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Fossil fishes from a lag deposit within the Upper Cretaceous Mancos Shale in New Mexico, USA, with comments on correlative Turonian–Coniacian time-transgressive lags in the Western Interior Seaway of North America

Harry M. Maisch IV [a, b, *], Martin A. Becker [c], Kenshu Shimada [d, e]

[a] School of Natural Sciences, Caldwell University, 120 Bloomfield Avenue, Caldwell, NJ 07006, USA
[b] Department of Physics and Mathematics, Bergen Community College, 400 Paramus Road, Paramus, NJ 07652, USA
[c] Department of Environmental Science, William Paterson University of New Jersey, 300 Pompton Road, Wayne, NJ 07470, USA
[d] Department of Environmental Science and Studies and Department of Biological Sciences, DePaul University, 2325 North Clifton Avenue, Chicago, IL 60614, USA
[e] Sternberg Museum of Natural History, Fort Hays State University, 3000 Sternberg Drive, Hays, KS 67601, USA

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ABSTRACT

A lag deposit between the Tocito Sandstone and Mulatto Tongue of the Upper Cretaceous Mancos Shale in Sandoval County, New Mexico, USA, contains a fossil assemblage of late Turonian–early Coniacian chondrichthyans and osteichthyans. This assemblage consists primarily of isolated teeth that derive from at least 26 taxa including: *Meristodonoides* sp.; *Ptychodus mortoni*; *P. mammillaris*; *Scapanorhyncus raphiodon*; *Protolamna* sp.; *Cretodus* cf. *C. semiplicatus*; *Cretodus* sp.; *Cretalamna* "*appendiculata*"; cf. *Eostriatolamia tenuiplicatus*; *Archaeolamna* cf. *A. kopingensis*; *Squalicorax* cf. *S. falcatus*; *S. deckeri; Squalicorax* sp.; *Paranomotodon*(?) sp.; *Rhinobatos lobatus*; *Ptychotrygon triangularis*; *Texatrygon hooveri*; *Pseudohypolophus mcnultyi*; *Ischyrhiza mira*; Chondrichthyes indet.; *Micropycnodon* cf. *M. kansasensis*; Pycnodontiformes indet.; Aspidorhynchidae indet.; *Protosphyraena* sp.; and *Enchodus* cf. *E. gladiolus*. The lag deposit formed along a series of outer shoreface and discontinuous sandbars in the southeastern corner of the San Juan Basin during eustatic sea-level fluctuation herein referred to as the Turonian–Coniacian Time Transgressive (TCTT) Event. This sea-level event and the concentration of fish remains into a lag deposit is also recorded at several other states within the Western Interior Seaway of North America. These stratigraphic properties have correlative potential across basins and states and provide a framework by which regional and eustatic sea-level events can be interpreted. Differences in coeval faunas found within these TCTT lags are bathymetrically controlled, related to the degree of taphonomic reworking, and proximity of the ancestral shoreline.

1. Introduction

During the Late Cretaceous, the Western Interior Seaway (WIS) inundated much of the center of North America forming various siliciclastic and calcareous deposits at numerous localized depositional basins within the primary seaway basin, including New Mexico (Molenaar, 1983; Kauffman, 1984; Cobban et al., 1994; Cumbaa et al., 2010; Scotese, 2014; Slattery et al., 2015). These localized basins generally formed by normal faulting and other structural complexities associated with orogenic events, and their accumulated sediments are well known to contain marine fossils, hydrocarbons, and other geologic resources (Kirk et al., 1978; Weimer, 1978; Bottjer and Stein, 1994; Martinson et al., 1998; Pecha et al., 2018). The largest transgression in the WIS is known to have occurred in the middle–late Turonian and resulted in the greatest inundation of the San Juan Basin in northwestern New Mexico (Molenaar, 1983; Cobban et al., 1994; Nummedal and Molenaar, 1995; Merewether et al., 2007). Numerous field studies in this basin have revealed a rich fossil record of Late Cretaceous invertebrates and vertebrates, including chondrichthyan and

* Corresponding author. School of Natural Sciences, Caldwell University, 120 Bloomfield Avenue, Caldwell, NJ 07006, USA.
E-mail address: hmaisch@caldwell.edu (H.M. Maisch).

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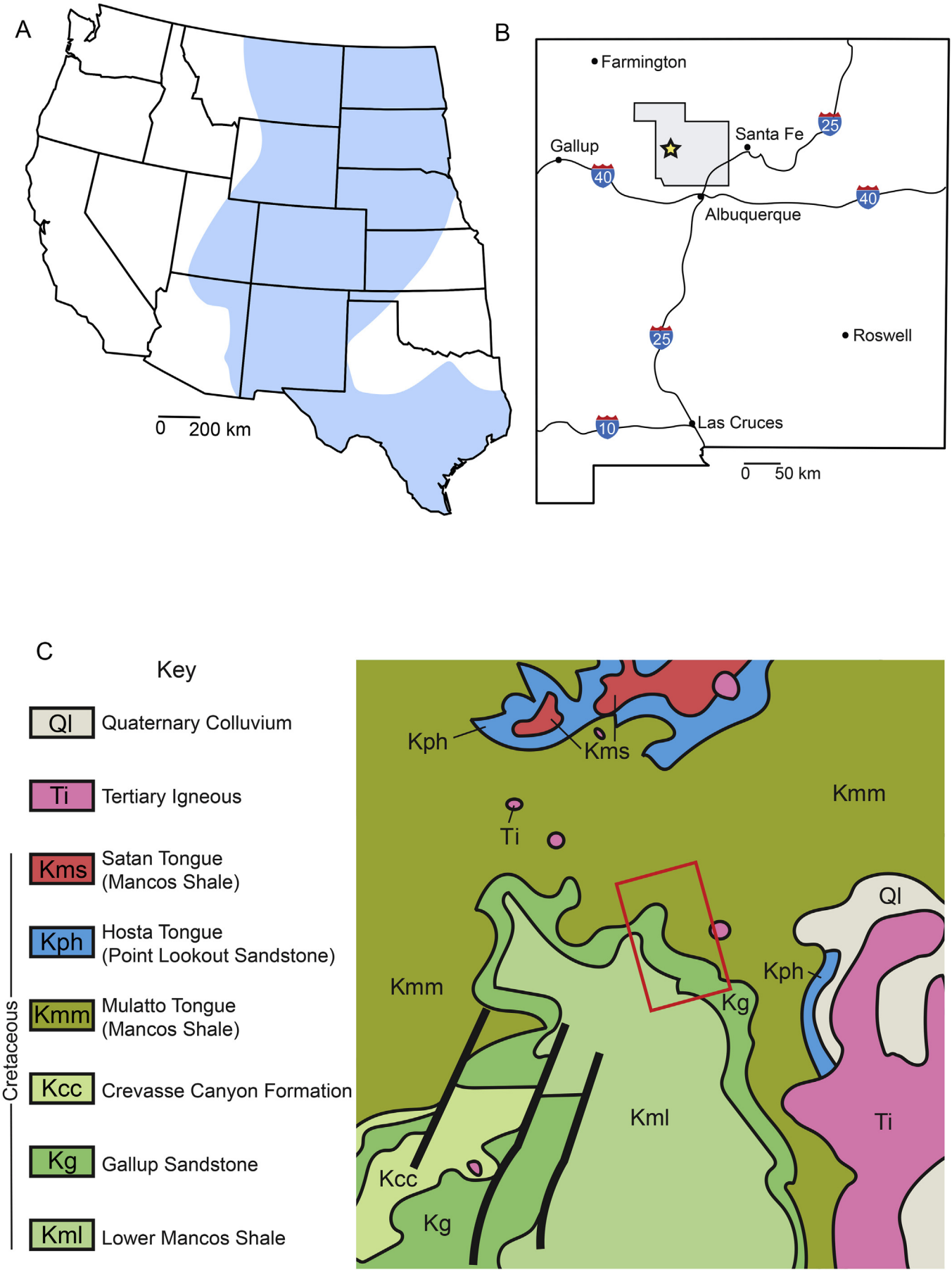
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B
Farmington
Santa Fe
Gallup
Albuquerque
Roswell
Las Cruces
25
40
10
0 50 km
C
Key
Ql Quaternary Colluvium
Ti Tertiary Igneous
Kms Satan Tongue (Mancos Shale)
Kph Hosta Tongue (Point Lookout Sandstone)
Kmm Mulatto Tongue (Mancos Shale)
Kcc Crevasse Canyon Formation
Kg Gallup Sandstone
Kml Lower Mancos Shale
Cretaceous
Kph
Kms
Kmm
Ti
Ql
Kg
Kml
Kcc

osteichthyan fishes (Bourdon et al., 2011; Fassett, 1974; Hunt and Lucas, 1992, 1993; Johnson and Lucas, 2003, 2004; Kirk and Zech, 1977; Lucas et al., 1988; Lucas and Speilmann, 2009; Pence et al., 1986; Scott et al., 2004; Sealey and Lucas, 2019; Speilmann et al., 2009, 2011; Williamson and Lucas, 1990; 1992; Williamson et al., 1989; Wolberg, 1985a, b).

In this study, we describe an assemblage of chondrichthyan and osteichthyan fossils collected from an upper Turonian–lower Coniacian lag deposit between the Tocito Sandstone and Mulatto Tongue of the Mancos Shale in the southeastern San Juan Basin. This lag deposit is exposed east of the Rio Puerco near the eastern border of the Chamisa Wilderness Study area and the western edge of Cerro Cochino in Sandoval County, New Mexico (Fig. 1). The concentration of described fossil remains within this lag is the product of regional and eustatic sea-level regression and transgression across the late Turonian–early Coniacian interval. Several other locations within the WIS also contain similar chondrichthyan and osteichthyan lags that became deposited specifically during the Turonian–Coniacian time-transgressive (hereafter referred to 'TCTT') event. These fossiliferous TCTT boundary lags form distinct stratigraphic horizons that are correlative across different regional basins and locations within the greater WIS basin, where several chondrichthyan taxa are common within these coeval lags and represent index fossils for the 'TCTT interval.' This study further interprets these TCTT boundary vertebrate-bearing lags in a sequence stratigraphic framework in order to recognize the time-transgressive nature of regional and eustatic sea-level cyclicity during the Late Cretaceous within the WIS.

2. Geographic and geologic settings

The field site and source of described fossils in this study occurs in the southeastern portion of the San Juan Basin, that is east of the Rio Puerco and near the eastern border of the Chamisa Wilderness Study area in Sandoval County, New Mexico, on US Bureau of Land Management (BLM) land (Fig. 1). This locality has previously been included in a New Mexico Geological Society fieldtrip guidebook and an unpublished master's thesis and is referred to locally as 'Shark Tooth Ridge' or NMNHM locality 2606 (Williamson and Lucas, 1992; Williams, 2006). Neither of these prior studies identified the occurrence of any osteichthyans or remains of chondrichthyans <2 mm. Both of these previous reports also interpret the El Vado Sandstone Member (Coniacian) of the Mancos Shale as the source of chondrichthyan teeth at this locality.

However, since then, the identification of Turonian–Coniacian strata in the San Juan Basin, including Shark Tooth Ridge, has been revised as described below. In this study, we refer to this specific fossil site as the 'Chamisa Field Site' because of its proximity to the Chamisa Wilderness Study Area and provide a detailed stratigraphic and paleontological analysis of collected chondrichthyans and osteichthyans from the locality.

To date, geologic quadrangle maps have not been compiled for the Chamisa Field Site and surrounding region. However, the current state geological map of New Mexico identifies the Chamisa Field Site occurring at, or in close proximity to, the Turonian–Coniacian boundary and the contact between the Gallup Sandstone and Mulatto Tongue, both of which are subunits within the Mancos Shale (New Mexico Bureau of Geology and Mineral Resources, 2003). The Gallup Sandstone (Turonian) has been interpreted as a regressive, shallow shoreface to beach sandstone consisting of six shallowing-upward sequences. These sequences include nearshore mudstones, shoreface sandstones, and coastal plain, carbonaceous interbedded sandstones and mudstones that extend from the western to the central part of the San Juan Basin before pinching out in proximity to the Chamisa Field Site (Molenaar, 1974, 1983; Tillman, 1986; Jones et al., 1991; Nummedal et al., 1993; Nummedal and Molenaar, 1995; Lin et al., 2019). The Mulatto Tongue (Coniacian) has been interpreted as a transgressive deposit of marine shales and fine-grained sandstones containing discontinuous sand units that include the Tocito and El Vado Sandstone Members (Lamb, 1968; Molenaar, 1983; New Mexico Bureau of Geology and Mineral Resources, 2003; Lin et al., 2019; Sealey and Lucas, 2019). Previous studies have proposed that these two sand units represent: 1) discontinuous portions of the Gallup Sandstone; 2) time-transgressive, reworked components of the underlying Gallup Sandstone; and 3) localized offshore, northwest-southeast trending sandbar deposits that formed parallel with the ancestral shoreline and within the Mulatto Tongue of the Mancos Shale (e.g., Molenaar, 1974, 1983; Tillman, 1986; Nummedal et al., 1993; Bottjer and Stein, 1994; Jennette and Jones, 1995; Nummedal and Molenaar, 1995; Valasek, 1995; Lin et al., 2019).

For this study, we follow the stratigraphic framework and mapping of Lin et al. (2019), Molenaar et al. (1996), New Mexico Bureau of Geology and Mineral Resources (2003), and Sealey and Lucas (2019), where the fossil-bearing lag deposit at the Chamisa Field Site occurs at the upper Tocito Sandstone–Mulatto Tongue contact (Fig. 2). Previous studies identified chondrichthyan teeth found at the Chamisa Field Site to occur in the El Vado Member of the Mancos Shale, but the El Vado Member consists of isolated sand lenses that: 1) reside stratigraphically higher than those of the Tocito Sandstone and have been well-studied further to the northeast; 2) have not been identified in the most recent lithostratigraphic interpretation of the southeastern section of the San Juan Basin; and 3) have been identified to have a middle–late Coniacian age which is inconsistent with the ages of the invertebrate and chondrichthyan fossils recovered from the Chamisa Field Site (e.g., Hedayati, 2008; Lin et al., 2019; Molenaar et al., 1996; Wood and Benavidez, 2017; also see Systematic paleontology and Discussion sections below).

A detailed measured section compiled in Figure 2 identifies the Mancos Shale sequence exposed at the Chamisa Field Site. This measured section consists of: 1) a lowermost platform of fine-grained sandstone within the Gallup Sandstone; 2) a succession of bioturbated sandy shales of the Mulatto Tongue; 3) a coarsening upwards and discontinuous sequence of the Tocito Sandstone; and 4) overlying sandy shales of the Mulatto Tongue (Fig. 3). The lag deposit between the Tocito Sandstone and Mulatto Tongue that is the focus of this study varies between 10 and 30 cm in thickness, is conglomeratic, cross-bedded, and extensively bioturbated, and contains an abundance of abraded vertebrate bones and teeth as well as infrequent, fragmentary invertebrate and carbonized wood remains (Figs. 4–11).

3. Materials and methods

The chondrichthyan and osteichthyan remains identified and described in this study consist primarily of teeth recovered in the field through a combination of: 1) surface collecting isolated and matrix specimens; 2) surface picking specimens from harvester ant nests; and 3) sieving fossiliferous surface sediment through

Fig. 1. Geographic and geologic settings. A, western United States and maximum extent of Late Cretaceous Western Interior Seaway during the Turonian; B, Chamisa Field Site (indicated by star) within Sandoval County, New Mexico, USA modified from Scotese (2014); C, regional geology of Late Cretaceous (Turonian–Coniacian) Mancos Shale and Tocito Sandstone–Mulatto Tongue contact within Sandoval County, including the Chamisa Field Site (rectangle on map) modified from the New Mexico Bureau of Geology and Mineral Resources (2003) Geologic Map of New Mexico, 1:500,000.

5.0–10.0 mm screens. In the laboratory, approximately 100 kg of this sediment was thoroughly rinsed through a series of stacked screens with mesh sizes between 0.5 and 5.0 mm, dried, and prospected for microscopic fossil remains with forceps under a binocular microscope. Isolated and matrix specimens included in this report were imaged with a Olympus SZ61 binocular microscope attached to an Infinity-2 digital camera or a Canon EOS Rebel T5 digital camera and measured using a digital caliper. Primary literature sources utilized for taxonomic descriptions below are: Becker et al. (2010); Bice and Shimada (2016); Cappetta (2012); Hamm and Cicimurri (2011); and Ouroumova et al. (2016). Field study and collection of fossils for this report was completed over two field seasons under BLM paleontological resource surface collection permit NM 19-01S. All fossil specimens in this study have been reposited in the invertebrate paleontology (IP) and vertebrate paleontology (VP) collections of the Academy of Natural Sciences (ANSP) at Drexel University, Philadelphia, Pennsylvania, USA under the catalog numbers ANSP IP 81680–81701 and ANSP VP 26300–26537.

4. Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Order Hybodontiformes Maisey, 1989
Family Hybodontidae Owen, 1846
Subfamily HYBODONTINAE Owen (1846)
Genus *Meristodonoides* Underwood and Cumbaa, 2010

Meristodonoides sp.

Fig. 5A–F

Material. Four isolated tooth fragments (figured teeth: ANSP VP 26300–26302 and one additional tooth ANSP VP 26303).
Description. The larger of the two tooth fragments measures 7.9 mm in total height and 5.4 mm in width. Teeth of this taxon exhibit a rounded, blunt main cusp with a medially positioned cutting edge. The lingual and labial tooth surfaces contain widely and irregularly spaced, longitudinal ridges.
Discussion. Teeth of *Meristodonoides* sp. can be readily distinguished from those of other chondrichthyans in the Chamisa Field Site assemblage, because they have main cusps with blunt apices and a rounded cross-section, a medially positioned cutting edge, and irregular longitudinal ridges on both the lingual and labial tooth surfaces. Teeth attributed to *Meristodonoides* from Upper Cretaceous deposits of North America also contain a single pair of broadly-spaced lateral cusplets with a smooth cutting edge that is continuous with the main cusp, and were previously assigned to another hybodontid genus, *Hybodus* (e.g., Underwood and Cumbaa, 2010). To date, several distinct *Meristodonoides* (*Hybodus*) species, including *M. butleri, M. montanensis,* and *M. rajkovichi,* have been reported from Albian–Campanian WIS deposits in Texas, Utah, Kansas, Wyoming, Montana, Alberta, and Saskatchewan (e.g., Beavan and Russell, 1999; Becker et al., 2010; Bice and Shimada, 2016; Bourdon et al., 2011; Cappetta and Case, 1999; Case, 1978, 1987; Cicimurri, 2001; Cook et al., 2008; Cumbaa et al., 2006; Eaton et al., 1999; Everhart, 2011; Hamm and Cicimurri, 2011; Johnson and Lucas, 2003; Ouroumova et al., 2016; Schubert et al., 2017; Speilmann et al., 2009; Thurmond, 1971; Underwood and Cumbaa, 2010; Welton and Farish, 1993; Williamson and Lucas, 1992; Williamson et al., 1989, 1993; Wolberg, 1985a,b). However, due to the recovery of only four fragmentary specimens from the Chamisa Field Site, we refrain from species-level taxonomic identification of *Meristodonoides* teeth in our sample.

