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Fish and Reptiles of the ReBecca's Hollow Site, Williams Fork Formation, Late Cretaceous (Edmontonian), Colorado & 'Between the Dinosaurs' Toes': Approaches to Exhibiting Microvertebrate Fossils in Museum Displays (With Emphasis on the Cretaceous Period)

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above-mentioned discipline.

**FISH & REPTILES OF THE REBECCA'S HOLLOW SITE, WILLIAMS FORK
FORMATION, LATE CRETACEOUS (EDMONTONIAN), COLORADO
&
'BETWEEN THE DINOSAURS' TOES': APPROACHES TO EXHIBITING
MICROVERTEBRATE FOSSILS IN MUSEUM DISPLAYS (WITH EMPHASIS ON
THE CRETACEOUS PERIOD)**

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(Edmontonian), Colorado & 'Between the Dinosaurs' Toes': Approaches to Exhibiting

Microvertebrate Fossils in Museum Displays (With Emphasis on the Cretaceous Period)

Thesis directed by Professor of Geological Sciences & Curator of Vertebrate Fossils Dr. Jaelyn J.

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The ReBecca's Hollow locality of the Late Cretaceous Williams Fork Formation (northwestern Colorado) yields a diverse, actinopterygian-dominated, vertebrate fauna from a freshwater environment. This assemblage is temporally correlative with the Horseshoe Canyon and St. Mary River Formations in Alberta but has many faunal similarities to Lancian localities from MT, WY, and the Dakotas. The discrepancy in fauna between the WFF and its Canadian contemporaries supports the hypothesis, proposed by others, for discrete faunal/climate zones between northern and central Laramidia across the Campanian-Maastrichtian boundary. The microvertebrate fossils from this locality provide important paleoecological data but, like other small fossils, are difficult to display and interpret in a museum setting. I propose a display method based on notions of worldbuilding and contextual learning that visually explain these specimens to museum audiences.

DEDICATION

This work is dedicated to my parents, Dr. Doris Bazzini Crothers and Colin Crothers, my brother Sean Crothers, and my aunt Dr. Maria Bazzini. They have all encouraged me to pursue my passions and provided me with endless support, wisdom, and love. Sean and I grew up with a love of dinosaurs, fish, and art and I am deeply grateful that we have both been able to pursue our creative dreams and continue to inspire one another.

Before beginning this project, I had been wrestling with my place within the arts and sciences, and my larger place in the vastness of time and space. I owe a tremendous debt to my family, who pushed me past my trepidations and inspired me to explore lost worlds and strange new ones.

ACKNOWLEDGEMENTS

I owe a huge thank you to my advisor Dr. Jaelyn Eberle, who served as the primary paleontological supervisor on this project. Jaelyn provided invaluable wisdom on the formatting, research style, and organization of this project, and I cannot express my gratitude enough for her making room for my artist's sensibilities in both this thesis and her laboratory.

The research conducted in this thesis would not have been possible without the input of my committee members, Dr. ReBecca Hunt-Foster, Dr. Don Brinkman, and Jim Hakala. Each provided valuable insight into the project's scientific and museological components. I must also thank Dr. Don Brinkman and Dr. Jim Gardner for hosting me during my visit to the Royal Tyrrell Museum of Paleontology in Drumheller, Alberta, and for providing tremendous help with the identification of the specimens from this assemblage.

The inception of this project is owed to my fellow Appalachian State University alumni Alyssa Wurtz, who originally helmed this faunal analysis as her undergraduate thesis. Alyssa's work provided me with an invaluable launch pad, and I hope that my continuation of this project does justice to her prior research.

The origins of this project are additionally owed to my Mesozoic mentor Dr. Andrew Heckert and his 2021-2024 field and lab crews from Appalachian State University's Department of Geological and Environmental Sciences, who collected and sorted thousands of fossil specimens, including the ones described in this work. These specimens are accessioned into the collections of the Utah Field House of Natural History State Park Museum, and thus I owe curator Dr. John Foster a thank you for his help in curating these specimens and his input on their identifications.

Funding for this project was provided, in part, by the University of Colorado Museum of Natural History's Museum Student Research Award. This funding was instrumental in securing my collections trip to Drumheller in August of 2024, and I am beyond grateful to the museum for providing me with this opportunity.

I finally must thank my friends and family for their support and encouragement with this project. Especially, my dear friends Luke Rose, Isaac Pugh, and Jeremiah Klinkerman, who I have come to embrace as my brothers in paleontology. This large interdisciplinary project has taken the better part of two years, but their enthusiasm and excitement for my work have kept me energized and excited to share it with them and the rest of the world.

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THESIS ORGANIZATION

This master's thesis has two components: (1) a standard paleontological analysis of the fish and reptiles of the Late Cretaceous Rebecca's Hollow locality in the Williams Fork Formation of Northwestern Colorado; and (2) a museological examination of how microvertebrate fossils are displayed and utilized in museum exhibitions. The first component of the thesis will be devoted solely to the systematic paleontology of 33 fish and reptile taxa, and an analysis of the guild structure of Rebecca's Hollow. The second component of this thesis discusses the problems that microvertebrate fossils pose in the context of museum displays, a discussion of contemporary methods of displaying these tiny fossils, and a philosophical meditation on how 'worldbuilding' may be useful to these displays. I conclude this section with a proposed visual solution to displaying microvertebrates.

INSTITUTIONAL ABBREVIATIONS

AMNH – American Museum of Natural History, New York, NY

DMNS – Denver Museum of Nature & Science, Denver, CO

MOR - Museum of the Rockies, Bozeman, MT

MWC - Museums of Western Colorado's Dinosaur Journey, Fruita, CO

RTMP - Royal Tyrrell Museum of Paleontology, Drumheller, AB

UCM – University of Colorado Museum of Natural History, Boulder, CO

UFHNS - Utah Field House of Natural History State Park Museum

USNM – United States National Museum of Natural History, Washington, D. C.

PART I

FISH & REPTILES OF THE REBECCA'S HOLLOW SITE, WILLIAMS FORK FORMATION, LATE CRETACEOUS (EDMONTONIAN), COLORADO

INTRODUCTION

Microvertebrate fossil sites provide a unique window into the biodiversity and ecology of extinct ecosystems, which have otherwise largely been erased from the geologic record. These sites and the taxa they preserve, provide useful frames of reference for modeling the dynamics of ecosystems, extinction patterns, and guilds (Estes 1964; Fiorillo, 1989; Brinkman, 1990; Brinkman, 2005; Baszio, 2008; Jamniczky et al., 2008; Brinkman, 2008; Longrich et al., 2012; Gardner & DeMar, 2013; Wynd et al., 2020). Mesozoic microvertebrate sites (especially those of Western North America) have been of particular interest to paleontologists because they yield small mammalian fossils from a variety of extant and extinct lineages, which are otherwise rare or absent from the fossil record (Clemens; 1966; Clemens et al., 1979; Archibald, 1982; Kelly, 2014). Mesozoic mammal fossils are particularly useful for biostratigraphic analysis and answering evolutionary questions regarding modern mammalian taxa (Wood et al., 1941; Lillegraven & McKenna, 1986; Hunter et al., 1997; Cifelli et al., 2004). Despite the dominance of mammals in the literature surrounding microvertebrate fossil sites, these localities also preserve diverse communities of contemporary chondrichthyans, actinopterygians, lissamphibians, squamates, testudines, and archosaurs, which often greatly outnumber mammals in both frequency and diversity (Estes 1964; Estes 1970; Greenwald, 1971; Sahni, 1974; Bryant 1989). Over the last four decades, considerable attention has been placed on the diversity and

