, 22, 24, 34, 35, 39, 47, 53, 57, 58, 60, 62, 69
 Dinosaur Park Formation 10, 14, 22, 24, 34, 35, 39, 47, 53, 57, 58, 60, 62, 69
 Dogfish sharks 18, 64
 Donoho Creek Formation 20, 38
 Dunvegan Formation 10, 36
 duraphagous 73
 Eagle Ford Group 36
 echinoids 2
 ecological analogue species 73
 Egypt 2, 20, 27, 35, 40, 68, 70
 Elasmobranchii Dermal Denticle Morphotype 1 13, 32, 45
 Elasmobranchii Dermal Denticle Morphotype 2 13, 41, 46
 Elasmobranchii Dermal Denticle Morphotype 3 13, 41, 47
 Elasmobranchii Placoid Scale Morphotype 1 13, 32, 45
 Elk Butte Member 9, 67
 Elopidae 13, 54
 Elopiformes 13, 54
 Emmons County 2, 8, 67
 Enchodontidae 14, 56
Enchodus 58, 63–65, 68–70, 72–74
Enchodus cf. *E. ferox* 1, 14, 15, 51, 58, 63–65, 68–70, 72, 74
Enchodus dirus 14, 15, 51, 56, 57, 63–65, 68, 72–74
Enchodus gladiolus 57
Enchodus mecoanalis 58
 Eocene 47, 54, 71, 72
 epipelagic 72
Erisichtbe nitida 52
 Escondido Formation 20, 27, 29
 estuarine 61–68, 74
 Europe 1, 6, 20, 21, 26, 27, 30, 36, 52, 68–70, 75
 euryhaline 34, 62, 69
 eurytopic 36, 64
 Eutaw Formation 20, 36
 evolutionary radiation 74
 extinction 1–3, 56, 69–75
 Fairpoint Member 9, 10, 14, 19, 21, 22, 24, 25, 27, 30, 35, 36, 48, 54, 57
 feeding competition 1
 feeding preferences 73, 74
 feeding types 1, 66
 Ferris Formation 22, 41
 floral 2
 fluvial 5, 34, 59, 62, 70
 food chain 64, 73
 Foraminifera 2, 72
 Foremost Formation 10, 20, 32, 34, 53
 “Formation No. 5” 2
 Fort Union Group 4, 7, 41, 70
 Fox Hills Sea 2, 5, 9, 20, 48, 60, 64, 66, 67, 69, 72, 74
 Fox Hills type area 1, 9
 France 20, 27, 29, 30, 36, 44
 freshwater 1, 10, 34, 48, 49, 51, 53, 54, 59–69, 73, 74
 Fruitland Formation 49
Galeocerdo cuvieri 29
Galeorhinus 2, 12, 15, 16, 30, 63, 65, 68, 69, 71, 74, 75
Galeorhinus girardoti 12, 15, 16, 30, 63, 65, 68, 69, 71, 74
 Gar 48, 62
 Gastropoda 2
 Gerhartsreiter Grabens 55, 56
 Glen Rose Formation 36
Ginglymostoma sp. 2, 10, 12, 15, 20, 21, 63, 65, 71, 74, 75
 Ginglymostomatidae 12, 20, 21
 Grayson Formation 36
 Great Britain 27, 54
 Greenhorn Formation 23, 38, 45, 47, 57
 Greenland 1, 68, 69, 75
 Guinea Corn Formation 27
 Gulf Coast 1, 53, 60, 66, 68, 69, 74
 habitat preferences 1
 Hanna Basin 22, 72
 Hell Creek Delta 1, 2, 7, 48, 53, 60, 62, 66, 67, 70, 75
 Hell Creek Formation 2, 4, 5, 7–9, 14, 24, 26, 27, 32, 34, 38, 39, 47–49, 53, 54, 62, 63, 67, 69–74
 Hexanchiformes 12, 14
 Holland 2, 19, 20, 26, 27
 holotype 16, 18, 25, 32, 34, 40–42, 44, 45, 49, 57
Hoploscaphites nebrascensis 1, 6–9, 67
Hoploscaphites nicolletii 1, 5–7, 9
 Hornerstown Formation 29, 70
 Hybodontidae 10, 12, 62, 63, 71, 74
 Hybodontiformes 9, 12
Hybodus 10, 12, 14, 15, 31, 62, 63, 65, 68, 71, 74