Order Incertae sedis
Family Ptychodontidae Jaekel, 1898
Genus *Ptychodus* Agassiz, 1835

Ptychodus mortoni (Mantell, 1836)
Figs. 5G–X, 11B

Material. Twelve isolated teeth (ANSP VP 26304–26315) and eight teeth in matrix (ANSP VP 26316–26323) (figured teeth: ANSP VP 26304–26308, and 26316).
Description. The largest median tooth measures 9.5 mm in total height and 10.3 mm in width whereas the largest lateral tooth measures 8.8 mm in total height and 9.8 mm in width. Teeth of this species have occlusal surfaces with a single, elevated, and conical cusp. Median teeth have a centrally located cusp, whereas lateral teeth are more elongate, asymmetric, and contain cusps that are off center. All teeth of this species possess ridges and grooves that emanate radially from the cusp apex that become less developed before terminating at or near the periphery of the crown. The edge of the crown is rounded and slightly overhangs the root base that is box-like and may exhibit a number of small, nutritive foramina.
Discussion. Ptychodus mortoni has been reported from numerous Coniacian–Campanian deposits globally (e.g., Blanco-Piñón et al., 2007; Shimada et al., 2010a; Cappetta, 2012; Hamm, 2020). From the WIS deposits, *P. mortoni* is known from Texas, New Mexico, Colorado, and Kansas (e.g., Williamson et al., 1989; Williamson and Lucas, 1990, 1992; Welton and Farish, 1993; Shimada, 1996; Cappetta and Case, 1999; Eaton et al., 1999; Johnson and Lucas, 2003; Shimada and Fielitz, 2006; Bourdon et al., 2011; Hamm and Cicimurri, 2011; Bice and Shimada, 2016). Teeth of *P. mortoni* are distinct from those of *P. mammillaris* Agassiz, 1835, *Pseudohypolophus mcnultyi* (Thurmond, 1971), and *Ptychotrygon triangularis* (von Reuss, 1844), that also occur in the Chamisa Field Site assemblage, because they contain a large, conical cusp with radially organized ridges and grooves across the entire occlusal surface. However, during the Late Cretaceous, numerous species of *Ptychodus* have been identified from isolated teeth, and interpreted as biostratigraphically important index fossils (e.g., Welton and Farish, 1993; Williams, 2006; Hamm, 2020). *Ptychodus* species with teeth appearing similar to those of *P. mortoni* include: *P. anonymus* Williston (1900); *P. atcoensis* Hamm and Cicimurri (2011); *P. mammillaris* Agassiz, 1835; *P. marginalis* Agassiz, 1835; *P. rugosus* Dixon (1850); and *P. whipplei* Marcou (1858). Teeth from these taxa exhibit noticeably different central cusp shapes, occlusal surface ornamentation, and may also have biostratigraphic ranges that differ from those of *P. mortoni* (Welton and Farish, 1993; Cappetta, 2012; Hamm, 2020). Additional information about *P. mortoni* and other *Ptychodus* taxa can be found in Cappetta (2012) and Hamm (2020).

Ptychodus mammillaris Agassiz, 1835

Fig. 5Y–Z

Material. Two teeth, one of which is fragmentary (ANSP VP 26324) and one tooth in matrix (ANSP VP 26325).
Description. Both specimens are represented by the apical portion of the cusp, the largest of which measures 2.8 mm in total height and 6.8 mm in width. Each specimen exhibits a series of well-defined, regularly spaced, transversely arranged ridges on the occlusal crown surface. These ridges and grooves become thinner further from the center of the cusp and are surrounded by numerous, irregular, fine concentric ridges and grooves.
Discussion. The teeth of *Ptychodus mammillaris* are distinct from those of *P. mortoni, Pseudohypolophus mcnultyi*, and *Ptychotrygon triangularis*, that also occur at the Chamisa Field Site by the presence of a series of well-defined, regularly spaced transverse ridges

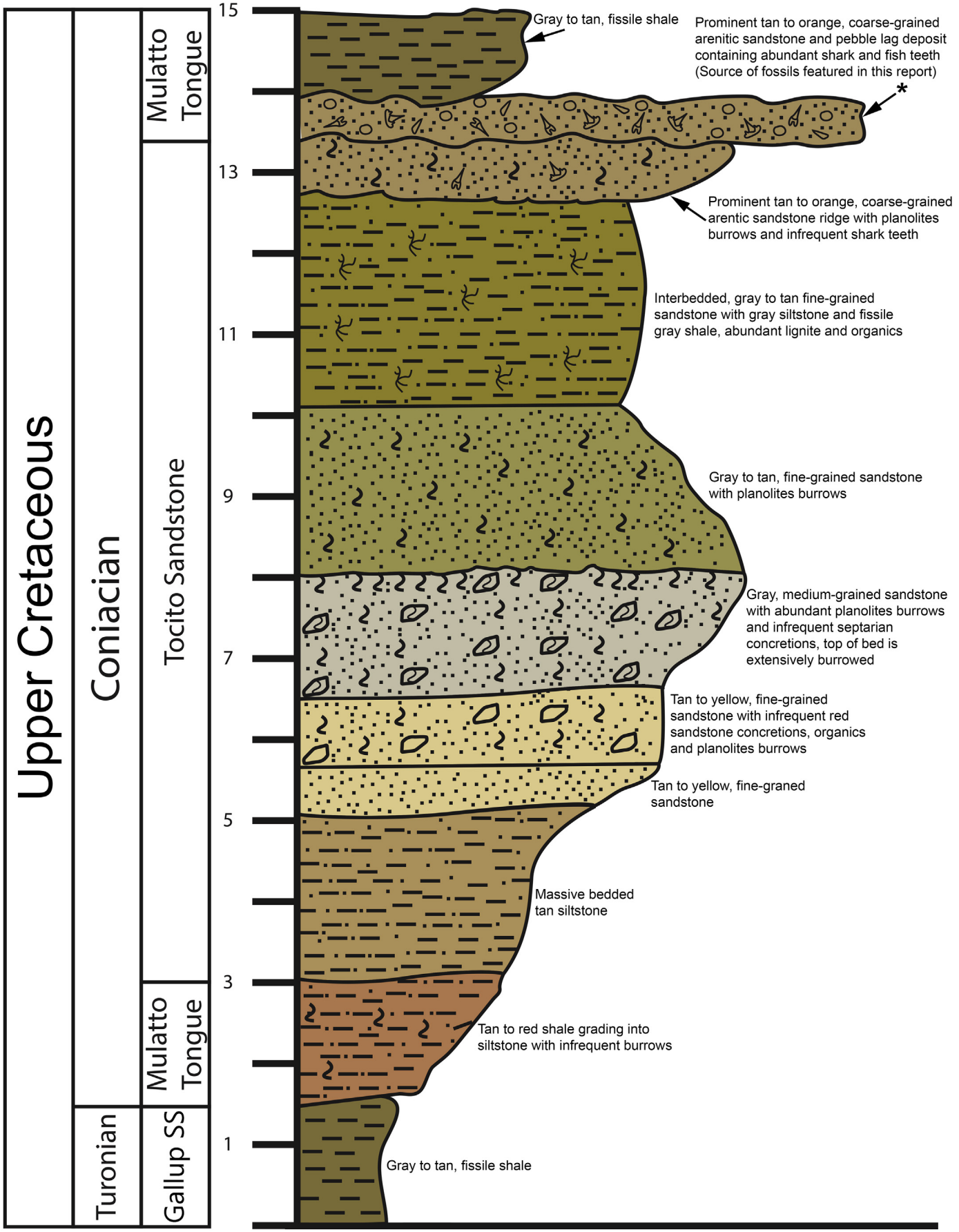
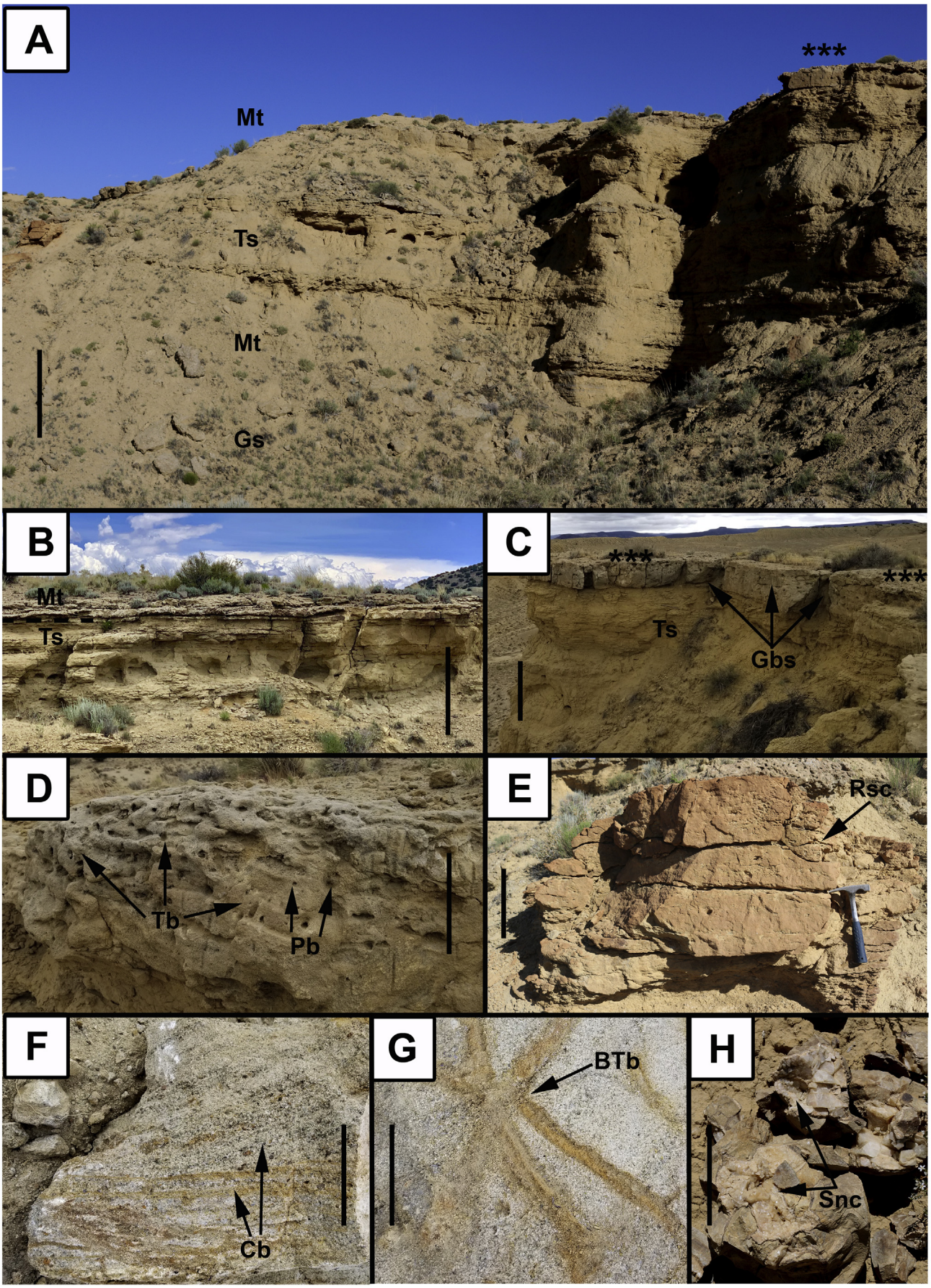


Fig. 2. Stratigraphic column of Upper Cretaceous (Turonian–Coniacian) formations exposed at the Chamisa Field Site in Sandoval County, New Mexico, USA described in this report. Note lag deposit and source of fossil fish remains featured in this study indicated by *. SS = sandstone. Vertical scale in meters.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occurring across a rounded cusp apex. Although teeth belonging to *Ptychodus anonymus* Williston (1900), *P. decurrens* Agassiz, 1835, *P. marginalis* Agassiz, 1835, and *P. whipplei* Marcou (1858), may appear similar to those of *P. mammillaris*, they possess either flatter or narrower cusps, uniquely ornamented occlusal surfaces, and have distinct biostratigraphic ranges. Our identification of these uncommon *Ptychodus* teeth in the Chamisa Field Site assemblage as *P. mammillaris* is in agreement with this taxon's Turonian–Coniacian biostratigraphic range (Williamson and Lucas, 1992; Williams, 2006; Hamm, 2020). *Ptychodus mammillaris* has been reported globally throughout the Turonian–Coniacian rocks in North America, Africa, Europe, and Asia (e.g., Antunes and Cappetta, 2002; Cappetta, 2012; Hamm, 2020). The North American record includes reports from WIS deposits in Texas, New Mexico, Arizona, Utah, Kansas, Wyoming, and South Dakota (e.g., Evetts, 1979; Williamson and Lucas, 1992; Welton and Farish, 1993; Williamson et al., 1993; Cicimurri, 1998, 2004; Cappetta and Case, 1999; Shimada and Everhart, 2003; Williams, 2006; Speilmann et al., 2009; Becker et al., 2010; Hamm and Cicimurri, 2011). For additional details on *Ptychodus* taxa, see discussion above on *P. mortoni* as well as Cappetta (2012) and Hamm (2020).

Order Lamniformes Berg, 1958
Family Mitsukurinidae Jordan, 1898
Genus *Scapanorhynchus* Woodward, 1889

Scapanorhynchus raphiodon (Agassiz, 1843)

Figs. 6A–H, 11A, E

Material. Thirteen isolated teeth (ANSP VP 26326–26338) and twelve additional teeth in matrix (ANSP VP 26339–26350) (figured teeth: ANSP VP 26326–26329, 26339, and 26340).
Description. The largest anterior tooth measures 27.3 mm in total height and 9.5 mm in width whereas the largest lateral tooth measures 14.4 mm in total height and 9.6 mm in width. Anterior teeth of this species have a narrow, erect main cusp with many faint, longitudinal striations on a convex lingual surface, and a smooth, nearly flat labial surface. A single pair of small, triangular to hook-like lateral cusplets may be present that are oriented in the same direction as the main cusp. A smooth cutting edge is present and is continuous between the main cusp and lateral cusplets. Lateral teeth have labiolingually compressed main cusps that are more triangular in shape and distally inclined. The roots of anterior and lateral teeth are holaulacorhizous, widely separated, and contain a lingual protuberance with a nutritive groove. Anterior tooth root lobes are rounded whereas those of lateral teeth are more compressed and spatulate.
Discussion. Extensive literature exists on *Scapanorhynchus raphiodon*, including reports from Cenomanian–Coniacian deposits globally (e.g., Niedzwiedźki and Kalina, 2003; Cappetta, 2012; Guinot et al., 2013; Retzler et al., 2013). From the WIS deposits, *S. raphiodon* is recorded in Texas, Kansas, New Mexico, Arizona, Utah, Colorado, Wyoming, Nebraska, and South Dakota (e.g., Becker et al., 2010; Bice and Shimada, 2016; Cappetta and Case, 1999; Cicimurri, 2001, 2004; Edwards, 1976; Hamm and Shimada, 2002; Johnson and Lucas, 2003; Ouroumova et al., 2016; Russell, 1988; Speilmann et al., 2009; Welton and Farish, 1993; Williamson and Lucas, 1990, 1992; Williamson et al., 1989, 1993; Wolberg, 1985). Teeth of *S. raphiodon* are distinct from those of *Archaeolamna* cf. *A. kopingensis* (Davis, 1890), *Cretalamna* "*appendiculata*" (Agassiz, 1843), and *Cretodus* sp. that also occur in the Chamisa Field Site assemblage by exhibiting narrower main cusps and cusplets, containing many longitudinal striations on the lingual surface of the main cusp, and having roots with a nutritive groove on the lingual protuberance. Teeth belonging to *S. texanus* (Roemer, 1849) have more developed lingual striations, attain larger overall sizes, and are known to occur later in the Cretaceous, distinguishing them from *S. raphiodon* (Welton and Farish, 1993; Niedzwiedźki and Kalina, 2003; Cappetta, 2012). Teeth from *Carcharias* and *Odontaspis* species may also appear similar to those of *S. raphiodon*, but they generally have more sigmoidal cusps (e.g., Welton and Farish, 1993; Hamm and Shimada, 2002; Cappetta, 2012). Teeth of *S. puercoensis* Bourdon et al., 2011, reported from the Hosta Tongue Member (Santonian) of the Point Lookout Sandstone of New Mexico may also appear similar to those of *S. raphiodon* from the Chamisa Field Site. However, teeth of *S. puercoensis* have been distinguished from those of *S. raphiodon* based on the presence of well-defined lateral cusplets in anterior teeth, a second pair of lateral cusplets in some lateral teeth, and narrower main cusps in all tooth positions. Although it is possible that teeth identified as *S. puercoensis* may belong to a distinct species, this taxon has not been reported elsewhere in New Mexico, the WIS, or globally. Moreover, the presence or absence of lateral cusplets has been shown to vary in various lamniform sharks individually, ontogenetically, or sexually in certain taxa (e.g., Applegate, 1965; Hubbell, 1996; Cappetta, 2012; van Vuuren et al., 2015). As such, we follow previous studies on Turonian–Coniacian chondrichthyans and consider these teeth from the Chamisa Field Site as *S. raphiodon* (e.g., Wolberg, 1985; Williamson and Lucas, 1992; Welton and Farish, 1993; Williamson et al., 1993; Speilmann et al., 2009; Becker et al., 2010; Hamm and Cicimurri, 2011; Cappetta, 2012; Bice and Shimada, 2016).