structure of non-mammalian Late Cretaceous microvertebrate communities (Brinkman, 1990; Eberth & Brinkman, 1997; Peng et al., 2001; Brinkman, et al., 2004; Brinkman, 2005; Garrison et al., 2007; Brinkman, 2008; Larson et al., 2010; Cullen et al., 2016; Brand et al., 2022; Wick & Brink, 2022). Many frames of inquiry such as their usefulness as biostratigraphic tools, environmental indicators, biodiversity gauges, and the ability to diagnose fragmentary teeth and vertebrae to the family or generic level have been attempted with fruitful results (Estes 1969; Carpenter 1982; Currie et al., 1990, Pearson et al., 2002; Heckert, 2004; Brinkman, 2005; Heckert & Lucas, 2006; Wilson, 2008; Longrich et al., 2011; Longrich et al., 2012; Brinkman et al., 2013; Brinkman et al., 2014; Brinkman et al., 2021; Wynd et al., 2020). These investigations have allowed researchers to reconstruct ancient ecosystems with a resolution that would have been unprecedented in previous decades.

Microvertebrate communities from the Late Cretaceous of the North American interior have been the subject of relatively intense inquiry over the last century. These faunas are particularly interesting to paleontologists because they record a relatively continuous record of the biota surrounding the transgressions and regressions of the Western Interior Seaway (an inland seaway that covered much of North America from the Early to Late Cretaceous) and the Cretaceous-Paleogene Mass Extinction (Estes et al., 1964; Estes et al., 1969, Estes et al., 1970; Archibald, 1982; Bryant 1989; Lofgren, 1995; Longrich et al., 2011; Longrich et al., 2012; Slattery et al., 2013; Wynd et al., 2020). Additionally, these sites are accessible to American and Canadian institutions, which have meticulously collected microvertebrate material via screenwashing and sediment sorting. This rich fossil record has allowed the development of four Late Cretaceous North American Land Mammal Ages (NALMA), which include (from oldest to youngest) the: Aquilan, Judithian, “Edmontonian”, Lancian (Russel, 1964; Russel, 1975;

Lillegraven & McKenna, 1986; Cifelli et al. 2004). Among the least understood of these ages is the informally recognized “Edmontonian”, best known from the late Campanian to early Maastrichtian St. Mary River Formation of Alberta (Sloan & Russell 1974; Russell 1975). This age is not defined by an endemic mammalian fauna, but rather a mosaic of Lancian and Judithian taxa. The rarity of known “Edmontonian” fossil sites is, in part, due to significant transgressions of the Western Interior Seaway during the latest Campanian and erosion from the early stages of the Laramide Orogeny (Fig. 1). Some of the best-known terrestrial fossiliferous units that are recognized as part of this faunal stage include the Horseshoe Canyon Formation of Alberta (Fox & Naylor, 1986; Cifelli et al. 2004), the El Gallo Formation of Baja California, Mexico (Lillegraven, 1972; Cifelli et al. 2004), the Prince Creek Formation of Alaska (Eberle et al., 2023) and the Williams Fork Formation of Colorado (Lillegraven, 1987; Diem, 1999; Cifelli et al. 2004). The lower part of the “Edmontonian” age overlaps with a separate faunal age known as the Kirtlandian land-vertebrate age of New Mexico, which was proposed by Sullivan & Lucas (2003; 2006) and defined based on the biostratigraphy of non-mammalian vertebrates. In terms of numerical age, the “Edmontonian” is generally recognized as c. 74-67.5 Ma (Cifelli et al., 2004), and the Kirtlandian is recognized as c. 75-72.8 Ma (Sullivan & Lucas, 2006). The Campanian-Maastrichtian boundary is recognized as 72.1 Ma by the Geological Society of America’s 2022 geological time scale, and thus the “Edmontonian” overlaps this boundary (Fig. 4). This temporal boundary in the Cretaceous was characterized by very high sea levels and a relatively cool and dry climate in northern regions of the North American interior (Specifically southern Alberta) during certain intervals (Quinney et al., 2013). The reason for these comparatively cooler climatic conditions at the Campanian-Maastrichtian has been linked to

changes in ocean circulation from tectonic activity, as inferred from isotopic data from foraminifera fossils and geophysics (Linnert et al., 2014).

The Williams Fork Formation of Northwestern Colorado is one of the best examples of a terrestrial “Edmontonian” unit in the contiguous United States (Cifelli et al., 2004). This Formation has been known to produce diverse fossil assemblages since at least the 1980s, but it has been only in the last three decades that rigorous paleontological analysis has revealed the Williams Fork Formation to contain a unique coastal ecosystem that existed alongside the better-known Canadian examples during one of the coldest climatic periods of the Cretaceous (Archibald, 1987; Diem, 1999; Brand et al., 2022). Previous analysis from this unit suggests a mixture of faunal influences from both northern and southern Laramidia and a temporally intermediate fauna with both Judithian and Lancian vertebrates (Brand et al., 2022).

The recently discovered ReBecca’s Hollow site of Rio Blanco County, CO is among the richest known microvertebrate sites in terms of quantity and biodiversity in the Williams Fork Formation. This deposit has produced at least 37 vertebrate taxa, with more expected to be unearthed with continued sampling. Among the novel features of this locality is the impressive diversity of actinopterygian fishes, lissamphibians, squamates, turtles, and archosaurs. Below I provide a description of the chondrichthyans, actinopterygians, testudines, and archosaurs from ReBecca’s Hollow. Auranos, caudatans, albanerpetontids, anguils, helodermatids, serpentes, as well as metatherians, and multituberculates, are known from this site and will be described in detail in a series of future publications. I compare ReBecca’s Hollow’s fish and reptile fauna to coeval faunal assemblages in the Horseshoe Canyon and St. Mary River Formations of Southern Alberta, which provides new inferences to be made about the environmental and climatic differences between northern and southern Laramidia during the “Edmontonian” age.