Hybodus sp. 10, 12, 14, 15, 62, 63, 65, 68, 71
Hypolophus malembeernis 47
 ?*Hypolophus mcultyi* 35, 36
Hypolophus sylvestris 36, 47
Hypsobatis 44
 Ichthyodectidae 13, 53, 71
 Ichthyodectiformes 13, 53
Igdabatis 42, 43
Igdabatis indicus 43
Igdabatis sigmodon 43
 India 29, 43
 inland paleocommunity 60
 insect 70
 invertebrate 1–3, 6, 64–67, 69, 70, 74
 Iron Lightning Member 5, 8, 9, 48, 62, 67
Ischyodus 2, 13, 15, 32, 47, 48, 62–65, 68, 69, 71, 73–75
Ischyodus bifurcates 48
Ischyodus dolloi 71, 73
Ischyodus rayhassi 13, 15, 32, 68, 73, 75
Ischyrhiza 13, 15, 32, 37, 38, 46, 62–65, 68, 69, 71, 73, 74
Ischyrhiza avonicola 13, 15, 37, 38, 62, 63, 65, 68, 69, 71, 73, 74
Ischyrhiza mira 37, 38
Ischyrhiza monasterica 37
Ischyrhiza scheideri 38, 46
Ischyrhiza texana 37
 Israel 26, 29, 70
 Jamaica 27
 Japan 26
 Kaskapu Formation 52

- Kemp Formation 2, 10, 18–24, 27–30, 35, 38–40, 68, 70, 71, 74
Kindleia fragosa 49, 51
 K-Pg boundary 2, 3, 5, 9, 26, 70–73
 Kristianstad Basin 18, 37, 58, 63, 69
 lacustrine 70
 lagoonal 1, 2, 9, 42, 61, 63–65, 67, 74
 Lamniform sharks 1, 16, 34, 25, 27, 32, 64, 70, 73, 75
 Lamniformes 12, 22, 28
 Lance Formation 7, 38, 47, 48, 51, 53, 60, 62, 66, 69
 Laramidia 66, 69
 Laramie Formation 38
 Lepisosteidae 13, 15, 48, 63, 65, 72, 74
 Lepisosteiformes 13, 48
 Lethbridge Coal 10, 14, 20, 22, 24, 35, 57
 Libya 27
 Linton Estuary 61, 63, 67
 Linton Member 2, 8, 61, 67
 lissamphibians 70
Lissodus 10, 14
 Lithostratigraphy 4
 Littig Formation 20, 27, 29
 Little Beaver Creek 6, 7
 Little Missouri River Badlands 5
 littoral zone 21, 64
 lizards 70
 Judith River Formation 10, 16, 20, 22, 31, 32, 35, 38, 39, 45, 46–49,
 53, 54, 57, 60, 66, 69, 70,
 Lebanon 58
 Logan County 3, 30, 42, 60, 75
 London Clay 47, 54
 macroflora 70
 Madagascar 29
 mammal 72
 Mancos Shale 36
 marginal marine facies 2
 marine tongues 2, 4, 5, 8, 48, 72, 74
 Marshalltown Formation 24, 29, 38
 Maryland 2, 21, 24–27, 29, 30, 36, 38, 40, 43, 47, 55, 59, 70
 Mediterranean 21, 70, 75
 Megafloa 2
Megasqualus orpiensis 69, 71
 Mekong Delta 56
Melivius 1, 13, 15, 49, 51, 62, 63, 65, 66, 68, 69, 72, 74
Melivius chauliodus 49
 Merchantville Formation 27, 58
 Mesaverde Formation 22, 29, 31, 35, 38, 40, 46, 47, 60
 Mexico 29
 Microstomatidae 13, 56
 Midcontinent 2, 3, 34, 37, 49, 60, 62, 67, 69–72, 75
 Milk River Formation 20, 32, 34
 Mississippi Embayment 1, 6, 68, 69, 74
 Missouri River Trench 4
 Missouri River Valley 2, 6–9, 67, 71
 Moberg Member 7, 9
 Molluscivore 1, 51, 74
 Monmouth Group 23, 24, 26, 46
 Moorville Chalk 27
 Morocco 20, 21, 26, 44, 58, 70, 73
 morphospecies 1, 59
 mosasaur 18, 64
Mosasaurus 2
 Mt. Laurel Formation 26, 53
Mustelus canis 45