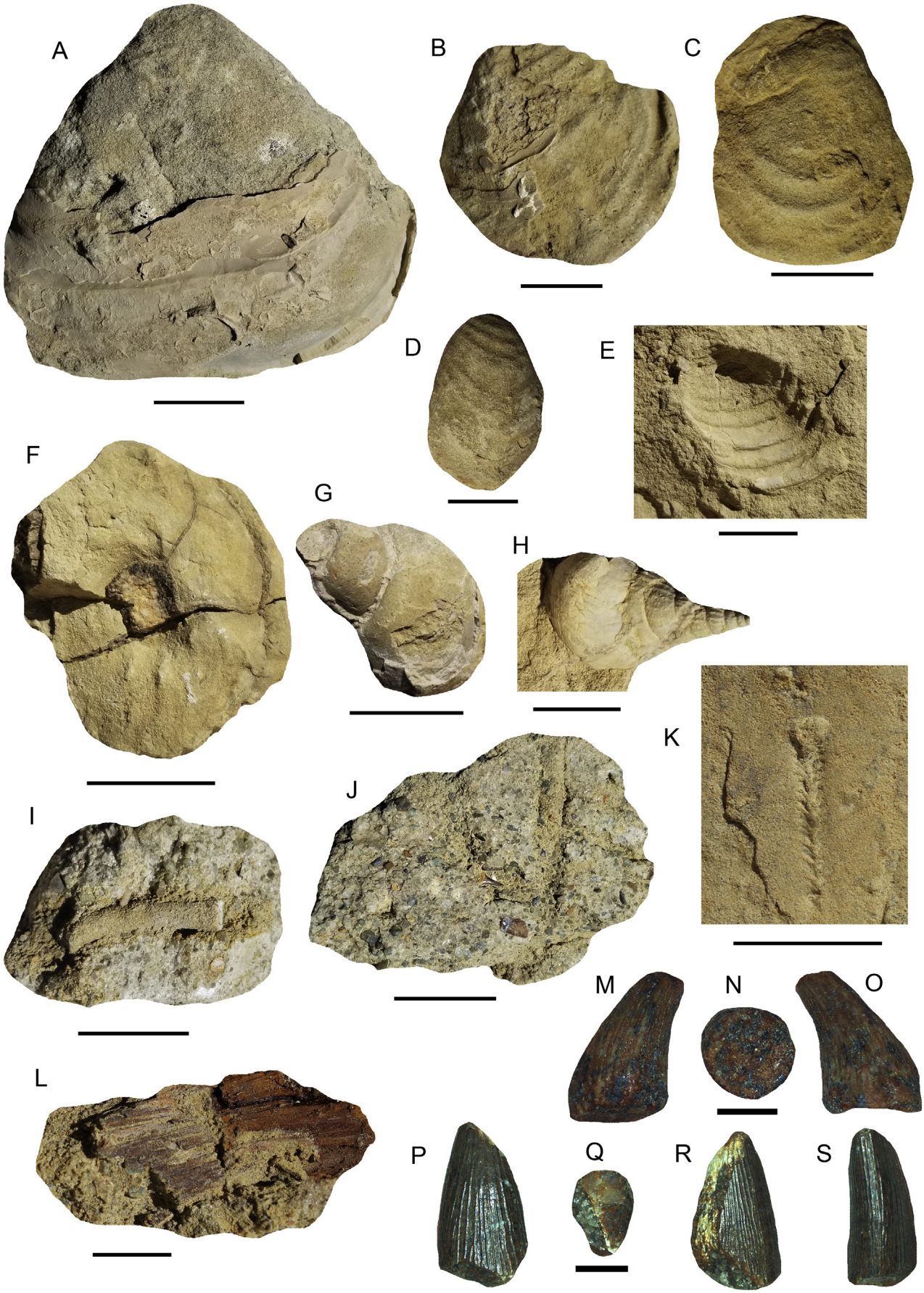
Family Otodontidae Glikman, 1964
Genus *Cretalamna* Glikman, 1958

Cretalamna "appendiculata" (Agassiz, 1843) sensu lato

Figs. 6I–T, 11C–D

Material. Fifteen isolated teeth (ANSP VP 26376–26390) and five teeth in matrix (ANSP VP 26391–26395) (figured teeth: ANSP VP 26376–26381, 26391, and 26392).
Description. The largest anterior tooth measures 13.9 mm in total height and 12.7 mm in width whereas the largest lateral tooth measures 13.5 mm in total height and 13.5 mm in width. Anterior teeth of this taxon have an erect, central main cusp and a single pair of broad, triangular lateral cusplets. The main cusp and distal cusplets of lateral teeth are distally inclined. All teeth are labiolingually compressed where the lingual surface is convex relative to the labial surface which is nearly flat. The roots of all teeth are holaulachorhizous, contain widely separated and angular root lobes

Fig. 3. Outcrop exposures, burrows and sedimentary features at the Chamisa Field Site, Sandoval County, New Mexico, USA. A, outcrop exposure utilized to measure the section depicted in Fig. 2 showing the Gallup Sandstone, lower Mulatto Tongue, Tocito Sandstone, and upper Mulatto Tongue of the Mancos Shale in ascending order. B, additional Tocito Sandstone–Mulatto Tongue exposure displaying prominent, gray, and bioturbated coarse sandstone bed overlying a succession of tan sandstones and siltstones. C, additional exposure of prominent, ridge-forming, gray, and bioturbated coarse sandstone bed immediately underlying the fossiliferous lag deposit. D, close-up view of extensive burrows of *Planolites* and *Thalassinoides* isp. in the coarse gray sandstone bed in Figs. 3B,C. E, large red sandstone concretion occurring near the middle of the measured section in Fig. 2.; F, cross-bedding in examined fossiliferous lag deposit; G, branching burrows of *Thalassinoides* isp. in examined fossiliferous lag deposit; H, septarian concretion containing calcite crystals from the Mulatto Tongue of the Mancos Shale. Abbreviations: Gs, Gallup Sandstone; Mt, Mulatto Tongue of the Mancos Shale; TS, Tocito Sandstone; Gbs, gray bioturbated sandstone; Tb, *Thalassinoides* isp. burrows; Pb, *Planolites* isp. burrows; Rsc, red sandstone concretion; Cb, cross-bedding; BTb, branching *Thalassinoides* burrows; Snc, septarian nodule calcite; ***, location of the fossiliferous lag deposit described in this report. Scale bars: A–B = 5 m; C = 2 m; D–E, H = 20 cm; and F–G = 10 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)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that form a shallow, U-shaped basal concavity, and have a flattened lingual root base. A faint lingual protuberance containing a nutritive foramen may be present.

Discussion. Teeth of *Cretalamna* "*appendiculata*" are distinct from those of *Archaeolamna* cf. *A. kopingensis*, *Cretodus* cf. *C. semiplicatus* (Agassiz, 1843), *Cretodus* sp., *Paranomotodon*(?) sp., and *Protolamna* sp. that also occur in the Chamisa Field Site assemblage because they are labiolingually compressed, lack well-developed lingual protuberances, and have broad, triangular lateral cusplets that are aligned with the main cusps. Teeth belonging to *Cretalamna woodwardi* Herman (1977), *Cretodus crassidens* (Dixon, 1850), *Haimirichia* (*Carcharias*) *amonensis* (Cappetta and Case, 1975), and other morphologically similar Late Cretaceous taxa can also be distinguished from those of *Cretalamna* "*appendiculata*" based on the aforementioned characteristics in addition to slight variations in cusplet orientation, overall size, biostratigraphic ranges, and paleobiogeographic distributions.

Cretalamna "*appendiculata*" is well-documented globally and has a biostratigraphic range of over 50 million years, ranging from the Albian–middle Eocene, which suggests it may represent a large species complex instead of a single, long-ranging species (e.g., Müller and Diedrich, 1991; Siverson, 1992, 1996; Mustafa, 2000; Antunes and Cappetta, 2002; Mustafa et al., 2002; Vullo, 2005; Shimada, 2007; Kennedy et al., 2008; Andreev and Motchurova-Dekova, 2010; Underwood and Cumbaa, 2010; Cappetta, 2012; Retzler et al., 2013; Siversson et al., 2015; Bice and Shimada, 2016). If *C.* "*appendiculata*" is regarded as a species complex, then it is possible that the teeth from the Chamisa Field Site may in fact belong to the Turonian and/or Coniacian-aged species: *C. appendiculata* (Agassiz, 1843) or *C. ewelli* Siversson et al. (2015), respectively (sensu Bice and Shimada, 2016; Siversson et al., 2015). With particular reference to the WIS deposits, *C.* "*appendiculata*" has been reported from Albian–Maastrichtian deposits in Texas, Kansas, New Mexico, Arizona, Utah, Colorado, Wyoming, Nebraska, South Dakota, Montana, and Saskatchewan (e.g., Becker et al., 2010; Bice and Shimada, 2016; Bourdon et al., 2011; Cappetta and Case, 1975, 1999; Cicimurri, 2004; Cumbaa et al., 2006; Gallardo et al., 2012; Hamm and Cicimurri, 2011; Jansen et al., 2013; Ouroumova et al., 2016; Martin and Stewart, 1977; McIntosh et al., 2013; Shimada, 1996, 2006; Shimada and Fielitz, 2006; Shimada et al., 2006; Siverson and Lindgren, 2005; Stewart and Martin, 1993; Underwood and Cumbaa, 2010; Welton and Farish, 1993; Williams, 2006; Williamson and Lucas, 1992; Wolberg, 1985a,b).

Family Odontaspididae Müller and Henle, 1839
Genus *Eostriatolamia* Glikman, 1980

cf. ***Eostriatolamia tenuiplicatus*** (Cappetta and Case, 1975)

Fig. 6U–Aa

Material. Three isolated teeth (ANSP VP 26404–26406).

Description. The largest tooth has a total height of 4.2 mm and width of 2.6 mm. Teeth of this taxon have striations on the crown surfaces that are especially well-developed on the labial face. The crown and lateral cusplets are thin and erect and a second pair of reduced lateral cusplets may occur. The root is bilobate and contains a faint nutritive groove.

Discussion. Teeth of *Eostriatolamia tenuiplicatus* are distinct from those of *Scapanorhynchus raphiodon*, *Archaeolamna* cf. *A. kopingensis*, and *Paranomotodon*(?) sp. that may appear similar and also occur in the Chamisa Field Site assemblage because they are much smaller, have thin, erect main cusps and cupslets, and exhibit labial and lingual crown surface ornamentation. Although these Chamisa Field Site teeth are uncommon and fragmentary, they appear most similar to those of *E.* (*Cenocarcharias*) *tenuiplicatus*. Teeth of *E. tenuiplicatus* were differentiated from *E. striatula* because they have a smaller and thicker size, cusp that is less inclined, and a greater amount of lingual tooth surface ornamentation (Cappetta and Case, 1999). However, Underwood and Cumbaa (2010) indicated that teeth of both taxa are highly variable, *Cenocarcharias* should be considered a junior synonym of *Eostriatolamia*, and *E. tenuiplicatus* and *E. striatula* may also be synonymous. *Eostriatolamia paucicorrugata* Underwood and Cumbaa (2010) differs from *E. tenuiplicatus* because teeth from the latter taxon may entirely lack surface ornamentation, contain larger lateral cusplets, and are only known from the northern part of the WIS (Underwood and Cumbaa, 2010). To date, *E. tenuiplicatus* has only been reported from Texas, Kansas, Colorado, Nebraska, and South Dakota (e.g., Cappetta and Case, 1975, 1999; Welton and Farish, 1993; Cicimurri, 2001; Cumbaa et al., 2006; Shimada et al., 2006; Shimada and Martin, 2008; Jansen et al., 2013).

Family Archaeolamnidae Underwood and Cumbaa, 2010
Genus *Archaeolamna* Siverson, 1992

Archaeolamna cf. ***A. kopingensis*** (Davis, 1890)

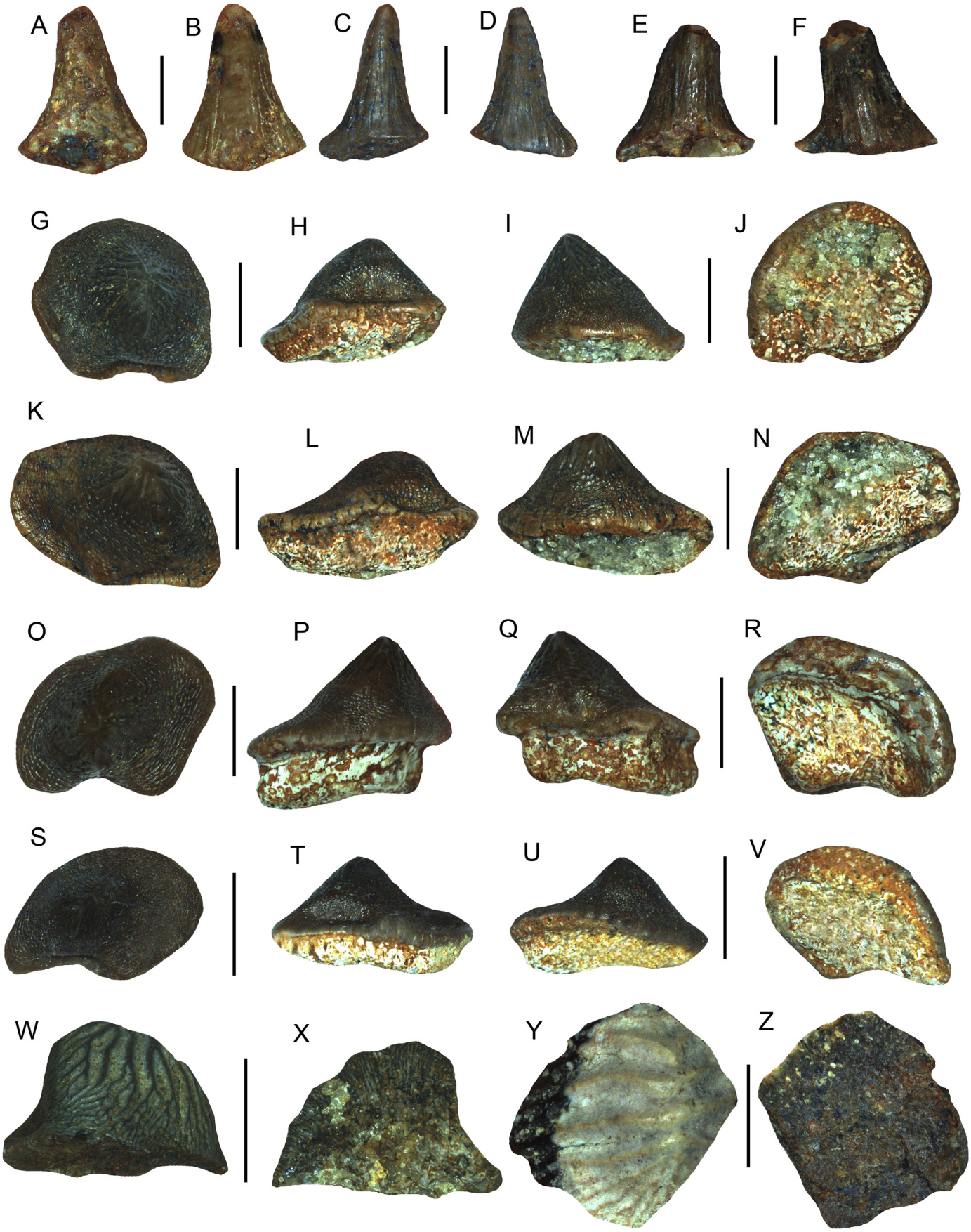
Figs. 6Bb–Hh, 11G

Material. Twelve isolated teeth (ANSP VP 26306–26371) and four teeth in matrix (ANSP VP 26372–26375) (figured teeth: ANSP VP 26360–26362, and 26372).

Description. The largest anterior tooth measures 24.4 mm in total height and 15.8 mm in width whereas the largest lateral tooth measures 7.7 mm in total height and 9.3 mm in width. Anterior teeth of this taxon have an erect, triangular main cusp with a single pair of lateral cusplets that are slightly taller than they are wide and are oriented away from the main cusp. Lateral teeth have distally inclined main cusps with distal lateral cusplets that are slightly smaller than the mesial cusplets. The main cusp and lateral cusplets of anterior and lateral teeth have a strongly convex lingual surface and slightly convex labial surface. A well-defined, smooth, and continuous cutting edge occurs between the main cusp and lateral cusplets. Between the crown and root on the lingual face is a well-marked tooth neck. The root is holaulachorhizous and robust and the root lobes are widely separated with a U-shaped basal concavity. A well-defined lingual protuberance is present and may exhibit one or more small, nutritive foramina.

Discussion. Teeth of *Archaeolamna* cf. *A. kopingensis* are distinct from those of *Cretalamna* "*appendiculata*", *Cretodus* sp., and *Protolamna* sp. that also occur in the Chamisa Field Site assemblage because they contain lateral cusplets that are angled away from the main cusp, lack tooth surface ornamentation, and have robust, rounded root lobes. The teeth of *Cretodus* spp. (e.g., *C. semiplicatus* and *C. houghtonorum* Shimada and Everhart, 2019) may bear some resemblance to those of *A.* cf. *A. kopingensis*, but teeth from these

Fig. 4. Representative non-fish fossils from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale Contact (Turonian–Coniacian), Sandoval County, New Mexico, USA. A–E, *Cremnoceramus deformis erectus* (Meek, 1877) inoceramid casts and mold (ANSP IP 81680–81684); F, cf. *Forresteria hobsoni* ammonite cast (ANSP IP 81688) from a septarian concretion; G–H, gastropod casts (ANSP IP 81689–81690) from the Mulatto Tongue of the Mancos Shale directly overlying examined fossiliferous lag deposit; I, Infilled *Planolites* isp. (ANSP IP 81694) burrow from the examined fossiliferous lag deposit; J, *Thalassinoides* isp. (ANSP IP 81695) burrow from the examined fossiliferous lag deposit (note *Scapanorhynchus raphiodon* tooth near center of rock); K, *Ancorichnus* isp. (ANSP IP 81691) burrow from the Mulatto Tongue overlying the lag deposit; L, carbonized wood fragment (ANSP IP 81701). M–O, indeterminant reptilian tooth (ANSP VP 26536); and P–S, fragmentary plesiosaurid tooth (ANSP VP 26532) recovered from examined fossiliferous lag deposit. Scale bars in A; F; J = 5 cm; B–E; G–I; K; L = 2 cm; and M–S = 1 cm. Reptilian tooth orientations: M, O, R = lateral; N, Q = basal; P = anterior; S = posterior.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taxa generally exhibit fine folds along the crown base, contain more labiolingually robust lateral cusplets and roots, and attain larger sizes (Welton and Farish, 1993; Becker et al., 2010; Hamm and Cicimurri, 2011; Cappetta, 2012; Bice and Shimada, 2016). Teeth of *Dallasiella willistoni* Cappetta and Case (1999), may also appear similar to small teeth of *A.* cf. *A. kopingensis*; however, they can be distinguished based on the presence of a well-developed nutritive groove on the lingual root surface and smaller overall size (Cappetta and Case, 1999; Hamm and Cicimurri, 2011; Cappetta, 2012).

Archaeolamna kopingensis has been reported globally from the Albian–Maastrichtian in North America, Europe, Asia, and Australia (e.g., Siverson, 1992, 1996; Vullo et al., 2007; Underwood and Cumbaa, 2010; Cappetta, 2012; Guinot et al., 2013). From the WIS deposits, *A. kopingensis* is known from New Mexico, Colorado, Kansas, Nebraska, Iowa, Nebraska(?), Alberta, and Saskatchewan (e.g., Shimada et al., 2006; Williams, 2006; Kennedy et al., 2008; Cook et al., 2008, 2011, 2013; Underwood and Cumbaa, 2010; Gallardo et al., 2012; Nagrodski et al., 2012; McIntosh et al., 2013; Meglei et al., 2013; Gorman et al., 2014; Bice and Shimada, 2016). Due to the nearly global distribution of *A. kopingensis* during the Late Cretaceous, and the variable degrees of tooth morphology that have been identified, this taxon may actually represent multiple species or subspecies (e.g., Cook et al., 2008; Siverson, 1992, 1996). In a study on Cenomanian chondrichthyans from Saskatchewan, Underwood and Cumbaa (2010) indicated that teeth of *A. kopingensis* have robust and gracile forms and a variety of subtle variations, including the presence of short longitudinal folds along the labial crown base of larger teeth likely representing ontogenetic or sexual heterodonty. These factors, and the often subtle morphological differences among *A. kopingensis*, *Cretalamna*, and *Cretodus* may also account for the paucity of occurrence data of *A. kopingensis* throughout the Turonian–Coniacian deposits of the WIS (e.g., Cumbaa et al., 2010; Underwood and Cumbaa, 2010; Cappetta, 2012). As such, we conservatively identify these teeth from the Chamisa Field Site as *A.* cf. *A. kopingensis* until additional taxonomic studies are conducted.

Family Pseudoscapanorhynchidae Herman, 1979
Genus *Protolamna* Cappetta, 1980a

Protolamna sp.