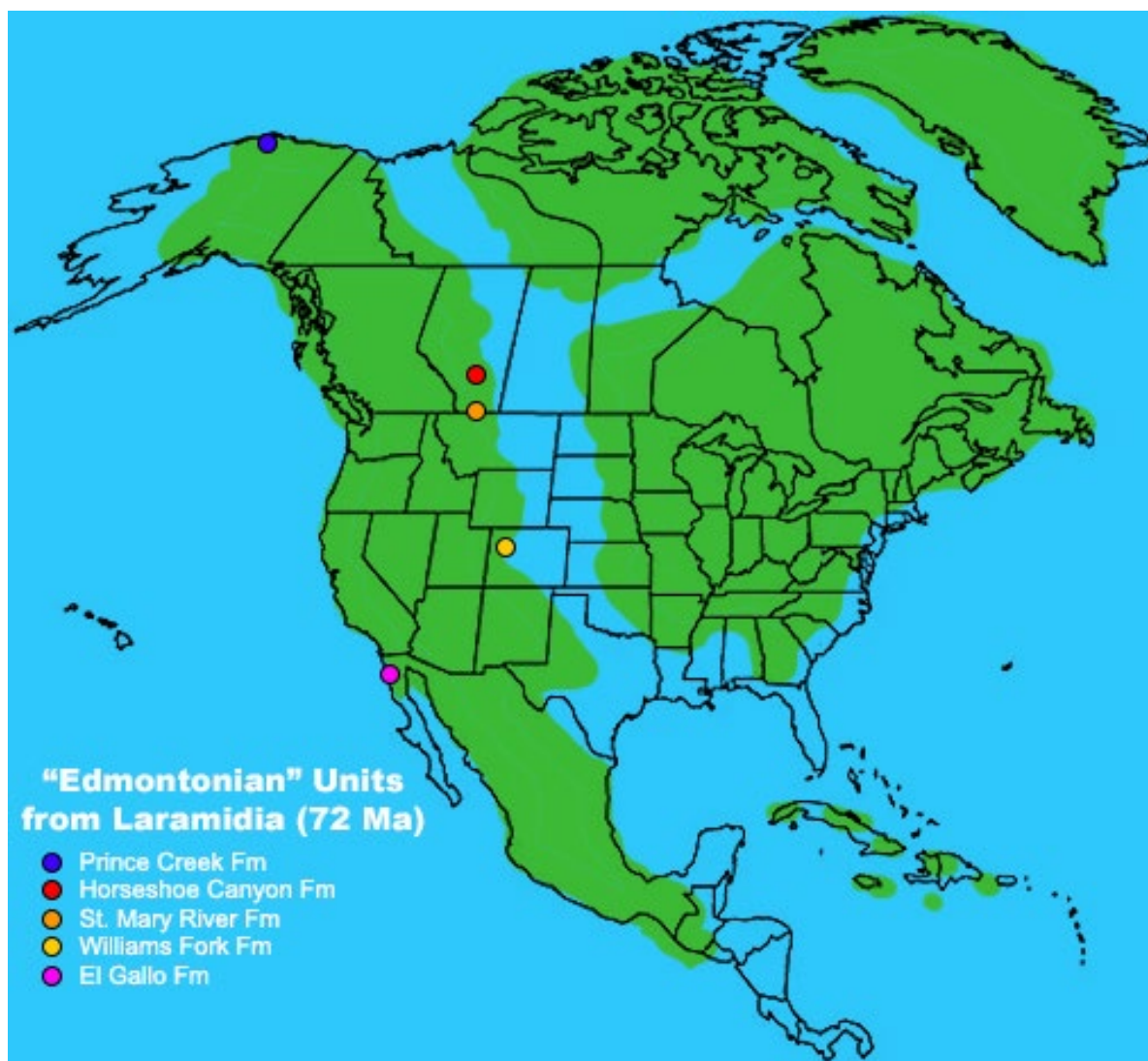


FIGURE 1. Palaeo-geographic map of late Campanian-early Maastrichtian (72 Ma) North American with well-known “Edmontonian” units marked. Adapted from Nyborg et al. (2014), Slattery et al. (2013), and Cifelli et al. (2004).

GEOLOGIC SETTING

The Williams Fork Formation is a Late Cretaceous sedimentary unit that outcrops along the Douglas Creek Arch in Northwestern Colorado (Fig. 2). This formation is the uppermost layer of the Mesaverde Group in the region and mainly consists of sandstones, interbedded with shales, mudstones, and lignites (Noll, 1988) (Fig. 3). The Williams Fork Formation has been interpreted as a fluvial deltaic system, which was deposited along the western shore of the epeiric Western Interior Seaway. The age of this unit has traditionally been inferred by ammonite zones, as it spans from the *Didymoceras cheyennense* to the *Baculites baculus* zones (Newman, 1987). These zones correlate to the numerical dates of c. 74.5-71.2 Ma (Gale et al., 2020). The dates from these ammonite zones place the Williams Fork Formation within the “Edmontonian” age (c. 74-67.5 Ma), and thus it is regarded as one of the key terrestrial rock units in this informal NALMA (Cifelli et al., 2004). Despite this historic age range, a detrital zircon date of 71.7 +/-1.8 Ma from Noll’s (1988) Sandstone C suggests that the Williams Fork Formation is largely Maastrichtian (Hunt-Foster et al., 2025) (Fig. 4). Locally the Williams Fork Formation overlies the Campanian marine Iles Formation and uncomfortably underlies the Eocene Wasatch and Green River Formations (Noll, 1988). Regionally, the Williams Fork Formation is overlain by the Cretaceous Lewis Shale and Lance Formation, which outcrops along the Rock Springs Uplift in Western Wyoming (Fig. 3) (Noll, 1988). The eastern portion of the Williams Fork Formation was likely shallow marine at certain intervals and ammonites are known from outcrops in Moffat County, CO (Newman, 1987). The presence of chondrichthyan teeth and denticles throughout this formation suggests a direct marine influence throughout the unit, but the frequent occurrence of fossils from freshwater turtles, crocodilians, lepisosteids, and amiids suggest a brackish to freshwater ecosystems. Most large fossilized bones from the Williams Fork Formation are

heavily water-worn and transported. Microvertebrate sites are relatively common in sandy channel scours and carbonaceous lenses (Eberle et al., 2024). The Williams Fork Formation is equivalent in age to the Bearpaw and upper Pierre Formations in Montana, North Dakota, South Dakota, and Wyoming, the lower Horseshoe Canyon and St. Mary River Formations of southern Alberta (Eberth & Kamo, 2022), the El Gallo Formation of Northern Mexico (Fastovsky, et al., 2020), the Meeteetse Formation of northern Wyoming (Shin, 2005), the upper Aguja Formation of Southwestern Texas, and possibly the Naashoibito Member of the Ojo Alamo Formation (formerly Kirtland Formation) in Northwestern New Mexico (Foster & Hunt-Foster, 2015).

The ReBecca's Hollow site is located on Bureau of Land Management land in Rio Blanco County, Colorado, in the badlands south of the town of Rangely (Fig. 5). This highly fossiliferous site is part of a carbonaceous mudstone lens that occurs between what Noll (1988) designated as Sandstone C and Sandstone D in the uppermost part of the lower half of the Williams Fork Formation. The fine organic sediment, the large quantity of small actinopterygian fossils, and the preservation of > 0.5 mm fossils suggest a shallow freshwater pond or oxbow lake environment. The dark organic sediment at ReBecca's Hollow is highly reactive to H₂O₂, and thus this chemical was used to prepare sediment from this locality. This site overlays the nearby J&M locality (part of a channel scour in Noll's Sandstone C) by approximately 8 meters (Noll, 1988).