Myledaphus 12, 15, 32, 34, 36, 46, 47, 62–65, 68, 69, 71, 73, 74
Myledaphus bipartitus 32, 34, 46, 47, 62, 71, 73
 Myliobatiformes 13, 40
Myliobatis aquila 42
 “*Myliobatis*” 1, 13, 15, 41, 43, 63, 64, 68, 69, 74
 “*Myliobatis*” *foxshillsensis* n.sp. 1, 13, 15, 41, 43, 63, 68, 74
 Navesink Formation 2, 4, 20, 26, 29, 54, 68, 70, 75
 NDGS: North Dakota Geological Survey 1, 3, 4, 15, 23, 42, 75
 ND: North Dakota State Fossil Collection 4, 28, 75
 nearshore 1, 10, 29, 36, 45, 62–66, 73, 74
 neritic 70
 Netherlands 21, 27
 Newcastle Sandstone 36
 New Egypt Formation 20, 27, 35, 41, 68, 69
 New Jersey 27, 29, 34, 35, 38, 39, 44, 46, 54, 57, 58, 69, 70, 75
 New Mexico 35, 38, 46–49, 69
 Niobrara Chalk 26, 29, 52, 53, 57
 nonmarine 62, 72
 No. 5 Greensand 58
 North Africa 2, 20, 30, 68–70, 75
 North American Land Mammal Age (NALMA) 72
 North American Midcontinent 2, 3, 34, 60, 62, 70
 Nurse sharks 21, 63, 74
 Odontaspidae 22
Odontaspis 2, 12, 15, 17, 22–25, 63–65, 68, 71, 74, 75
Odontaspis aculeatus 12, 15, 16, 24, 25, 63–65, 68, 71, 74
Odontaspis hardingi 23
 offshore marine 1, 36, 75
 Oldman Formation 32, 53
 omnivore 1, 64–66, 74
Onchopristis dunklei 46
 open ocean 6–65, 68, 73
Ophiomorpha 8, 61
 Otodontidae 12, 25
Otodus appendiculatus 26
 otolith 1, 2, 55, 56, 59, 62
 Ouled Abouan Phosphates 58
 Orectobififormes 12, 20
 Oxbow lakes 49, 62
 oyster assemblage 2
 Ozan Formation 20
 Pachycormidae 13, 51, 71
 Pachycormiformes 13, 51
Palaeogaleus 1, 12, 15, 16, 29, 30, 63, 65, 68, 69, 71, 74, 75
Palaeogaleus navarroensis 1, 12, 15, 16, 29, 30, 63, 65, 68, 69, 71, 74
Palaeogaleus vincenti 29, 30, 69, 70
Palaeohypotodus rutoti 69, 71, 73
 Palaeospinacidae 12, 31
 Paleobiogeography 69
 Paleocene 2, 16, 18, 25, 30, 36, 41, 43, 48, 53, 58, 68–73, 75
 paleoecological 3, 60, 61
 paleoecology 1, 2, 60
 paleofaunas 1–3, 29, 60, 61, 65, 75
 paleogeographic distribution 1
 paleogeography 1, 39, 60, 66, 67
 paludal 70
 Paluxy Formation 36
 palynoflora 70
 palynomorphs 70
 Panamanian Isthmus 20
Paralbula 13, 15, 51, 54, 62, 63, 65, 68, 72, 74
Paralbula cf. *P. casei* 13, 15, 51, 54, 62, 63, 65, 68, 71, 72, 74
Paranomotodon 27, 28

- Paranomotodon toddi* 1, 12, 15, 16, 27, 28, 63–65, 68–71, 74
Paraorthacodus 14
Paraorthacodus andersoni 1, 12, 15, 16, 31, 32, 63, 65, 68, 69–71, 74
Paraorthacodus conicus 16
Paraorthacodus eocaenus 16
Paratarpon 51, 62
Paratarpon? sp. 1, 51, 54, 63, 65, 68, 72, 74
 Paris Basin 20, 36
 Pawpaw Formation 36
 Pecan Gap Formation 20
 Peedee Formation 26, 27
 pelagic 1, 45, 57, 65, 66, 70, 72–75
 Pencil smelt 56, 62, 65, 74
 Pepper Formation 23, 36
 Perciformes 14, 58
 Phyllodontidae 54
 physical geography 66