Fig. 7A–I

Material. Twelve isolated teeth (ANSP VP 26396–26403) (figured teeth: ANSP VP 26396–26399).
Description. The largest tooth measures 11.7 mm in total height and 6.8 mm in width. Anterior teeth of this taxon have narrow, erect, smooth main cusps with nearly flat labial faces and convex lingual faces. A single pair of narrow, lateral cusplets is separated from the main cusp by a distinct notch and are more visible on the labial surface. Lateral teeth have distally inclined main cusps that are triangular in shape and contain lateral cusplets that are angled away from the main cusp. The cusps and cusplets of anterior and lateral teeth are lingually inclined and the labial crown base overhangs the root. The roots of anterior and lateral teeth are holaulochorhizous and robust, and have a well-defined lingual protuberance. Root lobes are elongated and taper to rounded bases where their mesial and distal edges are roughly parallel with each other. Root lobes are roughly equidimensional in anterior teeth whereas those of lateral teeth are asymmetrical with a smaller distal root lobe than the mesial one.
Discussion. Teeth of the genus *Protolamna* have been reported globally from rocks representing much of the Cretaceous (Valanginian–Maastrichtian) in North America, Africa, Europe, Asia, and Australia (e.g., Cappetta, 1975, Cappetta, 1980a, 2012; Cappetta and Case, 1999; Itoigawa et al., 1977; Kitamura, 2019; Noubhani and Cappetta, 1997, as *Cretodus* sp.; Siverson, 1997, as *Leptostyrax*; Siversson and Machalski, 2017). From the WIS deposits, *Protolamna* has only been reported from Cenomanian–Coniacian deposits in Texas, New Mexico, Wyoming, and Alberta (e.g., Cappetta and Case, 1999; Cicimurri, 2000; Cook et al., 2008; Hamm and Cicimurri, 2011; Welton and Farish, 1993; Williams, 2006 as *C. borodini*). Teeth of *Protolamna* sp. from the Chamisa Field Site are distinct from those of *Archaeolamna* cf. *A. kopingensis*, *Cretalamna* "*appendiculata*", and *Cretodus* sp. that also occur in the same fossil assemblage as they possess narrow main cusps and cusplets that lack surface ornamentation, have lingually inclined crowns, and have robust roots with elongated, parallel root lobes. Teeth of *Leptostyrax bicuspidatus* Williston (1900), *P. sokolovi* Cappetta (1980a), and *Pseudoscapanorhynchus compressidens* Herman (1977), can also be distinguished from those of *Protolamna* sp. from the Chamisa Field Site because they frequently contain one or more of the following characteristics: narrower cusps and cusplets, longitudinal enameloid furrows, mesiodistally compressed roots, longer and straighter root lobes, and a nutritive groove on the lingual root surface (Cook et al., 2008; Becker et al., 2010; Hamm and Cicimurri, 2011; Cappetta, 2012; Siversson and Machalski, 2017). Teeth of *P. roanokeensis* Cappetta and Case (1999), from the Albian of Texas may appear similar to those of *Protolamna* sp. described here; however, they generally have a small tooth neck and more divergent root lobes. In contrast, teeth of *P. carteri* Cappetta and Case (1999), from the Cenomanian of Texas appear nearly identical to those of *Protolamna* sp. from the Chamisa Field Site as they have main cusps that are erect and generally smooth, roots that are robust with a well-defined lingual protuberance, and root lobes with nearly parallel outer edges. However, as indicated by Siversson and Machalski (2017), teeth identified as *P. acuta* Müller and Diedrich (1991), from the Cenomanian of Germany appear very similar to those of *P. carteri*, and these two species may in fact be synonymous. Because of the taxonomic uncertainty of some *Protolamna* taxa, and the uncommon occurrence of *Protolamna* sp. in the Chamisa Field Site assemblage, we refrain from species-level taxonomic assignment for this taxon.

Genus *Cretodus* Sokolov, 1965

Cretodus cf. ***C. semiplicatus*** (Agassiz, 1843)

Fig. 7L–M

Material. One isolated tooth fragment (ANSP VP 26359).
Description. This tooth, although fragmentary, displays a robust, erect, smooth main cusp with a strongly convex lingual face and a slightly convex labial face. The tooth fragment measures 22.5 mm in total height and 20.4 mm in width. Well-defined longitudinal furrows occur on the lingual crown base. Lateral cusplets are broad, triangular, and oriented away from the main cusp, and contain cutting edges that are continuous with those of the main cusp. The tooth root is robust and bears a well-developed lingual protuberance.
Discussion. Recent taxonomic classification places *Cretodus* within Pseudoscapanorhynchidae (see Shimada and Everhart, 2019); however, complications in the proper species-level identification of *Cretodus* still occur as a result of earlier studies that have few or no

Fig. 5. Teeth of *Meristodonoides* and *Ptychodus* (Chondrichthyes) from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale contact (Turonian–Coniacian), Sandoval County, New Mexico, USA. A–F, *Meristodonoides* sp. (ANSP VP 26300–26302). G–X, *Ptychodus mortoni* (ANSP VP 26304–26308). Y, Z, *Ptychodus mammillaris* (ANSP VP 26324). All scale bars = 1 cm. Orientations: A, C, E, H, L, P, T = lingual view; B, D, F, I, M, Q, U = labial view; G, K, O, S, Y = occlusal view; J, N, R, V, Z = basal view; W = lateral view; X = interior view.

tooth illustrations, describe new species based on single teeth or fragmentary specimens, and/or lack adequate stratigraphic control (Cappetta, 2012; Shimada and Everhart, 2019). Schwimmer et al. (2002) conservatively suggested the vast majority of previously known *Cretodus* species, including *C. crassidens*, be synonymized with *C. semiplicatus*. However, this view has not been widely accepted, where the genus *Cretodus* is currently represented by five species: *C. crassidens*, *C. gigantea*, *C. houghtonorum*, *C. longiplicatus*, and *C. semiplicatus*, that can be subdivided into three distinct tooth grades (sensu Shimada and Everhart, 2019). It is presently understood that at least some *Cretodus* taxa were globally dispersed during the Cretaceous. In particular, the '*longiplicatus*/*semiplicatus*-grade' *Cretodus* likely originated in the shallow marine environment of western Eurasia during the late Early Cretaceous and became globally dispersed by the Late Cretaceous (Shimada and Everhart, 2019).

With particular reference to the Late Cretaceous and WIS, teeth of the '*semiplicatus*-grade' *Cretodus* (sensu Shimada and Everhart, 2019) have been reported from the Cenomanian–Turonian of Texas, New Mexico, Arizona, Colorado, Minnesota, South Dakota, Alberta, and Saskatchewan (Meyer, 1974; Wolberg, 1985; Williamson and Lucas, 1992; Welton and Farish, 1993; Williamson et al., 1993; Cappetta and Case, 1999; Case, 2001; Cicimurri, 2001; Shimada et al., 2006; Cumbaa et al., 2006, 2010; Cook et al., 2008; Speilmann et al., 2009); the '*crassidens*-grade' from Turonian–Coniacian deposits in Texas, New Mexico, Utah, Colorado, Wyoming, Kansas, Nebraska, South Dakota (e.g., Stewart and Martin, 1993; Welton and Farish, 1993; Cappetta and Case, 1999; Cicimurri, 2001, 2004; Shimada, 2006; Becker et al., 2010; Hamm and Cicimurri, 2011; Bice and Shimada, 2016; Ouroumova et al., 2016); and the '*houghtonorum*-grade from the middle Turonian of Kansas (Shimada and Everhart, 2019). Because of the fragmentary condition of the specimen described here, we refrain from decisively assigning the specimen to *Cretodus semiplicatus*, but rather only to *C.* cf. *C. semiplicatus*. The tooth identified as *C.* cf. *C. semiplicatus* here can be distinguished from those of *Archaeolamna* cf. *A. kopingensis*, *Cretalamna* "*appendiculata*", and *Protolamna* sp. that also occur in the Chamisa Field Site assemblage. Compared to teeth of those taxa, they are more robust, contain well-defined furrows along the lingual crown face, and are generally much larger in size. *Cretodus crassidens* (Dixon, 1850), *C. gigantea* (Case, 2001), *C. houghtonorum* Shimada and Everhart (2019), and *C. longiplicatus* Werner (1989), can also be distinguished from *C.* cf. *C. semiplicatus* teeth because they are more robust, may lack lingual furrows, and appear to have restricted biogeographic and biostratigraphic ranges (Cappetta, 2012; Shimada and Everhart, 2019).

Cretodus sp.

Fig. 7J–K, N–P

Material. Eight isolated teeth (ANSP VP 26351–26358) (figured teeth: ANSP VP 26351–26352).
Description. Teeth identified as *Cretodus* sp. here are robust and fragmentary, the largest of which measures 35.7 mm in total height and 17.0 mm in width. They exhibit an erect main cusp, triangular lateral cusplets, and nearly flat labial surfaces and highly convex lingual surfaces. The labial crown surface may slightly overhang the root and contain faint grooves along the basal crown margin near the lateral cusplets. In contrast, the lingual tooth surface may be smooth or contain enameloid folds that cover a large portion of the crown. The roots, although fragmentary, are robust and appear to contain a lingual protuberance.
Discussion. Teeth identified as *Cretodus* sp. from the Chamisa Field Site can be distinguished from teeth of *C.* cf. *C. semiplicatus* as well as those of *Archaeolamna* cf. *A. kopingensis*, *Cretalamna* "*appendiculata*", and *Protolamna* sp. due to more robust crowns with well-defined furrows near the crown base on both labial and lingual faces. Given the larger overall size and presence of well-defined furrows along the crown base, these teeth of *Cretodus* sp. may in fact belong to *C. crassidens* sensu lato (see Shimada and Everhart, 2019) that has been reported from similar Turonian–Coniacian deposits in New Mexico and elsewhere in the WIS (e.g., Welton and Farish, 1993; Cappetta and Case, 1999; Becker et al., 2010; Hamm and Cicimurri, 2011; Bice and Shimada, 2016). However, we refrain from species-level assignment of these teeth from the Chamisa Field Site given their fragmentary condition. Additional taxonomic and paleobiogeographic details on *Cretodus* taxa can be found in the discussion section for *C.* cf. *C. semiplicatus* in this study as well as in Cappetta (2012) and Shimada and Everhart (2019).

Family Anacoracidae Casier, 1947
Genus *Squalicorax* Whitley, 1939

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

Fig. 8A–L

Material. Nine isolated teeth (ANSP VP 26410–26418) and nine additional teeth in matrix (ANSP VP 26419–26427) (figured teeth: ANSP VP 26410–26415).
Description. The largest tooth measures 13.7 mm in total height and 12.3 mm in width; however, the root is incomplete. Teeth of this taxon are strongly labiolingually flattened and have a nearly flat labial surface and a slightly convex lingual surface. The main cusp bears finely serrated, mesial and distal cutting edges. The main cusp of anterior teeth is generally broad and triangular and may have a slight distal inclination, whereas that of non-anterior teeth exhibits a greater distal inclination and a well-developed distal heel. The tooth roots when preserved are bilobate with a rounded-rectangular shape, and have a wide, U-shaped concavity in between short lobes.
Discussion. Squalicorax is one of the most commonly reported Late Cretaceous chondrichthyan genera and is known globally from the Albian–late Maastrichtian marine deposits (Shimada, 2008; Cappetta, 2012). In the Chamisa Field Site assemblage, teeth identified as *S.* cf. *S. falcatus* resemble those of *S. falcatus*; however, subtle variations documented in the apical angle, tooth heel, and cusp shape and size of *Squalicorax* teeth during the Late Cretaceous suggests that teeth identified as a single species (e.g., *S. falcatus*) may in fact represent multiple species or subspecies within *Squalicorax* (e.g., Siverson et al., 2007; Cappetta, 2012). To date, over 40 species of *Squalicorax* have been identified although not all of these may be considered valid (Cappetta, 2012). Until a reassessment of *Squalicorax* is conducted, we tentatively refer these teeth from the Chamisa Field Site to *S.* cf. *S. falcatus*. Teeth of *S.* cf. *S. falcatus* described here are distinct from those of *S. deckeri* and *Squalicorax* sp. that also occur in the Chamisa Field Site assemblage by having larger, triangular, labiolingually compressed, and finely serrated main cusps and low, rounded-rectangular roots. Teeth of other *Squalicorax* taxa, such as *S. curvatus* (Williston, 1900), *S. kaupi* Agassiz, 1835, *S. priscoserratus* Siverson et al. (2007), and *S. pristodontus* Agassiz, 1835, can also be distinguished from those of *S.* cf. *S. falcatus* described here because they have either larger and more rounded main cusps and smaller distal heels, taller main cusps with well-developed distal heels, or erect, nearly symmetrical crowns that are more dorsoventrally compressed (e.g., Siverson et al., 2007; Shimada, 2008; Underwood and Cumbaa, 2010; Cappetta, 2012).

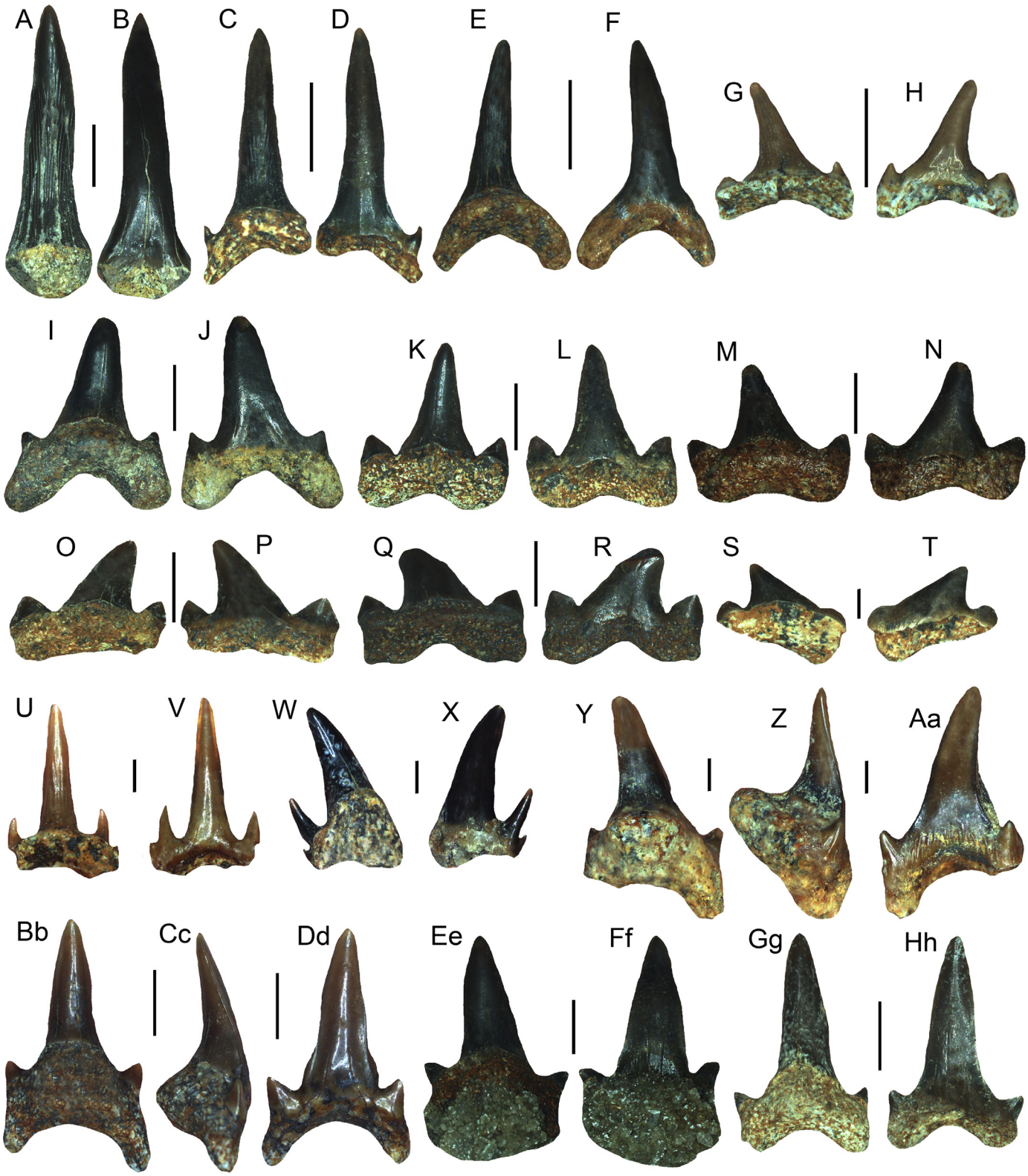


Fig. 6. Teeth of *Scapanorhynchus*, *Cretalamna*, cf. *Eostriatolamia*, and *Archaeolamna* (Chondrichthyes) from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale contact (Turonian–Coniacian), Sandoval County, New Mexico, USA. A–H, *Scapanorhynchus raphiodon* (ANSP VP 26326–26329); I–T, *Cretalamna* "*appendiculata*" (ANSP VP 26376–26381); U–Aa, cf. *Eostriatolamia tenuiplicatus* (ANSP VP 26404–26406). Bb–Hh, *Archaeolamna* cf. *A. kopingensis* (ANSP VP 26306–26362). Scale bars in A–R; Bb–Hh = 5 mm; S–Aa = 1 mm. Orientations: A, C, E, G, I, K, M, O, Q, S, U, W, Y, Bb, Ee, Ff = lingual view; B, D, F, H, J, L, N, P, R, T, V, X, Aa, Dd, Ff, Hh = labial view; Z, Cc = lateral view.

The species referable to *Squalicorax falcatus* or *S.* cf. *S. falcatus* has been reported throughout the Cenomanian–Santonian in North America, Europe, and Asia (e.g., Siverson et al., 2007; Cappetta, 2012). From the WIS deposits, it has been reported from Texas, Kansas, New Mexico, Arizona, Utah, Colorado, Wyoming, Nebraska, South Dakota, and Saskatchewan (e.g., Cappetta, 1973; Edwards, 1976; Wolberg, 1985; Case et al., 1990; Stewart and Martin, 1993; Welton and Farish, 1993; Williamson et al., 1993; Shimada, 1996; Cappetta and Case, 1999; Eaton et al., 1999; Cicimurri, 2001, 2004; Cumbaa et al., 2006; Shimada et al., 2006; Williams, 2006; Speilmann et al., 2009; Hamm and Cicimurri, 2011; McIntosh et al., 2013; Gorman et al., 2014; Bice and Shimada, 2016; Ouroumova et al., 2016). Additional details on *Squalicorax* taxa can be found in Cappetta (2012), Cappetta et al. (2014), Shimada (2008), and Siverson et al. (2007).

Squalicorax deckeri Bice and Shimada (2016)
Fig. 8M–X

Material. Eleven isolated teeth (ANSP VP 26428–26438) (figured teeth: ANSP VP 26428–26433).