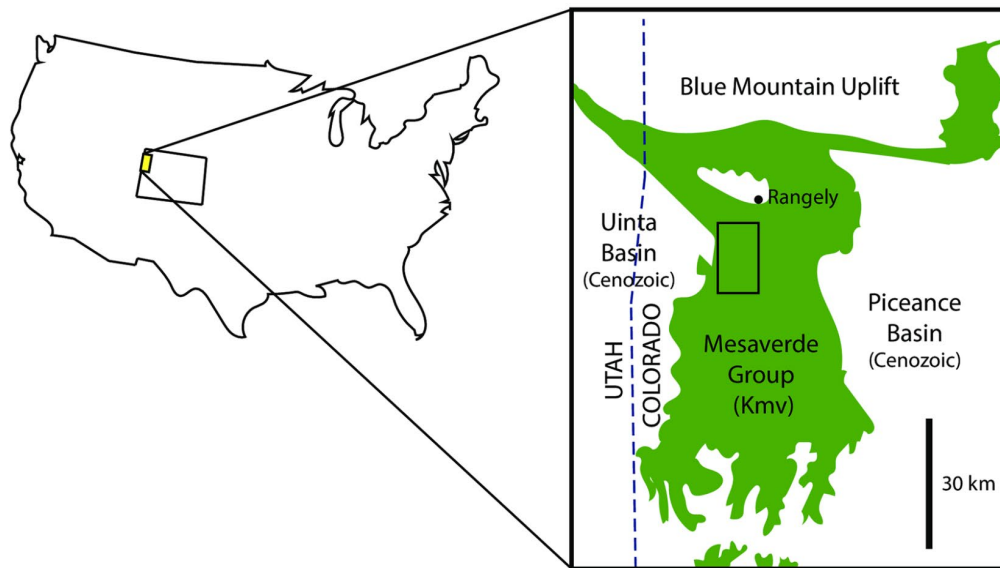


FIGURE 2. Map of Colorado (and neighboring Utah to the west) with the approximate location of the ReBecca's Hollow (site in rectangle). Modified from Eberle et al. (2024)

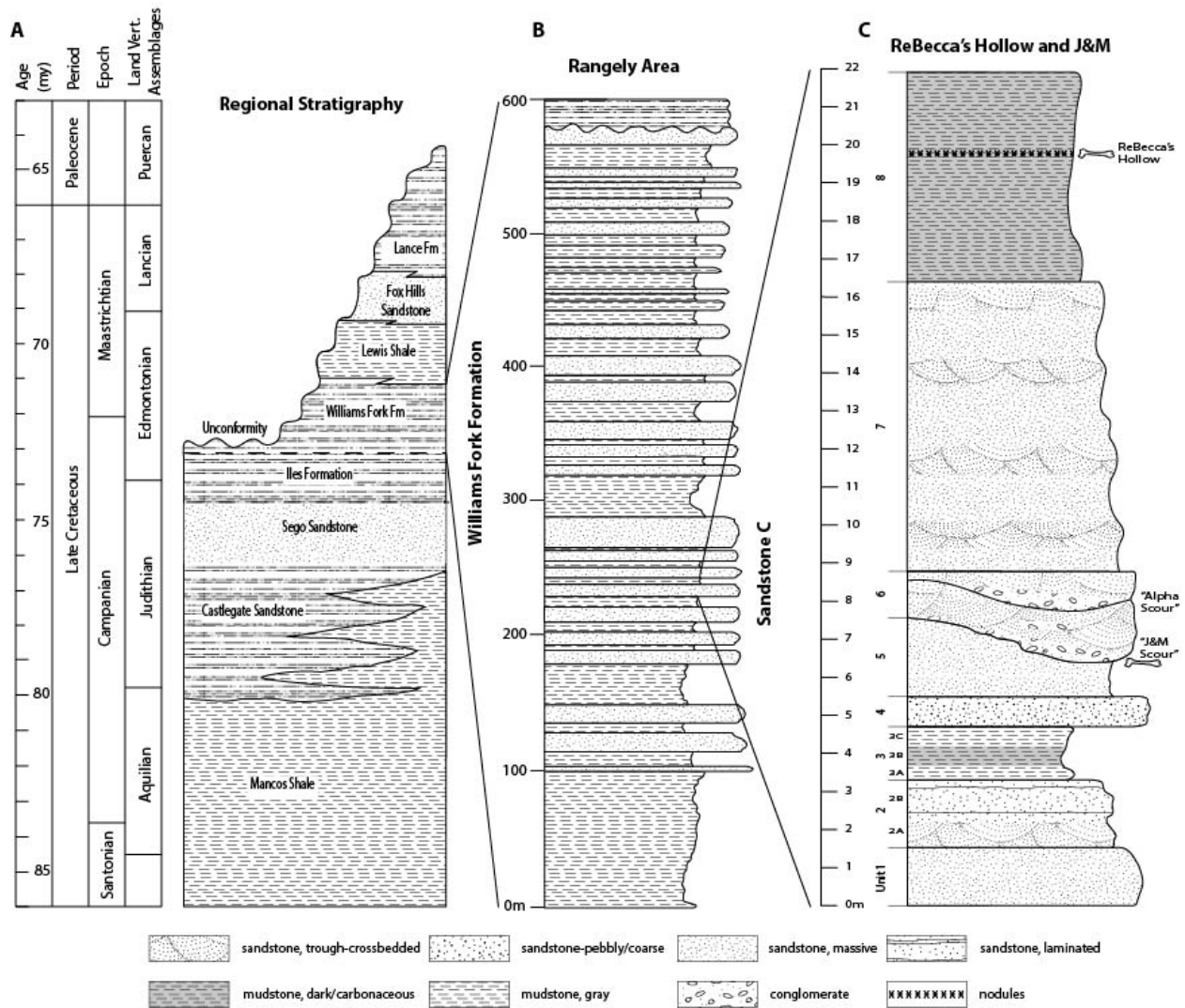


FIGURE 3. Generalized stratigraphic column of the Douglas Creek Arch (left), the Rangely Area of Rio Blanco County, CO (middle), and the ReBecca's Hollow and J&M localities (right). Stratigraphic column provided by John Foster, ReBecca Hunt-Foster, and Alyssa Wurtz and modified from Noll (1988).