 Pierre Formation 5–9, 18, 28, 30, 52, 53, 57, 58, 64, 65, 67
 piscivore 1, 64–66, 74
 placoid scales 1, 29, 45, 64
 plesiosaur 64
Plicatoscyllium sp. 64
Plicatoscyllium derameei 1, 11, 15, 20, 21, 63–65, 68, 69, 71, 74
Plioplatecarpus 18, 64
 Point Lookout Sandstone 35, 46, 47
Pollerspoeckia 54
Pollerspoeckia siegsdorfensis 1, 13, 15, 51, 54, 55, 63, 65, 68, 69, 72, 74, 75
Polygonodon rectus 53
Polygonodon vetus 53
Porthus angulatus 53
 predator 20, 49, 51, 52, 57, 62, 64–66, 70, 73, 74
 progradation 2, 66, 67
Protobathylagus effusus 56
Protoplatyrhina 34
Protoplatyrhina renae 12, 15, 34, 35, 45, 46, 63–65, 68, 71, 74
Protosphyraena 51, 52
Protosphyraena ferox 52
Protosphyraena gladius 52
Protosphyraena nitida 51, 52
Protosphyraena perniciosus 52
Protosphyraena sp. 1, 13, 15, 51, 52, 63–65, 70, 72–74
Protosphyraena tenuis 52
Pseudohypolophus 35–37
Pseudohypolophus ellipsi 36
Pseudohypolophus mcnultyi 13, 15, 32, 35, 36, 46, 63–65, 68, 71, 74
Pteranodon sp. 57
 Pterothrissidae 13, 54
Ptychotrygon 38–40
Ptychotrygon blainensis 52
Ptychotrygon greybullensis 13, 15, 32, 39, 40, 63–65, 68, 69, 71, 74
Ptychotrygon triangularis 52
Ptychotrygon vermiculata 52
Ptychotrygon winni 13, 15, 32, 38, 39, 63–65, 68, 69, 71, 74
 Ptychotrygonidae 13, 38, 71
 Pyrenees 43
Raja molassicus 46
 Rajidae 12, 37, 46
 Rajiformes 12, 32
 Raritan Formation 26
 Ratfish 1, 10, 32, 48
 reptilian 2, 53, 61
 Rhinobatidae 12, 32, 46
Rhinobatus latus 47
Rhinoptera 43
 Rhombodontidae 13, 43, 44, 72
Rhombodus 43, 44
Rhombodus andriesi 44
Rhombodus blinkhorsti 43
Rhombodus bondoni 44
Rhombodus carentonensis 44
Rhombodus levis 1, 13, 15, 41, 43, 44, 45, 46, 63–65, 68, 69, 71, 74
Rhombodus meridionalis 44
Rhombodus microdon 44
Rhombodus sp. 13, 15, 41, 44
 Ripley Formation 20, 59
 riverine 1, 64, 65, 74
 Russia 48
 salamanders 70
 Sannine Limestone 58
 Saskatchewan 23, 69
 Scandinavia 69, 75
 scavenger 1, 18, 29, 64–66, 74
 Sclerorhynchidae 13, 37, 71
 Scollard Formation 51
 sea level fluctuations 2, 60
 Selma Formation 26
Serratolamna 26
Serratolamna serrata 12, 15, 16, 26, 27, 63–65, 68, 70, 71, 73–75
 Serratolamnidae 12, 26
 Severn Formation 2, 21, 24–27, 29, 30, 36, 38, 40, 43, 47, 55, 59, 68, 70, 74
 shallow marine 1, 8, 60, 64, 68, 69, 71, 73, 74
 shark centrum 12, 16, 32
 Sharon Springs Member 53, 57
 Sheridan Delta 66
 shoreline 1–3, 6–8, 60, 62, 66, 67
 shoreline facies 2
 Siluriformes 13, 55
 Sioux Arch 8, 9, 67
 Sioux Uplift 60
 Six Flags Member 36
 SLU: Saint Lawrence University Paleontology Collection 4
 Smokey Hill Member 26, 53
 Soupfin sharks 63
 South Dakota 1, 2, 5, 7–10, 14, 19, 21–24, 27, 29, 34–36, 38, 39, 48, 53, 55–58, 62, 63, 67, 71
 Spain 36