Description. The largest anterior tooth measures 4.9 mm in total height and 5.2 mm in width whereas the largest lateral tooth measures 6.4 mm in total height and 6.0 mm in width. Teeth of this species are small where their crown is coarsely serrated and has a nearly flat labial face that slightly overhangs the bilobate root and a strongly convex lingual face. The main cusps of anterior teeth are triangular, nearly symmetrical, and may contain small mesial and distal shoulders. Lateral teeth have main cusps that are triangular, asymmetrical, and distally inclined and a well-developed distal heel separated from the main cusp by a notch. The root of anterior teeth may have a nearly flat basal surface, whereas the root of

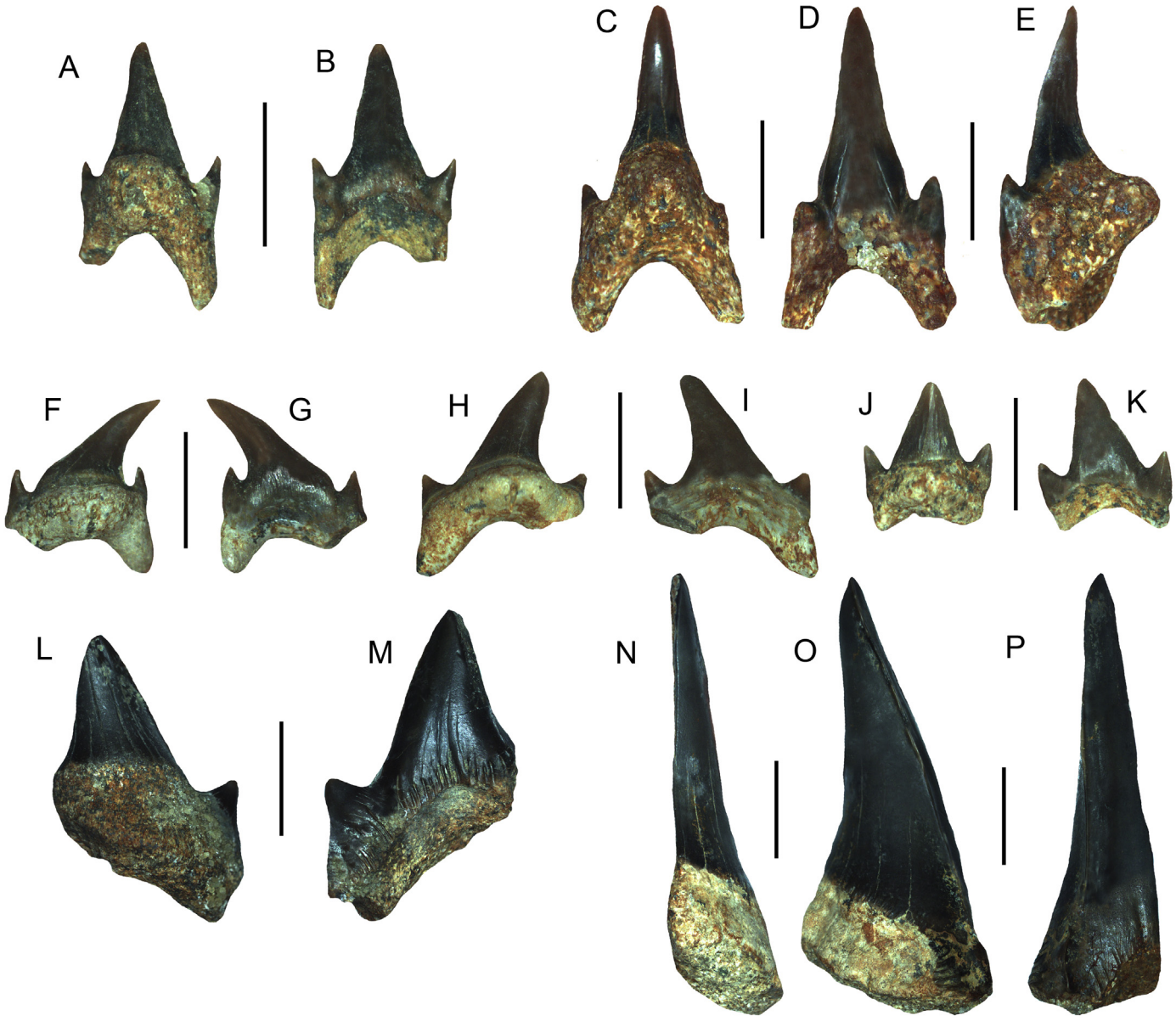


Fig. 7. Teeth of *Protolamna* and *Cretodus* (Chondrichthyes) from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale contact (Turonian–Coniacian), Sandoval County, New Mexico, USA. A–I, *Protolamna* sp. (ANSP VP 26396–26399); J–K; N–P, *Cretodus* sp. (ANSP VP 26351–26352); and L–M, *Cretodus* cf. *C. semiplicatus* (ANSP VP 26359). Scale bars in A–K = 5 mm; L–P = 10 mm. Orientations: A, C, F, H, J, L, N = lingual view; B, D, G, I, K, M, P = labial view; E, O = lateral view.

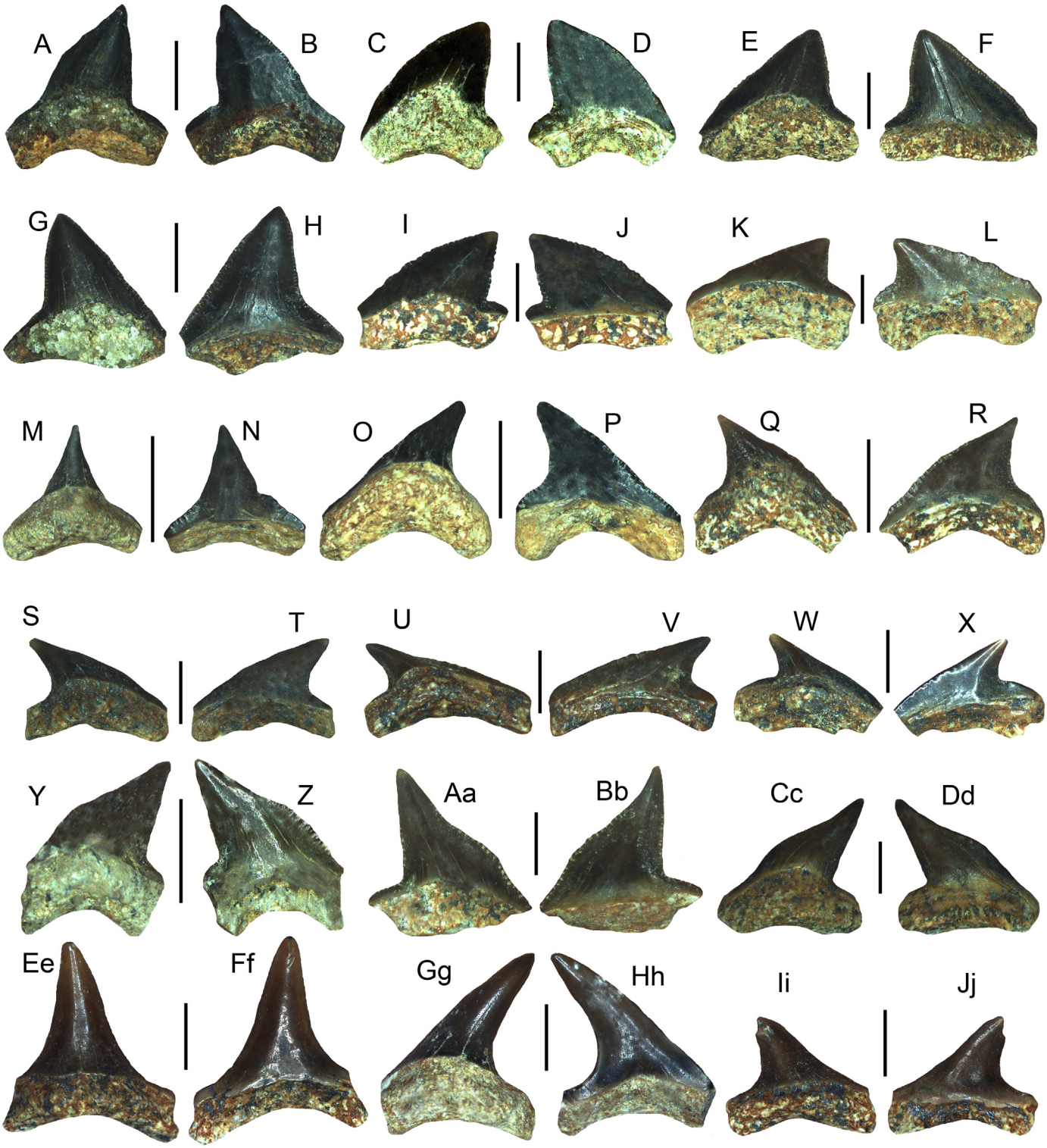
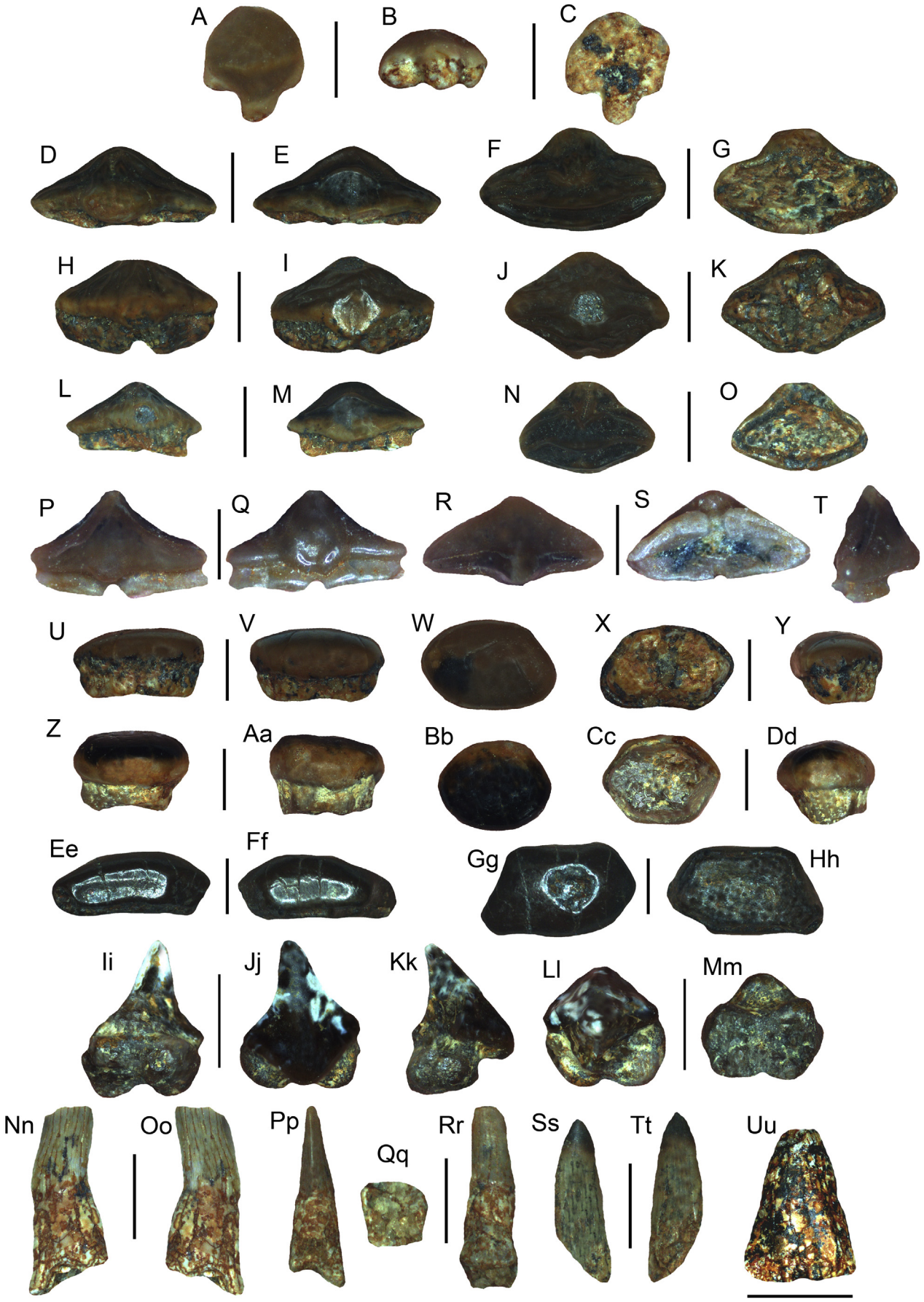


Fig. 8. Teeth of *Squalicorax* and *Paranomotodon* (?) (Chondrichthyes) from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale contact (Turonian–Coniacian), Sandoval County, New Mexico, USA. A–L, *Squalicorax* cf. *S. falcatus* (ANSP VP 26410–26415); M–X, *Squalicorax deckeri* (ANSP VP 26428–26433); Y–Dd, *Squalicorax* sp. (ANSP VP 26439–26441); Ee–Jj, *Paranomotodon*(?) sp. (ANSP VP 26407–26409). Scale bars in A–H; M–R; Y–Z; Ee–Jj = 5 mm; I–L; S–X; Aa–Dd = 2 mm. Orientations: A, C, E, G, I, K, M, O, Q, S, U, W, Y, Aa, Cc, Ee, Gg, Ii = lingual view; B, D, F, H, J, L, N, P, R, T, V, X, Z, Bb, Dd, Ff, Hh, Jj = labial view.

lateral teeth is widely separated and forms a more pronounced, U-shaped basal concavity.

Discussion. Teeth of *Squalicorax deckeri* are distinct from those of *S.* cf. *S. falcatus* and *Squalicorax* sp. that also occur in the Chamisa Field Site assemblage due to their smaller overall size, more acute cusp apex in anterior and lateral teeth, strongly convex lingual tooth surfaces, and thinner bilobate roots. Teeth of other *Squalicorax* taxa, including *S. pristodontus* and *S. kaupi*, can be distinguished from those of *S. deckeri* because they have much larger sizes, taller crowns with coarser serrations, lingual surfaces that are less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convex, and distinct biostratigraphic ranges (Siverson et al., 2007; Shimada, 2008; Cappetta, 2012; Bice and Shimada, 2016). *Squalicorax deckeri* can also be distinguished from *S. pawpawensis* Siverson et al. (2007), based on the presence of its strongly convex lingual tooth surface (Bice and Shimada, 2016).

Squalicorax deckeri is stratigraphically confined to the Turonian of the WIS (Bice and Shimada, 2016) where the species may have previously been identified as *Squalicorax* sp. (e.g., Cappetta and Case, 1999; Ouroumova et al., 2016). The identification of *S. deckeri* in the Chamisa Field Site assemblage may indicate that either the species extended into the early Coniacian in the WIS or its remains became reworked from the late Turonian into the early Coniacian. Additional details on the taxonomy and paleobiogeography of *Squalicorax* taxa can be found in the discussion on *S.* cf. *S. falcatus* discussion above, Bice and Shimada (2016), Cappetta (2012), Shimada (2008), and Siverson et al. (2007).

Squalicorax sp.

Fig. 8Y–Dd

Material. Six isolated teeth (ANSP VP 26439–26444) (figured teeth: ANSP VP 26439–26441).
Description. The largest tooth measures 13.5 mm in total height and 15.4 mm in width. Teeth of *Squalicorax* sp. from the Chamisa Field Site are slightly taller than they are wide and contain erect, irregularly serrated main cusps. The mesial cutting edge of the cusp has a distinct, distal bend roughly half-way between the root and cusp apex where serrations are coarsest, whereas serrations nearest to the cusp apex are fine or may even be absent. The distal cutting edge is straight, has a short and well-developed heel, and is finely serrated along the entire margin; however, serrations nearest to the cusp apex may be absent. In all teeth, the lingual face is convex, whereas the labial face is nearly flat. The root is holaulochorhizous, is more exposed on the lingual side, and forms a wide, shallow, U-shaped basal concavity.
Discussion. Teeth identified as *Squalicorax* sp. can be distinguished from those of *S.* cf. *S. falcatus* and *S. deckeri* that also occur in the Chamisa Field Site assemblage by having a distinct bend along the mesial tooth edge, irregular serration coarseness, and a consistently small distal heel. However, it is possible that the teeth of *Squalicorax* sp. described here represent variants of *S.* cf. *S. falcatus* due to ontogenetic and/or sexual heterodonty. Teeth of *Scindocorax novimexicanus* Bourdon et al. (2011), from the Santonian of New Mexico, are also somewhat similar to those of *Squalicorax* sp. from the Chamisa Field Site, but they are mesiodistally compressed, have main cusps that are more erect, and contain coarser serrations. Additional details on the taxonomy and paleobiogeography of *Squalicorax* taxa can be found in the *S.* cf. *S. falcatus* discussion in above, Bice and Shimada (2016), Cappetta (2012), Shimada (2008), and Siverson et al. (2007).

Family Incertae sedis
Genus *Paranomotodon* Herman in Cappetta and Case (1975)

Paranomotodon(?) sp.

Fig. 8Ee–Jj

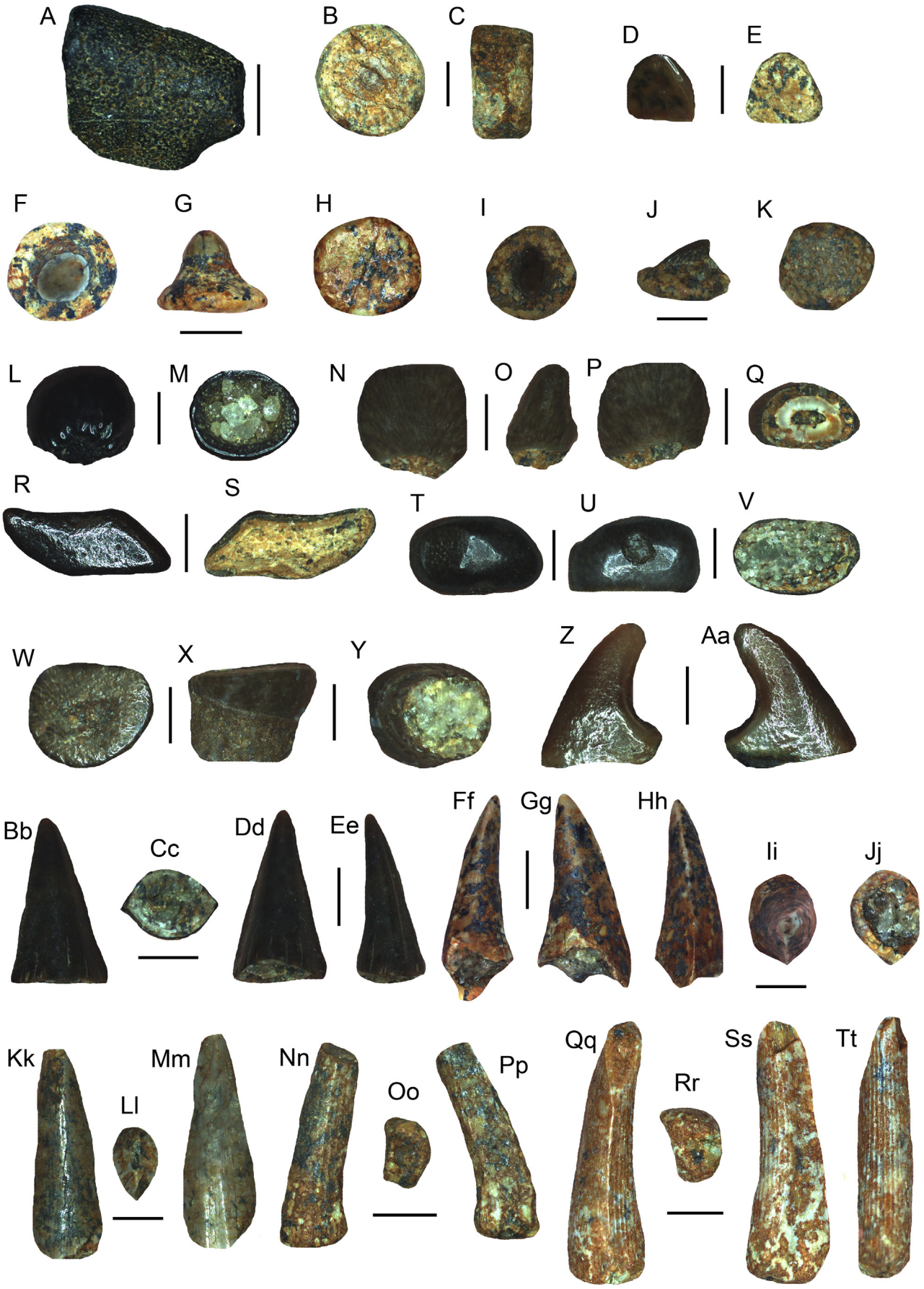
Material. Three isolated teeth (ANSP VP 26407–26409).
Description. The largest tooth measures 6.9 mm in total height and 6.5 mm in width. These teeth have a high, narrow, triangular main cusp with smooth, convex labial and lingual faces. The main cusp is distally inclined and contains sharp, complete cutting edges that extend onto the mesial and distal tooth heels where the distal heel is more developed than the mesial heel. The root is holaulochorhizous, has a well-developed lingual protuberance with a nutritive groove, and narrow, widely separated root lobes.
Discussion. Teeth attributable to *Paranomotodon* have been reported from the Cenomanian–Maastrichtian in North America, Africa, Europe, and Asia (e.g., Vullo, 2005; Cappetta, 2012; Guinot et al., 2013). From the WIS deposits, the genus has been reported from Turonian–Campanian deposits in Texas, Kansas, and New Mexico (e.g., Russell, 1988; Welton and Farish, 1993; Williamson et al., 1993; Shimada, 1996; Speilmann et al., 2009; Bice and Shimada, 2016). However, due to the uncommon and generally fragmentary occurrence of these *Paranomotodon*-like teeth in the Chamisa Field Site assemblage, we tentatively identify them as *Paranomotodon*(?) sp. They are distinct from those of *Archaeolamna* cf. *A. kopingensis* and *Scapanorhynchus raphiodon* that also occur in the Chamisa Field Site assemblage because they have smaller sizes, thinner and more distally inclined main cusps, contain mesial and distal tooth heels with continuous cutting edges, and lack lateral cusplets and crown surface ornamentation. The teeth of *Anomotodon* sp. may also appear similar to those of *Paranomotodon*(?) sp. teeth, but they contain more erect, lingually inclined main cusps and roots that are more robust and basally flattened (e.g., Cappetta, 2012; Bice and Shimada, 2016). *Paranomotodon*(?) sp. teeth can also be distinguished from those of *Dallasiella*, *Scapanorhynchus*, *Odontaspis*, and *Carcharias* taxa described from various Turonian–Coniacian WIS deposits because they lack lateral cusplets and have a mesial and distal heel.