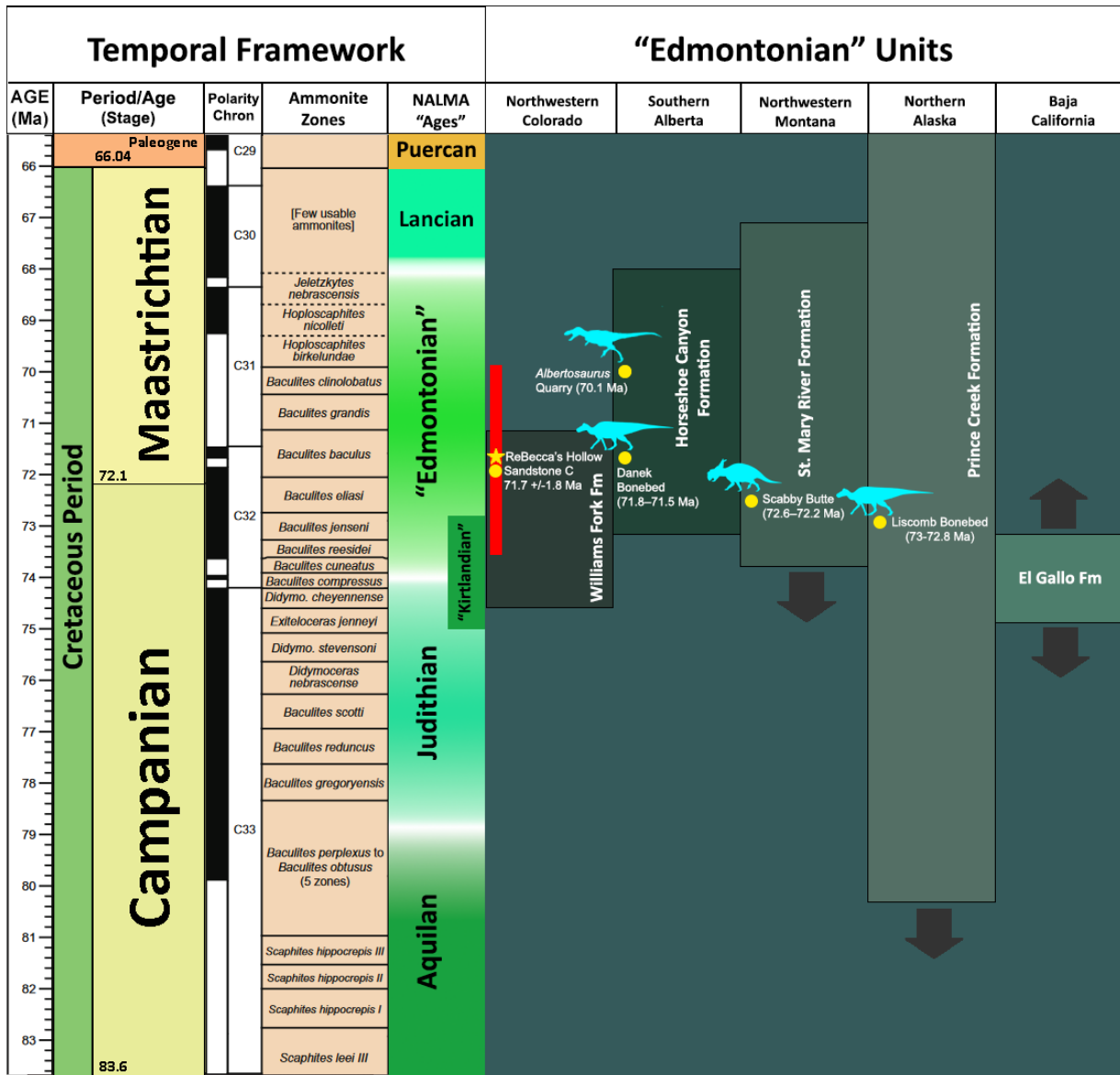


FIGURE 4. Temporal, paleomagnetic, and biostratigraphic context of well-known “Edmontonian” units. Yellow dots indicate localities with associated numerical dates. Red bar indicates the range of uncertainty for numerical date of Williams Fork Formation. Yellow star indicates an educated guess for the numerical age of the ReBecca’s Hollow locality. Blue dinosaur silhouettes represent the taxa that dominate the bonebeds of their respective localities. Dark arrows indicate uncertainty of dates for geologic formations. Modified from Eberth & Kamo (2020), Ramezani et al. (2022), Gale et. al. (2020), Sullivan & Lucas (2006), Cifelli et al. (2004), Druckenmiller et al. (2023), and Fastovsky (2020). The zircon date from the Williams Fork Formation was provided by Hunt-Foster et al. (2025)

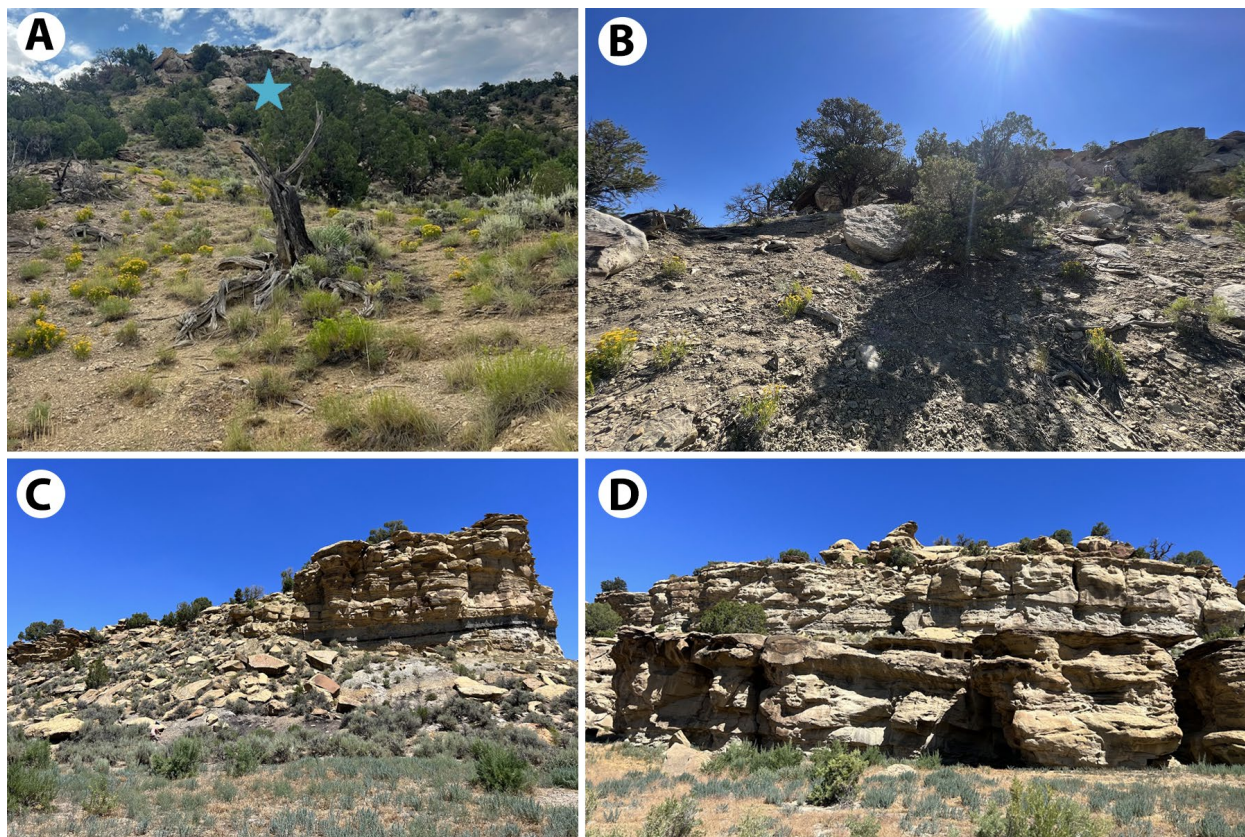


FIGURE 5. Williams Fork Formation (Late Cretaceous) exposures south of Rangely, CO. (A) UFHNH locality SCP 2019-2 (ReBecca’s Hollow). Blue star denotes fossiliferous horizon. (B) Closeup of fossiliferous horizon at ReBecca’s Hollow. (C-D) Sandstone buttes neighboring UFHNH locality SCP 2019-2.

MATERIALS AND METHODS

The fossils described in this unit are accessioned and repositied in the collections of the Utah Field House of Natural History State Park Museum in Vernal, UT. They were collected with permits on Bureau of Land Management land by field crews from Appalachian State University and the Utah Field House of Natural History State Park Museum in May of 2021 and May of 2022, with permits obtained by Dr. John Foster. Sediment was recovered from this site in bulk and screen-washed in Heckert's Paleontology Undergraduate Research Lab on Appalachian State University's Campus (Boone, NC). The sediment was placed in paint sieves and suspended in a solution of water and hydrogen peroxide. This process oxidized the organic clay clinging to the fossils, which fell away from the larger bone and rock clasts in the paint sieves. After the sediment was freed from the clay particles and dried, it was then poured into a series of circular metal sieves at mesh sizes of 4 mm, 2 mm, 1 mm, and 0.05 mm. The differing sediment sizes were then recovered, and fossils were picked using metal tweezers and paint brushes. The fossils described in this thesis were photographed and figured using a ZEISS Axio Zoom V16 in Eberle's lab at CU Boulder and a KEYENCE VHX 3000 3D Microscope in Heckert's lab at Appalachian State.