 spawning 64
 Species A.—Indetermined Shark Centrum 12, 16, 28, 32
 Species B.—Indetermined Rhinobatid Centrum 12, 37, 51
 Species C.—Indetermined Teleost Tooth 13, 51
 Species D.—Indetermined Teleost? Bone Fragment 14, 51, 59
 Species E.—Vertebral Morphoserries Type IB-2 of Brinkman 14, 51, 59
 Species F.—Vertebral Morphoserries Type IIIA-1 of Brinkman 14, 51, 59
 Species G.—Indetermined Teleost Scale 14, 51, 59
 Species H.—Indetermined Teleost Scale 14, 51, 60
Squalicorax 28, 29, 64
Squalicorax kaupi 29
Squalicorax pristodontus 1, 12, 15, 16, 28, 29, 64, 65, 68, 70, 71, 73–75
 Squalidae 12, 16
 Squaliformes 12, 16
Squalus 1, 16, 18, 64, 71
Squalus ballingsloevensis 1, 10, 12, 16, 18, 63, 64, 69, 71, 74, 75
Squalus minor 18, 69, 71
Squalus sp. 10, 12, 15, 18, 63–65, 74

- Squatina* 1, 2, 8, 19, 20, 22, 71, 75
Squatina hassei 10, 12, 15, 18–20, 22, 63–65, 68, 69, 71, 74, 75
 Squatinidae 12, 18
 Stoneville facies 9, 35
 Stump Site Natural Area 4
 Sweden 1, 14, 16, 18, 37, 58, 68, 69
 Switzerland 46
 Synechodontiformes 12, 31
Synechodus 2, 16, 31, 32, 71, 75
Synechodus andersoni 16, 32
Synechodus turneri 1, 10, 12, 15, 16, 31, 32, 63, 65, 68, 71, 73
Synechodus striatus 31
 Syria 29
 Taylor Marl 27, 29, 38
 Teapot Sandstone Member 14, 22, 31, 38
 temperate waters 63
 tempestite beds 61
 Tethyan 20, 67–70, 75
 Texas 1, 68, 69, 74
 Texas Gulf Coast 2, 10, 18–24, 26–30, 35, 36, 38–40, 43, 44, 45, 47, 58, 70, 74
Texatrygon hooveri 40
 Thresher shark 45
 tidal-flat 60
 tidal influence 1, 63–65, 74
 Tiger shark 29, 64
 Timber Lake Member 5–9, 32, 36, 40, 42, 57, 60, 66, 67
 Tombigbee Sand 36
 Tongue River Formation 34, 53
 trace fossils 2
 Trail City Member 5, 7, 9
 Transcontinental Arch 67
 Travis Peak Formation 36
 Tremp Formation 43
 Tres Hermanos Formation 38
 Triakidae 12, 29
 tritor 2, 48
 trophic preferences 65
 tropical waters 18, 21, 49, 59, 63
 Tunisia 29
 Turner Sandstone Member 36
 University of North Dakota Paleontology Collection 4
Vinctifer 52
Vorbisia 55, 62
Vorbisia vulpes 13, 15, 51, 55, 62, 63, 65, 68, 70, 72, 74
 Walnut Formation 36
Walteraja 37
Walteraja exigua 1, 12, 15, 32, 37, 63–65, 68, 69, 71, 74, 75
 Weno Formation 36
 Western Interior 5, 9, 10, 53, 57, 66, 68, 69
 Western Interior Seaway (WIS) 1, 2, 5, 8, 9, 20, 24, 28, 30, 34, 36, 39, 53, 56, 60, 62, 66, 68, 70–75
 Wobbeong sharks 19, 22, 63, 64, 74
Wodebousia spinata 1, 8, 61
 Wolfe City Formation 36, 43
 Woodbine Formation 23, 36, 40, 45
 Wyoming 2, 22, 29, 31, 35, 36, 38–41, 46, 47, 51, 53, 62, 66, 72
Xiphactinus 53
Xiphactinus audax 53
Xiphactinus vetus 1, 13, 16, 51, 53, 57, 63–65, 68, 69, 72–74

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