Superorder Batomorphii Cappetta, 1980b
Order Rajiformes Berg, 1940
Family Rhinobatidae Müller and Henle, 1838
Genus *Rhinobatos* Linck, 1790
Rhinobatos incertus Cappetta (1973)

Fig. 9A–C

Material. One isolated tooth (ANSP VP 26456).
Description. The tooth is small, measuring 0.5–1.5 mm in maximum dimension and has a smooth, rounded-globular occlusal surface, a round labial face that extends over the root, and a distinct lingual face with an enlarged, central uvula located between two lesser developed protuberances. The root is displaced lingually, is holaulochorhizous, and contains two root lobes separated by a single nutritive groove. A nutritive foramen is present on each side of the lateral-most lingual protuberances near the crown-root junction, and a single large, centrally located foramen occurs between the root lobes on the basal root surface.
Discussion. Teeth of *Rhinobatos incertus* are distinct from oral teeth of *Ischyrhiza mira* Leidy (1856a), *Pseudohyplophus mcnultyi* (Thurmond, 1971), and *Ptychotrygon triangularis* (von Reuss, 1844) that also occur in the Chamisa Field Site assemblage by having a much smaller size, a smooth, rounded occlusal surface, and a distinct lingual uvula that is located between two smaller lingual protuberances. Additional *Rhinobatos* taxa with teeth similar to

Fig. 9. Teeth of *Rhinobatos*, *Ptychotrygon*, *Texatrygon*, *Pseudohypolophus*, and *Ischyrhiza* (Chondrichthyes) from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale contact (Turonian–Coniacian), Sandoval County, New Mexico, USA. A–C, *Rhinobatos incertus* (ANSP VP 26456). D–O, *Ptychotrygon triangularis* (ANSP VP 26463–26465). P–T, *Texatrygon hooveri* (ANSP VP 26475). U–Hh, *Pseudohypolophus mcnultyi* (ANSP VP 26457–26458). Ii–Mm, tooth of *Ischyrhiza mira* (ANSP VP 26445), Nn–Tt, rostral spine of *I. mira* (ANSP VP 26446–26447), and (Uu) root portion of rostral spine of *I. mira* (ANSP VP 25455). Scale bars in A–Mm = 2 mm; Nn–Uu = 5 mm. Orientations: A, F, J, N, R, W, Bb, Gg, Ll = occlusal view; C, G, K, O, S, X, Cc, Hh, Mm, Qq = basal view; B, E, I, M, Q, V, Aa, Ff, Ii = lingual view; D, H, L, P, U, Z, Ee, Jj = labial view; T, Y, Dd, Kk, Pp = profile view; Nn–Oo; Rr–Uu = dorsal or ventral view.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those of *R. incertus* include: *R. casieri* Herman (1977), *R. kiestensis* Cappetta and Case (1999), *R. lanonianensis* Cappetta and Case (1999), and *R. lobatus* Cappetta and Case (1999). With the exception of *R. casieri* that has been documented from the Santonian of Belgium and the Campanian of New Jersey and has an distinctly elongated central lingual uvula, teeth from these other *Rhinobatos* taxa have only been documented from Turonian–Coniacian deposits of Texas (Cappetta and Case, 1975, 1999; Herman et al., 1997; Hamm and Cicimurri, 2011). *Rhinobatos lanonianensis* has a distinct transverse ridge across the top of the occlusal surface and an irregularly scalloped labial crown edge that is unlike that seen in teeth of *R. incertus*. However, teeth of *R. lobatus* similar to those of *R. incertus* because they have a rounded occlusal surface and labial crown edge, may bear a faint transverse ridge on the occlusal surface, and also contain a large lingual uvula in between two smaller protuberances. It has been suggested that teeth identified as *R. lobatus* are from females and those with taller, pointed crowns identified as *R. kiestensis* may in fact belong to *R. lobatus* males (e.g., Everhart, 2007; Underwood and Cumbaa, 2010; Bice and Shimada, 2016). Variable degrees of sexual heterodonty have previously been documented in *Rhinobatos* taxa, and further complications in the proper identification of isolated *Rhinobatos* teeth may be a result of seasonal heterodonty such that the teeth of females and males generally exhibit flat, low crowns except during the mating season where male teeth may exhibit taller, pointed crowns (e.g., Kajiura and Tricas, 1996; Herman et al., 1997; Everhart, 2007; Underwood and Cumbaa, 2010; Cappetta, 2012; Bice and Shimada, 2016). As a result, *R. kiestensis* may be synonymous with *R. lobatus*, and the restricted biostratigraphic and geographic distribution of *R. lobatus* and *R. kiesensis* to the Turonian–Coniacian of Texas suggests that *R. lobatus* may in fact be a junior synonym of *R. incertus*.

Rhinobatous incertus appears to be restricted to the Albian–Campanian deposits of the WIS and has been reported from Texas, New Mexico, Colorado, Kansas, Nebraska, South Dakota, Alberta, and Saskatchewan (e.g., Cappetta, 1973; Edwards, 1976; Stewart, 1990; Welton and Farish, 1993; Cappetta and Case, 1999; Cicimurri, 2001; Everhart, 2007; Speilmann et al., 2009; Underwood and Cumbaa, 2010; Gallardo et al., 2012; Nagrodski et al., 2012; Cook et al., 2013; Bice and Shimada, 2016; Ouroumova et al., 2016). It is reasonable to assert that the small tooth size of *Rhinobatos* spp., including those of *R. incertus*, could have contributed to taphonomic and collecting biases (e.g., winnowing, abrasion, and the lack of bulk sampling) that may have obscured the understanding of chondrichthyan diversity and paleobiogeographical resolution. In fact, as a result of taxonomic uncertainties and taphonomic and collecting biases, it is quite plausible that "*Rhinobatos* sp." previously reported from other Cretaceous localities may be synonymous with *R. incertus*. If so, this species must have had a more expansive distribution than is currently recognized. Until additional studies on teeth of extant and extinct *Rhinobatos* are conducted, we follow Bice and Shimada (2016) and Everhart (2007) and identify the tooth of *Rhinobatos* from the Chamisa Field Site as *R. incertus*.

Suborder Sclerorhynchoidei Cappetta, 1980b
Family Ptychotrygonidae Kriwet, Nunn, and Klug (2009)
Genus *Ptychotrygon* Jaekel, 1894

Ptychotrygon triangularis (von Reuss, 1844)

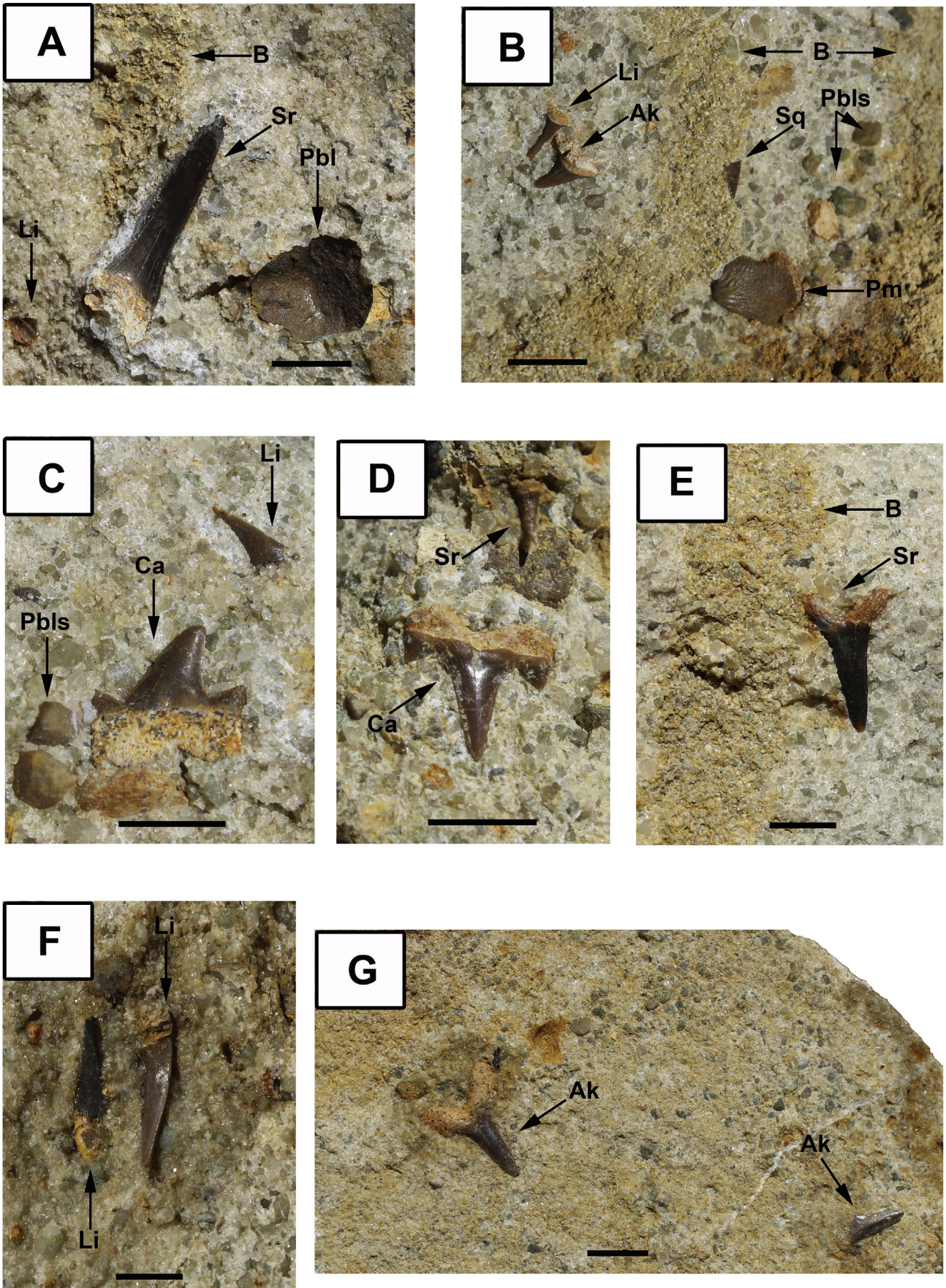
Fig. 9D–O

Material. Ten isolated teeth (ANSP VP 26463–26472) and two teeth in matrix (ANSP VP 26473–26474) (figured teeth: ANSP VP 26463–26465).

Description. The largest tooth measures 3.1 mm in total height and 5.6 mm in width. These teeth have low, rounded, and subtriangular crowns. The occlusal surface of the crown has a distinct crest with three labially-positioned transverse ridges. The crown surface is generally smooth in between the transverse ridges, and wear facets are frequently preserved. The labial and lingual crown surfaces overhang the root and form low aprons. The lingual apron generally contains a small, circular depression for articulation with adjoining teeth. The tooth root has a flat basal surface that is bisected by a central groove and forms two triangular attachment surfaces.

Discussion. Ptychotrygon triangularis has been reported throughout the Albian–Maastrichtian in North America, Europe, and Africa (e.g., Cappetta, 1973; Cappetta and Case, 1975; Cappetta, 1980b; Kriwet, 1999a; Cappetta, 2012; Villalobos-Segura et al., 2021). From the WIS deposits, *P. triangularis* is known from Texas, New Mexico, Utah, Kansas, Colorado, Nebraska, South Dakota, and Alberta (Cappetta, 1973; Wolberg, 1985; Russell, 1988; Williamson et al., 1989, 1993; Stewart and Martin, 1993; Welton and Farish, 1993; Beavan and Russell, 1999; Cappetta and Case, 1999; Cicimurri, 2001, 2004; Johnson and Lucas, 2003; Shimada et al., 2006; Becker et al., 2006, 2010; Speilmann et al., 2009; Jansen et al., 2013; Ouroumova et al., 2016; Schubert et al., 2017). Teeth of *P. triangularis* are distinct from those of *Pseudohypolophus mcnultyi* and *Rhinobatos incertus* that also occur in the Chamisa Field Site assemblage, characterized by a subtriangular outline in occlusal view, a rounded crown with multiple, labially-positioned transverse ridges, and a root base bisected into two triangular attachment surfaces. Teeth belonging to *Ptychotrygon eutawensis* Case et al. (2001), *P. vermiculata* Cappetta (1975), and *Texatryon hooveri* (McNulty and Slaughter, 1972) are also distinct from those of *P. triangularis* by containing one or more of the following characteristics: faint furrows in between the occlusal surface ridges, a labial crown surface that noticeably overhangs the root base, a taller crown with a single well-defined transverse ridge, large protruding labial and lingual aprons, and/or distinct biostratigraphic ranges (e.g., Welton and Farish, 1993; Becker et al., 2006; Bourdon et al., 2011; Cappetta, 2012). Although a thorough taxonomic review of species of *Ptychotrygon* is needed, we assign our *Ptychotrygon* specimens to *P. triangularis* because they appear identical to previously identified specimens of *P. triangularis* from other Turonian–Coniacian WIS deposits (e.g., Welton and Farish, 1993; Cicimurri, 1998; Cappetta and Case, 1999; Becker et al., 2004; Shimada et al., 2006; Bourdon et al., 2011; Hamm and Cicimurri, 2011; Cappetta, 2012; Bice and Shimada, 2016).

Fig. 10. Chondrichthyan elements and teeth of *Micropycnodon*, Pycnodontiformes indet., Aspidorhynchidae indet., *Protosphyraena*, and *Enchodus* (Chondrichthyes and Osteichthyes) from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale contact (Turonian–Coniacian), Sandoval County, New Mexico, USA. A, cartilage fragment of indeterminant chondrichthyan (ANSP VP 26476); B–C, vertebral centrum of indeterminant chondrichthyan (ANSP VP 26477); D–K, dermal denticles of indeterminant chondrichthyans (ANSP VP 26480–26482). L–M, *Micropycnodon* cf. *M. kansasensis* (ANSP VP 26490) (note ornamented occlusal surface); N–Q, incisiform tooth of Pycnodontiformes indet. (ANSP VP 26506). R–S, *Anomoedus*-like molariform Pycnodontiformes indet. tooth (ANSP VP 26485); T–Y, molariform Pycnodontiformes indet. teeth (ANSP VP 26494–26495) (note wear facet); Z–Aa, pharyngeal Pycnodontiformes indet. tooth (ANSP VP 26510); Bb–Ee, Aspidorhynchidae indet. tooth (ANSP VP 26529); Ff–Mm, *Protosphyraena* sp. teeth (ANSP VP 26523–26524); Nn–Tt, *Enchodus* cf. *E. gladiolus* teeth (ANSP VP 26516–26517). Scale bars in A = 5 mm; B–Y; Bb–Tt = 2 mm; Z–Aa = 1 mm. Orientations: A = exterior view; B = articular view; C = lateral view; D, F, I = apical view; E, H, K = basal view; G, J, M, Q, S, V, Y, Cc, Jj, Oo, Rr = basal view; L = oblique occlusal view; N = labial view; O, U, X, Z, Aa, Ee, Ff, Hh = profile view; R, T, W, Ii, Ll = occulusal view; Bb, Tt = labial view; Dd, Gg, Kk, Ss = lingual view; Nn = lateral view; Pp, Qq = medial view.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Genus *Texatrygon* Cappetta and Case, 1999

Texatrygon hooveri (McNulty and Slaughter, 1972)

Fig. 9P–T

Material. One isolated tooth (ANSP VP 26475).
Description. The tooth is small and measures 2.5 mm in maximum dimension. The crown is erect, triangular, and smooth. A single, mesiodistally oriented transverse ridge occurs across the center of the occlusal surface. A prominent labial protuberance can be seen in occlusal view and both the labial and lingual crown surfaces overhang the root and form low aprons. The lingual apron contains a small, circular depression for articulation with adjoining teeth. The tooth root has a slightly concave basal surface that is bisected by a central groove and forms two triangular attachment surfaces.
Discussion. To date, *Texatrygon hooveri* has only been reported from the Turonian of the WIS in Texas, Arizona, and Nebraska (McNulty and Slaughter, 1972; Welton and Farish, 1993; Williamson et al., 1993; Cappetta and Case, 1999; Hamm and Cicimurri, 2011; Cappetta, 2012; Ouroumova et al., 2016). Teeth of *T. hooveri* are distinct from those of *Ptychotrygon triangularis*, *Pseudohypolophus mcnultyi,* and *Rhinobatos incertus* that also occur in the Chamisa Field Site assemblage, and are characterized by a narrow, subtriangular outline in occlusal view, a smooth, erect crown, labial protuberance, and a weakly concave root base bisected into two triangular attachment surfaces. *Ptychotrygon rubyae* Williamson et al. (1993), identified from the Turonian of Arizona, has been synonymized with *T. hooveri*. We assign this specimen to *T. hooveri* because it appears identical to those previously identified from Turonian–Coniacian WIS assemblages and is the only *Texatrygon* species known prior to the Campanian (e.g., Cappetta and Case, 1999; Hamm and Cicimurri, 2011; Cappetta, 2012).