The taxonomy of Brinkman's 2022 Guidebook of the Dinosaur Park Formation was used as the primary model for the systematic paleontology of this thesis. Additional taxonomy of osteichthyans and reptiles was followed from Brand et al. (2022) and Wick & Brink (2022) for osteichthyan systematics.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order HYBODONTIFORMES Patterson, 1966

Family HYBODONTIDAE Owen, 1846

Meristodonoides Underwood & Cumbaa, 2010

cf. Meristodonoides sp.

Fig. 9, H

Referred Specimen and Locality: UFHNNH 19295, an incomplete tooth from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Meristodonoides*: Kiowa Formation, Kansas (Albian); Trinity Group, Texas (Albian or Aptian); Dakota Group, Kansas (Cenomanian); Coleraine Formation, Minnesota (Cenomanian); Ashville Formation, Saskatchewan (Cenomanian); Carlile Shale, Kansas and Nebraska (Turonian); Atco Point Formation, Texas (Coniacian); Point Lookout Sandstone, New Mexico (Santonian); Eutaw Formation, Mississippi (Santonian–Campanian); Belly River Group, Montana and Alberta (Campanian); Mesaverde Formation, Wyoming (Campanian); Demopolis Chalk, Mississippi (Campanian); Blufftown Formation, Georgia (Campanian); Black Creek Group, North Carolina (Campanian); Marshalltown Formation, Delaware (Campanian); Northumberland Formation, British Columbia (Campanian); Monmouth Group, New Jersey (Campanian-Maastrichtian).

Description: UFHNNH 19295 is an incomplete tooth, approximately 5.8 mm from the base of the crown to its broken tip (Fig. 9, H). The tooth crown features a tall main cusp with narrow carinae

running up both lateral sides. The main cusp is curricular in cross-section and features a series of short longitudinal striations around the junction with the root, on both the anterior and posterior sides. These features are consistent with the description of *Meristodonoides* by Underwood & Cumbaa (2010). The root is not preserved, and neither are the lateral cusplets. The incomplete nature of UFHNSH 19295 (especially the absence of the lateral cusplets) does not allow UFHNSH 19295 to be assigned to a species, but the tall central cusp and lack of a labial boss differentiate it from the contemporary hybodont genus *Lonchidion*. Additionally, the damaged nature of the tooth does not facilitate its identification as an anterior or lateral tooth. The identification of UFHNSH 19295 was aided by personal communication with Don Brinkman in August of 2024.

Discussion: Originally described as *Hybodus rajkovichi* by Case (2001), most examples of this hybodontid in the Cretaceous of North America were reassigned to a new genus *Meristodonoides* by Underwood & Cumbaa (2010). This genus is generally regarded as a cosmopolitan shallow marine/brackish taxon, with an expansive geographic range in North America, Europe, and Asia from the Tithonian Stage of the Jurassic to the early Maastrichtian of the Cretaceous (Underwood 2020; Brinkmann 2005; Brinkman 2008). UFHNSH 19295 is one the only known chondrichthyan present at the ReBecca's Hollow locality and represents the first occurrence of this genus in the Williams Fork Formation (an example of *Chiloscyllium* was recovered from ReBecca's Hollow as the systematics were largely completed and will be included in a future publication). *Meristodonoides* is the second known hybodont from the Williams Fork Formation, as Brand et al. (2022) reported *Lonchidion griffisi*, as well as several other elasmobranch taxa, from the nearby J&M site.

Chondrichthyans are well-known from freshwater facies across Laramidia throughout the Cretaceous and have generally been regarded as proxies for marine influence from the Western

Interior Seaway (Estes 1964; Estes & Berberian 1970; Estes et al. 1969). Despite this deduction, Wynd et al. (2020) found that chondrichthyan diversity through the Hell Creek Formation was seemingly not affected by the retreat of the epeiric seaway, thus creating some ambiguity around the nature of their ecology. The presence of cf. *Meristodonoides* in an environment near the Western Interior Seaway is therefore not surprising, but the lack of other elasmobranch taxa is a curious feature of ReBecca's Hollow, especially when compared to the neighboring chondrichthyan-rich J&M site. Cook et al. (2014) found that occurrences of the hybodont *Lonchidion* in non-marine Laramidian deposits were correlated with warm climatic conditions. Because an example of "*Hybodus* sp." (likely *Meristodonoides*) is known from the contemporary Horseshoe Canyon Formation of Alberta, Canada, it does not seem this genus is much of an indicator of paleoclimatic condition, as this unit is thought to represent a relatively cool climate with a distinct faunal zone (Larson et al. 2010; Quinney et al. 2013).

Superclass OSTEICHTHYES Huxley, 1880

Class ACTINOPTERYGII Klein, 1885

Order ACIPENSERIFORMES Berg, 1940

Family ACIPENSERIDAE Bonaparte, 1831 (s. Bemis et al., 1997)

cf. Acipenseridae gen. et sp. indet.

Fig. 9, L

Referred Specimen and Locality: UFHNNH 19284, a fragment of sculpted dermal bone, likely cranial, from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFHNH 19284 is a fragment of sculpted dermal bone, approximately 2.5 mm in length (Fig. 9, L). This fragmentary bone is ornamented with distinctive anastomosing ridges and pits seen in living and extinct examples of sturgeon skulls (Hilton & Grande, 2006). UFHNH 19284 lacks the ganoid covering of lepisosteid dermal bones and the linear striations seen in amiid skull bones. The fragment is too incomplete to designate to a region of the skull or more precise taxonomic identification, but the smooth ridging and small pits are distinctive enough to identify the bone as likely being from the skull, rather than a dermal scute (Estes 1964; Hilton & Grande 2006).

Discussion: Acipenserid fossils are known from numerous freshwater facies across the Cretaceous of North America, from the Cenomanian to the latest Maastrichtian (Vavrek et al. 2014; Hilton & Grande 2006). This group has survived into the present day and currently consists of 27 recognized species (Hung, 2017). Archibald (1987) reported the occurrence of a possible acipenseriform fossil from the Williams Fork Formation, and thus this specimen is the second report of this group in the unit. Unfortunately, no specimen number, element, locality, or collection number was given for Archibald's fossil, making it impossible to confirm. Currently, modern sturgeons are known from subarctic to subtropical waters in North America and Eurasia (Hung, 2017). Sturgeon fossils are usually uncommon in microvertebrate sites, with some authors owing this to their anadromous lifestyle (Estes 1970; Bryant 1989). If UFHNH 19284 represents a sturgeon, its presence at ReBecca's Hollow is not surprising as they are well known from Cretaceous freshwater facies, including the contemporaneous Horseshoe Canyon Formation in Alberta (Larson et al., 2010).

Order LEPISOSTEIFORMES Hay, 1929

Family LEPISOSTEIDAE Owen, 1825

Atractosteus Rafinesque, 1820

Atractosteus sp.