Rhinobatoidei Fowler, 1941
Family Incertae sedis
Genus *Pseudohypolophus* Cappetta and Case, 1975

Pseudohypolophus mcnultyi (Thurmond, 1971)

Fig. 9U–Hh

Material. Six isolated teeth (ANSP VP 26457–26462) (figured teeth: ANSP VP 26457–26459).
Description. The largest median tooth measures 5.3 mm in maximum dimension. These teeth have low, smooth, slightly convex crowns with rounded edges that overhang the root on all sides. Median teeth are mesiodistally elongated and have rhomboidal occlusal surfaces, whereas lateral teeth are generally smaller than median teeth and are elliptical. The roots are holaulochorhizous, low, and thinner than the crowns, and several small nutritive foramina may be present near the crown. A well-developed nutritive groove containing a centrally located basal foramen separates the pentagonal root lobes.
Discussion. Teeth attributed to *Pseudohypolophus* have been reported throughout the Aptian–Santonian in North America and Asia (e.g., Eaton et al., 1999; Cook et al., 2008; Cappetta, 2012). From the WIS deposits, *P. mcnultyi* has only been reported from Cenomanian–Maastrichtian deposits in Texas, New Mexico, Nebraska, South Dakota, and Alberta (e.g., Thurmond, 1971; Cappetta and Case, 1975, 1999; Williamson and Lucas, 1992; Stewart and Martin, 1993; Welton and Farish, 1993; Williamson et al., 1993; Johnson and Lucas, 2003; Cicimurri, 2004; Becker et al., 2004, 2010; Cook et al., 2008; Speilmann et al., 2009; Ouroumova et al., 2016). Teeth of *P. mcnultyi* are distinct from those of *Ptychotrygon triangularis* and *Rhinobatos incertus* that also occur in the Chamisa Field Site assemblage as they possess much larger, smooth, rhomboidal-elliptical occlusal surfaces and thin roots with pentagonal root lobes. *Pseudohypolophus ellipsis* Case et al. (2001), was identified from the Santonian of Georgia and differentiated from *P. mcnultyi* on the basis of having a larger tooth size and elliptical shape, but this species is based on a single lateral tooth. Teeth of *Hypolophodon sylvestris* White (1931), are somewhat similar to those of *P. mcnultyi*; however, they have a folded lingual surface with a distinct uvula, roots that are well-separated from the crown, and are known to occur in the early Cenozoic (Cappetta, 2012). Additionally, teeth of *Protoplatyrhina hopii* Williamson et al. (1993), and *P. renae* Case (1978), can be distinguished from those of *Pseudohypolophus mcnultyi* due to the presence of smaller, flatter occlusal surfaces and a heart-shaped root base. Moreover, teeth of *Protoplatyrhina renae* teeth bear a lingual uvula that is not seen in *P. hopii* or *Pseudohypolophus mcnultyi*.

Order Sclerorhynchiformes Kriwet, 2004
Family Sclerorhynchidae Cappetta, 1974
Genus *Ischyrhiza* Leidy, 1856a

Ischyrhiza mira Leidy (1856a)

Fig. 9Ii–Uu

Material. One isolated oral tooth (ANSP VP 26445), nine isolated rostral spine fragments (ANSP VP 26446–26454), and one rostral spine root (ANSP VP 26455) (figured specimens: ANSP VP 26445–26447, and 26455).
Description. Rostral spines, that measure up to 8.1 mm in our sample, have long, dorsoventrally flattened crowns with smooth cutting edges that extend from the crown apex to slightly above the crown-root junction. Their dorsal and basal crown surfaces are weakly convex and may contain faint ridges near the crown base. The root of rostral spines is longer than the crown and widens near the base where it is divided into two root lobes with multiple grooves forming a scalloped appearance. The oral tooth measures 2.8 mm in maximum dimension, is erect, triangular, and contains convex labial and lingual faces. Their crown surface is smooth and forms a large, rounded labial uvula overhanging the lingually offset root that has a flat basal surface separated into two attachment surfaces by a nutritive groove.
Discussion. The rostral spine of *Ischyrhiza mira* can be readily distinguished from those of all other taxa in the Chamisa Field Site assemblage based on their relatively straight, dorsoventrally compressed crowns, and large, scalloped root base. In contrast, oral teeth of *I. mira* may appear similar to those of *Ptychotrygon triangularis* and *Rhinobatos incertus* in the Chamisa Field Site assemblage; however, teeth of these taxa are not as erect and have rounded occlusal surfaces that may bear several distinct ridges or grooves. The rostral spine of *I. avonicola* Estes (1964), can be distinguished from those of *I. mira* by possessing short, stubby, hook-like crowns and shorter, splayed roots. Rostral spines similar to those of *I. avonicola* identified as *I. texana* Cappetta and Case (1975), have since been transferred to the genus *Kiesteus* Cappetta and Case, 1999. Additionally, rostral spines identified as *I. schneideri* Slaughter and Steiner (1968), have been problematic

Fig. 11. Matrix specimens containing chondrichthyan teeth from the Tocito Sandstone–Mulatto Tongue of the Mancos Shale lag deposit (Turonian–Coniacian), Sandoval County, New Mexico, USA (note taphonomically worn and oriented teeth, the concentration of teeth, and the infilled *Thalassinoides* isp. burrows seen in A–G). A, ANSP VP 26339; B, ANSP VP 26316; C, ANSP VP 26391; D, ANSP VP 26392; E, ANSP VP 26340; F, ANSP VP 26483; G, ANSP VP 26372. Abbreviations: Li=Lamniformes indeterminate; B = burrow; Sr=*Scapanorhynchus raphiodon*; Pbl = pebble(s); Ak = *Archaeolamna* cf. *A. kopingensis*; Sq = *Squalicorax* sp.; Pm=*Ptychodus mortoni*; Ca=*Cretalamna* "*appendiculata*." All scale bars = 10 mm.

because they resemble those of *I. mira* and were interpreted to represent a subspecies of *I. mira* (i.e., *I. mira schneideri* Slaughter and Steiner, 1968) or a distinct, ancestral taxon (Williamson et al., 1993; Cicimurri, 2004). However, we follow the current interpretation that *I. schneideri* is not a valid taxon and identify the rostral spines from the Chamisa Field Site as *I. mira* (e.g., Cappetta, 2012; Sternes and Shimada, 2018). To date, *I. mira* has been identified from Turonian–Maastrichtian deposits of the WIS in Texas, New Mexico, Arizona, Utah, Kansas, Nebraska, Montana, and Alberta (e.g., McNulty and Slaughter, 1964; Slaughter and Steiner, 1968; Cappetta, 1973; Case, 1978; Wolberg, 1985; Russell, 1988; Williamson et al., 1989, 1993; Williamson and Lucas, 1992; Welton and Farish, 1993; Case and Cappetta, 1997; Beavan and Russell, 1999; Cappetta and Case, 1999; Johnson and Lucas, 2003; Speilmann et al., 2009; Becker et al., 2010; Bourdon et al., 2011; Hamm and Cicimurri, 2011; Bice and Shimada, 2016; Ouroumova et al., 2016; Schubert et al., 2017; Sternes and Shimada, 2018).

Chondrichthyes indet. 1

Fig. 10A

Material. One calcified cartilage fragment in matrix (ANSP VP 26476).
Description. The calcified cartilage fragment exposes a pitted and stellate exterior surface that ranges between 1 and 2 mm thick. The specimen is convex and C-shaped when viewed laterally.
Discussion. The calcified cartilage specimen from the Chamisa Field Site is dark in color and appears to be phosphatized. The pitted, stellate external surface is similar to calcified cartilage specimens from the rostrum and jaws of *Ischyrhiza mira* previously reported from the Late Cretaceous by Becker et al. (2002, 2005) and Sternes and Shimada (2018). Whereas the specimen is interpreted to be from a chondrichthyan, it is small and too fragmentary, precluding further taxonomic identification.

Chondrichthyes indet. 2

Fig. 10B–C

Material. Three isolated vertebrae (ANSP VP 26477–26479) (figured specimen: ANSP VP 26477).
Description. The specimens are represented by isolated calcified vertebral centra that are small, weakly-amphicoelous, and circular in outline in articular view. The largest specimen has a diameter of 7.1 mm and an anteroposterior length of 4.4 mm. The presence or absence of radial lamella and nutritive foramina is uncertain from external observation.
Discussion. Isolated chondrichthyan vertebrae similar to those from the Chamisa Field Site are relatively common in the Late Cretaceous and Cenozoic marine deposits (e.g., Lucas et al., 1985; Welton and Farish, 1993; Becker et al., 2002, 2008, 2011; Blanco-Piñón et al., 2005; Maisch et al., 2014, 2019; Bice and Shimada, 2016; Schubert et al., 2017). The abundance of lamniform, rajiform, and sclerorhynchiform teeth in the Chamisa Field Site assemblage suggests that these isolated vertebrae may belong to one or more of these taxa; however, the uncertainty in potentially diagnostic taxonomic features, including radial lamella and nutritive foramina, does not allow for further taxonomic identification.

Chondrichthyes indet. 3

Fig. 10D–K

Material. Three isolated dermal denticles (ANSP VP 26480–26482).
Description. The isolated dermal denticles (or thorns) are small (up to 4.3 mm in maximum dimension), circular–triangular in shape, and have external surfaces with well-developed, convex enameloid cusps that are straight, posteriorly inclined, or nearly flat. Their base is flat to weakly concave, and nutritive foramina are absent.
Discussion. Similar to isolated vertebrae, dermal denticles of chondrichthyans are relatively common in the Late Cretaceous and Cenozoic marine deposits (e.g., Welton and Farish, 1993; Williamson et al., 1993; Becker et al., 2002; Shimada et al., 2006; Bourdon et al., 2011; Hamm and Cicimurri, 2011; Reinecke et al., 2011; Cappetta, 2012; Maisch et al., 2019). However, the morphology of chondrichthyan dermal denticles is highly variable across the body and within a single species (e.g., Gravendeel et al., 2002; Serra-Pereira et al., 2008; Cappetta, 2012; Sibert et al., 2016; Dillon et al., 2017; Ankhelyi et al., 2018). Thus, further taxonomic identification of dermal denticles from the Chamisa Field Site is not possible at the present time.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887
Superorder Neopterygii Regan, 1923
Order Pycnodontiformes Berg, 1940
Family Pycnodontidae Agassiz, 1833
Genus *Micropycnodon* Hibbard and Graffham, 1945

Micropycnodon cf. ***M. kansasensis*** (Hibbard and Graffham, 1941)

Fig. 10L–M

Material. Four isolated molariform teeth (ANSP VP 26490–26493) (figured tooth: ANSP VP 26490).
Description: The molariform (i.e., likely prearticular and/or vomerine) teeth are small (up to 1.5 mm in maximum dimension) and circular in occlusal view. The occlusal surface is convex and contains multiple, irregular ridges and grooves that form crenulations surrounding a shallow concavity on part of the occlusal surface. The basal surface of molariform teeth is concave and exposes porous dentine.
Discussion. Identifying isolated pycnodont teeth to specific genera or species has generally been regarded as problematic due to overall similarities in pycnodont tooth morphology. However, the specimens described here from the Chamisa Field Site bear a strong resemblance to those previously identified as *Micropycnodon kansasensis*, where we conservatively refer them to as *M.* cf. *M. kansasensis* (e.g., Hibbard and Graffham, 1941; Cumbaa et al., 2006; Shimada et al., 2006; Speilmann et al., 2009; Becker et al., 2012; Cronin and Shimada, 2019). They are distinct from those of other small, globular fish remains from the Chamisa Field Site, such as teeth of Pycnodontiformes indet. as well as *Pseudohypolophus mcnultyi* and *Rhinobatos incertus*, because of their small, circular, convex crowns with crenulations surrounding a shallow concavity. Molariform teeth belonging to other pycnodonts including *Anomoedus* sp., *Gyrodus* sp., and *Phacodus* sp., may resemble those of *M.* cf. *M. kansasensis*; however, they lack partially crenulated occlusal surfaces and commonly attain larger sizes (e.g., Hooks et al., 1999; Kriwet, 1999b; Cumbaa et al., 2006; Shimada and Everhart, 2009). Currently, the genus *Micropycnodon* appears to be restricted to the WIS deposits with records from the Cenomanian–Santonian in New Mexico, Colorado, Kansas, South Dakota, and Saskatchewan (e.g., Hibbard and Graffham, 1941, 1945; Dunkle and Hibbard, 1946; Russell, 1988; Stewart, 1990; Shimada, 1996; Cicimurri, 2001; Shimada and Fielitz, 2006; Shimada et al., 2006; Cumbaa et al., 2006, 2010, 2013; Everhart, 2007; Shimada and Martin, 2008; Gallardo et al., 2012; Nagrodski et al., 2012; Cronin and Shimada, 2019).

Genus Pycnodontiformes indet.

Fig. 10N–Aa

Material. Four isolated incisiform teeth (ANSP VP 26506–26509); twelve isolated molariform teeth (ANSP VP 26494–26505), five

isolated *Anomoedus*-like molariform teeth (ANSP VP 26485–26489), one isolated phyrangeal tooth (ANSP VP 26510), and five molariform teeth in matrix (ANSP VP 26511–26515) (figured teeth: ANSP VP 26485, 26494, 26495, 26506, and 26510).
Description. Incisiform (i.e., dentary and premaxillary) teeth generally have a labiolingually flattened, lingually-inclined, robust, rounded chisel- or peg-like crown (maximum crown height of 3.5 mm) and a columnar root, if preserved, that is slightly longer than the crown. Molariform (i.e., prearticular and vomerine) teeth generally possess a robust rounded crown with a circular, oval, or reniform outline and commonly with a circular–oval wear facet (maximum crown height of 2.5 mm). The root of molariform teeth is porous and not as wide as the crown, but if the root is not preserved, the basal tooth surface exposes the dentine with a deep cavity. The pharyngeal ('throat') tooth has a laterally compressed, hook-to claw-like crown (maximum crown height of 3 mm).
Discussion. In general, pycnodonts were laterally-compressed, deep-bodied fishes that inhabited shallow marine waters worldwide from the Triassic–Eocene, and to date numerous species have been identified based on articulated skeletons, associated dentitions, jaw fragments, or isolated teeth (e.g., Hooks et al., 1999; Kriwet, 1999b, 2002; Nursall, 1996a,b; Shimada and Everhart, 2009; Shimada et al., 2010b; Vullo, 2005; Vullo et al., 2017, 2019). In the WIS pycnodont remains, including isolated teeth, are relatively common, particularly in shallow nearshore marine deposits (e.g., Becker and Chamberlain, 2012; Becker et al., 2010, 2012; Bice and Shimada, 2016; Cumbaa et al., 2006, 2010; Case and Schwimmer, 1988; Hussakof, 1947; Ouroumova et al., 2016; Russell, 1988; Schubert et al., 2017; Shimada, 2006; Shimada and Everhart, 2009; Shimada et al., 2006, 2010b; Speilmann et al., 2009). Teeth from the Chamisa Field Site included in Pycnodontiformes indet. here may be represented by multiple taxa, such as *Anomoedus*, *Gyrodus*, *Hadrodus*, and/or *Phacodus* (but not *Micropycnodon*), but their exact taxonomic identification is difficult on the basis of isolated teeth. Instead, we group them into distinct morphotypes after Becker et al. (2012). These morphotypes are grouped based on overall similarity in shape and location in the vomerine, prearticular, dentary, premaxillary and pharynx regions. In general, premaxillary and dentary teeth are incisiform, vomerine and prearticular teeth are molariform, and pharyngeal teeth are claw-shaped and laterally compressed (e.g., Applegate, 1992; Becker et al., 2012; Nursall, 1996a,b; Poyato-Ariza, 2005; Poyato-Ariza and Wenz, 2002).

Order Aspidorhynchiformes Bleeker, 1859
Family Aspidorhynchidae Nicholson and Lydekker, 1889
Genus Aspidorhynchidae indet

Fig. 10Bb–Ee

Material. Three isolated teeth (ANSP VP 26529–26531) (figured tooth: ANSP VP 26529).
Description. The largest tooth measures 5.4 mm in total height and 3.9 mm in mesiodistal width. Their crowns are short, triangular, erect, contain convex labial and lingual faces with faint vertical striations and a slight lingual inclination, and exhibit well-defined, smooth mesial and distal cutting edges. The tooth root is absent, the tooth base is slightly concave, and forms a tapered ellipse outline.
Discussion: The family Aspidorhynchidae currently includes six genera, including *Aspidorhynchus* and *Belonostomus*, that are known to occur throughout the WIS deposits (e.g., Cumbaa et al., 2006, 2010; Bice and Shimada, 2016; Ouroumova et al., 2016; Van Vranken et al., 2019). Although their sub-familial taxonomic identification is difficult, teeth of Aspidorhynchidae indet. described here are distinct from those of other fish taxa from the Chamisa Field Site in that they possess triangular, faintly-striated crowns with well-defined cutting edges that give tapered, ellipse-like outline in basal view.

Order Pachycormiformes Berg, 1940
Family Pachycormidae Woodward, 1895
Genus *Protosphyraena* (Leidy, 1857)

Protosphyraena sp.

Fig. 10Ff–Mm

Material. Five isolated tooth fragments (ANSP VP 26523–26527) and one tooth in matrix (ANSP VP 26528) (figured teeth: ANSP VP 26523 and 26524).
Description. The largest tooth fragment measures 10.8 mm in total height and 4.9 mm in width. The tooth crowns are erect, mesiodistally compressed, and slightly lingually inclined. The labial and lingual faces are weakly convex and contain very fine vertically oriented striations, whereas a cutting edge is present on the mesial and distal margins. The tooth base is slightly concave and exposes porous dentine.
Discussion. Teeth of *Protosphyraena* sp. are distinct from those of other fish taxa from the Chamisa Field Site, including Aspidorhynchidae indet. and *Enchodus gladiolus* (Cope, 1872), by possessing mesiodistally compressed teeth with well-defined mesial and distal cutting edges and very fine, vertically-oriented striations. Although isolated teeth of *Protosphyraena* sp. may be relatively abundant in many Late Cretaceous marine vertebrate assemblages around the world, previous studies indicate that rostral and fin elements are more taxonomically diagnostic (e.g., Stewart, 1988), and as a result, we identify the isolated teeth from the Chamisa Field Site simply as *Protosphyraena* sp. From the WIS deposits, the genus *Protosphyraena* has been reported from the Cenomanian–Campanian in Colorado, Kansas, Iowa, South Dakota, Saskatchewan, and Alberta (e.g., Witzke, 1981; Russell, 1988; Stewart, 1988; Cumbaa and Tokaryk, 1999; Cicimurri, 2001; Everhart et al., 2004; Liggett et al., 2005; Shimada et al., 2006; Shimada and Fielitz, 2006; Cumbaa et al., 2006, 2013; Parris et al., 2007; Shimada and Martin, 2008; Gallardo et al., 2012; Nagrodski et al., 2012; Bice and Shimada, 2016).

Order Aulopiformes Rosen, 1973
Suborder Enchodontoidei Berg, 1940
Family Enchodontidae Woodward, 1901
Genus *Enchodus* Agassiz, 1835

Enchodus cf. ***E. gladiolus*** (Cope, 1872)

Fig. 10Nn–Tt

Material. Six isolated teeth (ANSP VP 26516–26521) and one tooth in matrix (ANSP VP 26522) (figured teeth: ANSP VP 26516 and 26517).
Description. Teeth are represented by mesiodistally compressed, sigmoidal crowns that are slightly inclined lingually, and measuring up to 11.3 mm in total height. The lingual face is more convex than the labial face, but both faces exhibit well-defined striations from the apex to the tooth base, whereas the mesial and distal edges exhibit a smooth cutting edge. The tooth base is rootless and the exposed dentine is generally flat or weakly concave.
Discussion. Teeth of *Enchodus* are distinct from those of other fish taxa from the Chamisa Field Site, including Aspidorhynchidae indet. and *Protosphyraena* sp., because they have a narrow sigmoidal crown with well-defined longitudinal striations. Currently, four species of *Enchodus* are recognized in North American that are known to have similar tooth morphologies and overlapping biostratigraphic ranges: *E. dirus* Leidy (1857), *E. gladiolus*

Cope (1872), *E. petrosus* Cope (1874), and *E. shumardi* Leidy (1856b) (e.g., Goody, 1976; Fielitz, 2002; Becker et al., 2010; Bice and Shimada, 2016). The *Enchodus* teeth from the Chamisa Field Site are most similar to those of *E. gladiolus* identified in other Turonian–Coniacian WIS deposits, and thus we conservatively refer these teeth to as *E.* cf. *E. gladiolus*. Although numerous *Enchodus* species have been identified globally throughout the Late Cretaceous (e.g., Cavin et al., 2012; Chalifa, 1996; da Silva and Gallo, 2016), in the WIS, *E. gladiolus* has been reported from Turonian–Maastrichtian deposits in New Mexico, Colorado, Wyoming, Kansas, Arkansas, Nebraska, Iowa, Saskatchewan, and the Northwest Territories (e.g., Goody, 1976; Fielitz, 1996, 2002; Martin et al., 1998; Cumbaa and Tokaryk, 1999; Robb, 2004; Shimada and Fielitz, 2006; Shimada et al., 2006; Cumbaa et al., 2006, 2013; Parris et al., 2007; Schein and Lewis, 2007; Cumbaa and Murray, 2008; Shimada and Martin, 2008; Becker et al., 2010; Gallardo et al., 2012; Jansen et al., 2013; Gorman et al., 2014; Bice and Shimada, 2016; Ouroumova et al., 2016).

5. Discussion

5.1. Taxonomic composition and paleoecology of the Chamisa fish assemblage

The chondrichthyan and osteichthyan taxa in the Chamisa assemblage consist of nektonic and benthic marine vertebrates that had wide geographic distributions during the Late Cretaceous. These fish taxa are primarily represented by isolated teeth with the greatest abundance associated with *Scapanorhynchus*, *Archaeolamna, Squalicorax, Ptychodus*, Pycnodontiformes indet., and *Enchodus*. Invertebrate remains including ammonites, inoceramids, gastropods, and decapod crustaceans also occur in the Chamisa assemblage as steinkerns, shell fragments, and ichnofossils (Fig. 4). However, vertebrate and invertebrate taxa with deep water affinities were noticeably absent.

The Chamisa chondrichthyans and osteichthyans have tooth morphologies that are indicative of grasping, clutching, and crushing dentitions ideal for consuming small fishes and a variety of soft and shelled invertebrate prey items (e.g., Applegate, 1965; Cumbaa et al., 2010; Becker et al., 2012; Cappetta, 2012). In particular, teeth of *Scapanorhynchus raphiodon* and *Archaeolamna* cf. *A. kopingensis* are well-suited for feeding upon a variety of small vertebrates including chondrichthyans and osteichthyans whereas *Squalicorax* taxa (*Squalicorax* cf. *S. falcatus*, *S. deckeri*, *Squalicorax* sp.) are generally accepted to have been opportunistic predators or scavengers in shallow marine environments capable of tearing flesh from a variety of vertebrates (e.g., Schwimmer et al., 1997; Shimada and Cicimurri, 2005; Becker and Chamberlain, 2012; Ehret and Harrell, 2018; Shimada and Hanks, 2020). In contrast, *Ptychodus* taxa (*P. mortoni* and *P. mammilaris*), *Rhinobatus incertus*, *Pseudohypolophus mcnultyi*, *Ptychotrygon triangularis*, and *Ischyrhiza mira* represent durophagous, benthic chondrichthyans and contain teeth that form pavement-like dentitions well-suited for crushing and grinding a variety of invertebrate prey items (e.g., ammonites, inoceramids, and rudists) and may occasionally have also preyed on small vertebrates (e.g., Kauffman, 1972; Welton and Farish, 1993; Cappetta, 2012; Bice and Shimada, 2016; Hamm, 2020).

Pycnodonts (*Micropycnodon* cf. *M. kansasensis* and Pycnodontiformes indet.) also have pavement-like dentitions consisting of incisiform, molariform, and pharyngeal teeth ideal for nibbling and crushing a variety of invertebrates, whereas *Enchodus* cf. *E. gladiolus* and *Protosphyraena* sp. had teeth designed for grasping and piercing prey (e.g., Becker et al., 2012; Kriwet, 2001; Stewart and Carpenter, 1990). Additionally, it has been suggested that *Enchodus* sp. formed large schools and as a result were preyed upon by various chondrichthyans, osteichthyans, and marine reptiles including plesiosaurs (e.g., Becker et al., 2013; Shimada and Everhart, 2003). The occurrence of a diverse assemblage of chondrichthyans and osteichthyans in addition to a variety of invertebrates and isolated plesiosaur teeth in the Chamisa assemblage (Figs. 4–11) suggests a dynamic, shallow marine food web existed in northwestern New Mexico during the TCTT event (e.g., Stewart and Carpenter, 1990; Shimada and Everhart, 2003).

The taxonomic homogeneity of the fish taxa identified in Table 1 demonstrates the highly mobile nature of both benthic and nektonic taxa in the WIS during the TCTT event. In particular, representatives of *Ptychodus*, *Scapanorhynchus*, *Squalicorax*, *Ptychotrygon*, *Ischyrhiza,* Pynodontiformes, and *Enchodus* are nearly ubiquitous throughout the WIS during the entire Late Cretaceous (e.g., Kriwet and Benton, 2004; Cappetta, 2012). However, variability in chondrichthyan and osteichthyan species between states and across the WIS may be the combined result of differences in bathymetry, water temperature, salinity, distance from shore, substrate, trophic structure, and taphonomic, collecting, and taxonomic (nomenclatural) biases (Shimada, 1996; Cappetta and Case, 1999; Merewether et al., 2007; Becker et al., 2010; Cumbaa et al., 2010; Hamm and Cicimurri, 2011; Cappetta, 2012; Bice and Shimada, 2016).

5.2. Formation of the Tocito Sandstone–Mulatto Tongue lag deposit

At the Chamisa Field Site, we follow Tilman (1986) and Lin et al. (2019) and interpret the Tocito Sandstone as a series of discontinuous, outer shoreface sandbars deposited at the seaward extent of the ancestral shoreline in the southeastern corner of the San Juan Basin (see Fig. 1 of Lin et al., 2019). These sandbars represent erosional lenses within the Mulatto Tongue that pinch out to the east with increasing distance from the ancestral shoreline. Although originally assigned to the Gallup Sandstone, these

Table 1
Chondrichthyan and osteichthyan taxa found in Turonian–Coniacian Western Interior Seaway lag deposits identified in the text. Note that osteichthyans were not reported from the Texas locality.

Taxa	Location		
	New Mexico: Chamisa Locality, Tocito Sandstone –Mulatto Tongue (This Study)	Texas: Acadia Park–Atco Formation (Hamm and Cicimurri, 2011)	Kansas: Codell Sandstone–Fort Hays Limestone (Shimada, 1996; Bice and Shimada, 2016)
Chondrichthyans			
Meristodonoides	X	X	X
Ptychodus	X	X	X
Scapanorhynchus	X	X	X
Protolamna	X	X	
Cretodus	X	X	X
Cretalamna	X	X	X
cf. *Eostriatolamia*	X		
Archaeolamna	X		X
Squalicorax	X	X	X
Paranomotodon	X		X
Rhinobatos	X	X	X
Ptychotrygon	X	X	X
Texatrygon	X	X	
Pseudohypolophus	X	X	
Ischyrhiza	X		X
Osteichthyans			
Micropycnodon	X	NA	X
Pycnodontiformes	X	NA	X
Aspidorhynchidae	X	NA	
Protosphyraena	X	NA	X
Enchodus	X	NA	X

sandbars are thought to have accumulated during a sea-level regression in the early late Turonian and directly after the maximum sea-level transgression in New Mexico (Molenaar, 1974, 1983; Nummedal et al., 1993; Nummedal and Molenaar, 1995). Subsequent transgression during the early Coniacian resulted in preservation of these sandbar lenses directly above a prominent unconformity within the Mulatto Tongue of the Mancos Shale (Fassett, 1974; Hook and Cobban, 2013; Hook et al., 2012, Figs. 2–3). In this same framework, the lag deposit that resides at the upper contact between the Tocito Sandstone and Mulatto Tongue of the Mancos Shale would represent sediments and fossils that have been taphonomically reworked into these outer shoreface sandbars during wave-based erosion and a regressive-transgressive sea-level cycle across the TCTT interval (Walaszczyk and Cobban, 2000; Merewether et al., 2007; Hook and Cobban, 2013). This regional sea-level event is also recognized throughout the WIS (Cobban et al., 1994; Hancock and Walaszczyk, 2004; Merewether et al., 2007; Nielsen et al., 2008) and as KTu5-KCo1 in third order eustatic sea-level cycles of Haq (2014).

Multiple lines of evidence found at the Chamisa Field Site and in the lag deposit reinforce this viewpoint and include: 1) the laterally-discontinuous, lenses-like nature of the Tocito Sandstone that forms an erosion resistant platform; 2) the well-sorted, rounded and cross-bedded quartz sand and pebbles that reside at the top of the Tocito Sandstone and prominent lithology change with the overlaying Mulatto Tongue; 3) the concentration of abraded chondrichthyan and osteichthyan teeth at the top of the Tocito Sandstone; 4) the chronological ranges of the chondrichthyan taxa identified in this report (i.e., mixing of Turonian and Coniacian species: see Systematic paleontology section above); and, 5) the occurrence of the biostratigraphically significant inoceramid bivalve *Cremnoceramus deformis erectus* (Meek, 1877) in the lowermost Mulatto Tongue of the Mancos Shale and directly above the lag deposit (Fig 4:A–E; also see Hancock and Walaszczyk, 2004; Walaszczyk and Cobban, 2000).

5.3. Correlative properties of the Turonian–Coniacian unconformity and vertebrate-bearing lags in WIS

Details of the correlative nature of the regional Turonian–Coniacian unconformity identified in this study were compiled by Merewether et al. (2007). As a general trend, their research indicated that the WIS retreated to the south during the late Turonian and exposed formations in more northerly states to the greatest duration of erosion. States further to the south, including New Mexico, experienced less erosion during this regression, but they were the first to receive sedimentation during subsequent transgression in the early Coniacian. Based on molluscan fossil zonation and radiometric ages: 1) the duration of the TCTT erosional hiatus is estimated from 5.1 m.y. in northeastern Nebraska to 0.5 m.y. in northeastern New Mexico; and, 2) rates of transgression ranged from 1340 km/m.y. between southeastern Colorado and northwestern Wyoming, and 400 km/m.y. between southeastern Colorado and northeastern Nebraska (Merewether et al., 2007).

Table 1 compares the fish taxa contained within the Tocito Sandstone–Mulatto Tongue lag deposit in the Chamisa Field Site to those found at, or near, the TCTT interval in Texas and Kansas in the basal Atco Formation and Codell Sandstone respectively (Shimada, 1996; Hamm and Cicimurri, 2011; Bice and Shimada, 2016). Although these aforementioned localities do not formally identify concentrations of chondrichthyans and osteichthyans as lags, many of the same, or similar species to those found in the Chamisa Field Site occur as concentrations within relatively thin beds <1 m of sandstone above unconformable contacts in the Acadia Park and Blue Hill Shale formations.

It is also noteworthy that the Texas and Kansas localities outcrop along the eastern margin of the WIS almost due north of one another and are separated by approximately 925 km. The New Mexico locality in this study crops out along western margin of the WIS and is separated from the Texas and Kansas localities by approximately 1100 km. We interpret the chondrichthyan and osteichthyan taxa found in these three states to represent lags, and for the discussion that follows, originated during the same regional and eustatic late Turonian–early Coniacian regressive-transgressive sea-level event documented by Merewether et al. (2007) and third order eustatic sea-level cycles KTu5–KCo1 of Haq (2014).

Several other localities across the WIS including Colorado, South Dakota and Wyoming may also have vertebrate-bearing lags that are the product of this late Turonian–early Coniacian sea-level event, but they require additional field study (e.g., Edwards, 1976; Evetts, 1979; Cicimurri, 2004). In general, the overall faunal similarities in multiple states preserving TCTT strata attest to the highly mobile nature of chondrichthyans and osteichthyans and their ability to migrate across the shallow shelf platform within the WIS even as sea-level fluctuated.

5.4. Sequence stratigraphic versus lithostratigraphic interpretations of TCTT vertebrate-bearing lags

Differences in how the chondrichthyan and osteichthyan lags seen in Table 1 are studied and correlated between states may be related to the use of sequence stratigraphic versus lithostratigraphic principles (e.g., Donovan, 1993; Mancini et al., 1996; Haq, 2014; Lin et al., 2019). In this regard, the unconformity identified by Merewether et al. (2007) during the late Turonian–early Coniacian would represent a sequence stratigraphic framework and stratal surface by which chondrichthyan and osteichthyan lags identified in Table 1 can be correlated within the WIS. In our view, placement of these lags in a traditional lithostratigraphic framework creates correlative complications. These correlative complications are the result of bathymetric differences, degrees of taphonomic reworking, and the time transgressive nature of lag deposit formation. This type of framework also places individual lags seen in these three states as latest Turonian or early Coniacian age. However, the biostratigraphy of associated chondrichthyans in these lags discussed in the 'Systematic paleontology' section above and seen in Table 1 clearly demonstrates mixing of latest Turonian and early Coniacian genera and species. These genera and species, as represented primarily by teeth, can be viewed as erosion-resistant bioclasts that have experienced multiple periods of exhumation and reburial during the late Turonian–early Coniacian regressive-transgressive sea-level event in the WIS. In our view, the late Turonian–early Coniacian bounding unconformity would therefore better represent: 1) a time-transgressive surface; and, 2) that associated chondrichthyan and osteichthyan lags found in these WIS states be recognized as time-averaged marker beds. These marker beds would also provide distinct stratigraphic horizons by which regional and eustatic sea-level cycles could be recognized and correlated including those identified by Merewether et al. (2007) and KTu5–KCo1 of Haq (2014) as described in this report.

Vertebrate-bearing lag deposits similar to the one found between the Tocito Sandstone and Mulatto Tongue of the Mancos Shale in New Mexico are relatively common in Late Cretaceous and Cenozoic shallow marine sediments in the US. Specifically, these lag deposits: 1) form during regressive-transgressive regional and eustatic sea-level events; 2) can be recognized in outcrop as

stratigraphic horizons that reside at the contacts between geologic formations, members or units; and, 3) occur directly above unconformites between shale and sandstone, marl and limestone or clay and sand (e.g., Cicimurri, 2004; Hancock and Walaszczyk, 2004; Shimada et al., 2006; Cumbaa et al., 2006, 2013; Becker et al., 2010; Underwood and Cumbaa, 2010; Hamm and Cicimurri, 2011; Schubert et al., 2017; Maisch et al., 2019). The chronology of chondrichthyans and associated invertebrate fossils found within these lags also provide stage to sub-stage boundary age resolution (Hancock and Walaszczyk, 2004; Williams, 2006; Becker et al., 2010; Hamm and Cicimurri, 2011; Cappetta, 2012; Hamm, 2020). These sequence stratigraphic and biostratigraphic properties have correlative potential across basins and states (e.g., Evetts, 1979; Becker et al., 2010; Cumbaa et al., 2010; Hamm and Cicimurri, 2011; Maisch et al., 2014). In fact, several controversial studies have even proposed transatlantic correlation of the TCTT event between New Mexico and western Europe based on the occurrence of inoceramid bivalves including *Cremnoceramus deformis erectus* identified in this study (see Hancock and Walaszczyk, 2004; Walaszczyk et al., 2014; Krause and Braunberger, 2016).

Future opportunity may exist to apply the sequence stratigraphic correlative methods identified in this study to other localities where chondrichthyan and osteichthyan lag deposits occur along unconformities. For example, Cumbaa et al. (2010) utilized a bentonite layer to analyze contemporaneous mid-Cenomanian chondrichthyan and osteichthyan concentrations at five localites in the WIS between Alberta and Kansas. Their study indicated that these concentrations occurred along unconformities and distinct lithology changes within relatively narrow beds. These beds were identified 2 m or more below to 1.5 m above the bentonite bed and 40Ar/39Ar ages ranged between 94.96 ± 0.5 Ma and 93.3 Ma. This range in ages occurs during at least two, third-order sea-level cycles of Haq (2014), including KCe4 and KTu1, where the sequence bounding unconformities may provide a chronostratigraphic framework and datum by which changes in chondrichthyan and osteichthyan faunas can be interpreted and correlated across broad geographic areas of the WIS.

6. Conclusions

1. In the Chamisa Field Site study area, the Tocito Sandstone represents a series of discontinuous and erosional offshore sandbar lenses occurring within the Mulatto Tongue of the Mancos Shale. These lenses were deposited above the Turonian–Coniacian boundary and formed during the late Turonian regression-early Coniacian transgression of regional and eustatic sea-level. This sea-level event also formed an unconformity that can be traced throughout the WIS (sensu Haq, 2014; Lin et al., 2019; Merewether et al., 2007; Molenaar, 1983).
2. The upper contact between the Tocito Sandstone and Mulatto Tongue contains a lag deposit with chondrichthyans and osteichthyans of known chronologies from both the Turonian and Coniacian (see 'Systematic Paleontology' above). These vertebrate fossils have been reworked and mixed during this late Turonian regression-early Coniacian transgression sea-level event (e.g., Merewether et al., 2007; Haq, 2014).
3. The Turonian–Coniacian interval unconformity and chondrichthyan and osteichthyan lag deposit identified in this study can be traced into Texas and Kansas and possible other states in the WIS. These two states also have lags with the same, or similar Turonian–Coniacian chondrichthyans and osteichtyans directly below, or above the Turonian–Coniacian boundary (Hamm and Cicimurri, 2011; Bice and Shimada, 2016). We interpret these chondrichthyan and osteichthyan lags to be the product of the same sea-level event recognized at the Chamisa Field Site study area.
4. The Turonian–Coniacian chondrichthyan and osteichthyan lag deposits and unconformity in these three states form a chronostratigraphic surface by which regional and eustatic, regressive-transgressive sea-level cyclity can be identified and correlated across shorelines, basins and states of the WIS (sensu Haq, 2014; Merewether et al., 2007).
5. The methods utilized in this study are applicable elsewhere and may represent a means to reconcile traditional lithostratigraphic interpretations and the correlative nature of time transgressive vertebrate fossil lags or concentrations in the stratigraphic record (e.g., Donovan, 1993; Cumbaa et al., 2010).

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