Fig. 6, I-J

Referred Specimens and Locality: UFHNH 20733, 2 lateral line (left and right) scales from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Late Cretaceous North American Distribution of *Atractosteus*: Demopolis Formation, Mississippi (Campanian); Aguja Formation, Texas (Campanian); Belly River Group, Montana & Alberta (Campanian); Mesaverde Formation, Wyoming (Campanian); St. Mary River Formation(?), Alberta (Campanian-Maastrichtian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, Montana (Maastrichtian); Frenchman Formation, Saskatchewan (Maastrichtian).

Description: UFHNH 20733 are two lateral line scales from lepisosteids. These specimens measure 15.5 x 8 mm (UFHNH 20733B) and 22.5 x 15 mm (UFHNH 20733A) (length by height) (Fig. 6, I-J). The scales are both rhomboid in shape and have a bony base with a ganoid covering on the exterior side. Both have the lateral line canal on the interior of the posterior end of the scale (found only on the lateral line scales) (Grande, 2010). Both scales have a shallow dorsal peg and a long, low anterodorsal process. UFHNH 20733A sports a slightly more prominent dorsal peg than that of UFHNH 20733B, with the former almost completely reabsorbed by the upper tip of the scale. The shallow dorsal peg on these ganoid scales is thought

to be diagnostic of the genus *Atractosteus*, with the smaller *Lepisosteus* having a taller and more prominent dorsal peg (Grande, 2010).

Discussion: *Atractosteus* (the genus which includes the modern alligator gar, *Atractosteus spatula*) is among the most common and widespread vertebrate fossils in Laramidian microvertebrate sites (Brinkman, 2008; Sankey, 2008; Sahni, 1974; Stein, 2021). Historically, most Laramidian gar fossils were placed in the species *Lepisosteus occidentalis* (originally named *Lepidotus occidentalis* by Leidy in 1856, and recombined by Cope in 1877) (Estes, 1964; Estes, 1969; Greenwald, 1971; Carpenter, 1979; Breithaupt, 1982, Bryant 1989). *Lepisosteus occidentalis* was subsequently placed into the genus *Atractosteus* by Wiley (1976) based on cranial comparisons made by Estes (1964). This taxonomic revision was embraced by Brinkman (1990), Peng et al. (2001), Neuman & Brinkman (2005), and Brinkman (2022) in their identifications of the lepisosteids present in the Campanian Dinosaur Park Formation of Alberta. To complicate the taxonomy of Laramidian gar, Gottfried and Krause (1998) found *Atractosteus* to be a subgenus of *Lepisosteus*. Grande (2010) later found *Atractosteus* to be a valid genus, with one of its distinguishing morphological characteristics being thicker ganoid scales with a less-developed pen and socket than those of *Lepisosteus*. Additionally, Grande (2010) stated that the lateral line scales of *Atractosteus* have a short low dorsal peg, rather than a tall developed one as in *Lepisosteus* (a designation later embraced by Eberle et al. (2014) in their description of Eocene gar from the Canadian Arctic). Despite thousands of gar fossils being known from Laramidian sites, the designation of these remains to one genus or the other remains problematic. Lepisosteids have been reported from the Williams Fork Formation by Archibald (1987) and Brand et al. (2022), but neither designated these fossils to a genus. This is the first report of this genus in the Williams Fork Formation. This genus is extant in the present and represented by

three living species (*A. spatula*, *A. tristoechus*, and *A. tropicus*) (Brownstein & Lyson, 2022). Modern examples of this fish are present in fresh and brackish waters around warm lowland ecosystems in the Mississippi Basin, Central America's Gulf Coast, and the Caribbean. Although gar fossils are common in the Williams Fork Formation, Lepisosteids are absent in the contemporaneous Horseshoe Canyon, likely due to this unit being in colder high-latitude environments with discrete faunal zones (Larson et al., 2010). Curiously, *Lepisosteus* was reported from the Scabby Butte locality area in the roughly contemporaneous and slightly more southern St. Mary River Formation of Alberta by Langston (1975). Because Langston did not describe these specimens, provide specimen numbers, or give an explanation as to why they were referred to this genus, I suspect that this occurrence is that of Holostean A or B as defined by Brinkman (1990). The presence of these fish in the Williams Fork Formation, and its absence in the Horseshoe Canyon appears to provide further evidence of these units representing discrete faunal/climatic zones (Larson et al., 2010, Quinney et al., 2013, Foster & Hunt-Foster, 2015, Brand et al., 2022).

Lepisosteidae n. gen et sp.

Fig. 6, F

Referred Specimens and Locality: UFHNNH 19294, tooth from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian Stage, Late Cretaceous).

Description: UFHNNH 19294 is a 4 mm long conical tooth with a series of deep striations radiating and large enamel folds along the base of the crown (Fig. 9, F). The tooth is slightly recurved and has no carinae along its sides. One of the curious features of this specimen is a lack

of an enamel cap or any break in the enamel structure from the base to the tip of the crown. This tooth best matches an undescribed lepisosteid from the Late Cretaceous of Utah (Brinkman, personal communication in January of 2025). This taxon will be described in an upcoming publication. This potential new taxon is the first of its kind to be reported in the Williams Fork Formation and expands the known osteichthyan diversity of this formation.

Lepisosteidae gen. et indet.

Fig. 6, A, B, C, D, E, G, H, K

Referred Specimen and Locality: UFHNH 19280, 21 vertebral centra; UFHNH 19281, 27 tooth crowns and 3 jaw fragments with teeth; UFHNH 20181, tooth, UFHNH 20199, hundreds of ganoid scales; UFHNH 19280, vertebra centra; UFHNH 20196 cranial elements; UFHNH 20731, hundreds of ganoid scales; UFHNH 20713, lepidotrichia from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Lepisosteids are among the most common vertebrate remains at ReBecca's Hollow that are referable to the family level. UFHNH 20181 and UFHNH 20731 represent thousands of ganoid scales from the lateral, dorsal, and lateral line regions of the gar (following Yang et al., 2014) and personal communication with Don Brinkman in August of 2024). These scales range in completeness from isolated fragments of ganoion to complete scales with intact dorsal pegs and anterolateral processes. Rhomboid scales lacking a lateral line canal are referable to the flanks of the fish, while thick rounded scales originate from the dorsal region (Fig. 6, C). UFHNH 20181 contains several examples of lateral line scales with a posterior canal on the bony base on the interior side, but they are too incomplete to be referred to as a genus. UFHNH 19281

and UFHNH 20181 are collections of conical minutely striated teeth with bulbous translucent tips and restricted crown bases that are typical of this family (Fig. 6, D-E). These teeth range in size from less than 1 mm to 5mm in height. UFHNH 19281 is a batch of three jaw element fragments with striated acrodont tooth sockets (Fig. 6, A, D). In two of the specimens, a row of smaller marginal sockets runs parallel to larger mesial teeth. These fragments are too incomplete to designate to a region in the skull. UFHNH 19280 contains numerous pneumatic opisthocoelous vertebrae (most of which are represented as partial centra) (Fig. 6, K). UFHNH 20196 is a batch of dermal skull elements with ornamented ganoid coverings (Fig. 6, H). Most of these elements are broken and not referable to a specific region of the skull but have the typical ganoid ornamentation of this family of fish. UFHNH 20713 represents dozens of isolated fin rays with enamel covering on the exterior side (Fig. 6, G) It cannot be said as to what fish or region of the body these elements come from, as lepidotrichia on holostean-grade fish generally do not change much from fish to fin as figured in Grande (2010) (Fig. 82), but these elements are nearly identical to lepisosteid lepidotrichia figured in Wink & Brink, 2022 (Fig. 2, H).

Discussion: Lepisosteid fossils are well-known across the Late Cretaceous and Early Cenozoic of North America and are thought to have served as a keystone family in freshwater and brackish environments along the Western Interior Seaway (Estes & Berberian, 1970).

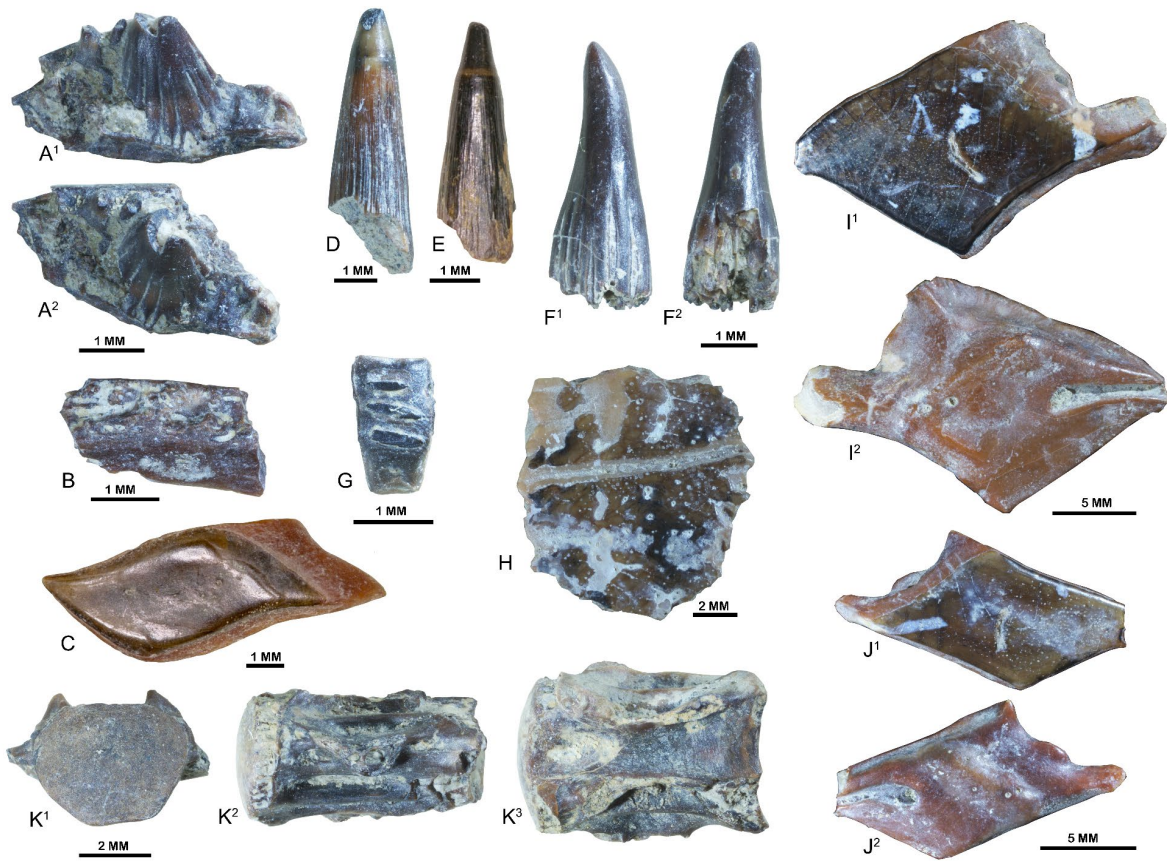


FIGURE 6. Lepisosteid specimens from ReBecca's Hollow (SCP 2019-2). (A) UFHNH 19281A, jaw element in (A¹) medial view (A²) occlusal view. (B) UFHNH 19281B, jaw element in dorsomedial view. (C) UFHNH 20199, lateral ganoid scale in lateral view. (D) UFHNH 19281C tooth in lateral view. (E) UFHNH 19281E, tooth in lateral view. UFHNH 19294, Lepisosteidae n. gen et sp. in (F¹) lateral view and (F²) lingual view. (G) UFHNH 20713, lepidotrichia in lateral view. (H) UFHNH 20196, dermal skull element in exterior view. (I) UFHNH 20733A, *Atractosteus* sp. right lateral line scale in (I¹) lateral view (I²) medial. (J) UFHNH 20733B, *Atractosteus* sp. Left lateral line scale in (J¹) lateral view (J²) medial. (K) UFHNH 20183, vertebral centrum in (K¹) anterior, (K²) left lateral view, and (K³) dorsal view.

Order AMIIFORMES Hay, 1929

Family AMIIDAE Owen, 1825

Subfamily VIDALAMIINAE Grande and Bemis, 1998

Melvius Bryant, 1988

cf. *Melvius* sp.

Fig. 7

Referred Specimens and Locality: UFHNNH 19273, 27 isolated marginal teeth; UFHNNH 20187, 3 isolated marginal teeth; UFMNH 20742, partial vertebral centrum; UFMNH 20741, partial vertebral centrum; UFMNH 20739, partial vertebral centrum; UFMNH20740, partial vertebral centrum from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Melvius*: Straight Cliffs Formation, Utah (Turonian-Campanian); Milk River Formation, Alberta (Santonian); Iron Springs Formation, Utah (Santonian-Campanian); Masuk Formation, Utah (Campanian); Mesaverde Formation, Wyoming (Campanian); Fort Crittenden Formation, Arizona (Campanian); Cabollona Group, Sonora, Mexico (Campanian); Difunta Group, Coahuila, Mexico (Campanian); Aguja Formation, Texas (Campanian); Judith River Formation, Montana (Campanian); Wahweap Formation, Utah (Campanian); Fruitland Formation, Utah (Campanian); Kirkland Formation, Utah (Campanian); Kaiparowits Formation, Utah (Campanian); Mesaverde Formation, Wyoming (Campanian); Williams Fork Formation, Colorado (Campanian-Maastrichtian); Lance Creek Formation, Wyoming (Maastrichtian); Hell Creek Formation, Montana (Maastrichtian).

Description: UFHNNH 19273 and UFHNNH 20187 represent isolated teeth that measure 1.3 to 6 mm in crown height and .5 - 4 mm in width of the base (Fig. 7, E-F). The teeth have developed

mesial carinae on each side but lack serrations and the enamel is smooth and semi-translucent. The carinae begin at the base of the crown as rounded wing-like projections and grade into the body of the crown towards the tip. The teeth are widest at their base and end in an elongated sharp acrodin tip. This tooth style is consistent with vidalamiine amiids (Grand & Bemis, 1998; Cidade et al., 2022). These teeth are similar in size and morphology to those featured in Brand et al. (2022) (Fig. 5), Brinkman et al. (2013) (Fig. 10.8), Eaton et al. (2014) (Fig. 3), Wick & Brink (2022) (Fig. 3), and Bryant (1988) (Fig. 12), all of which have been referred to *Melvius*. Brand et al. (2022) concluded that the morphology of these teeth was consistent with a vidalamiine. Some of the teeth preserve a partial bony root attached to the crown, while others appear to be shed crowns. *Melvius* is the only known genus of vidalamiine in the Cretaceous of Western North America, thus teeth of this morphology have frequently been assigned to this taxon.

UFHNNH 20742, UFHNNH 20739, UFHNNH 20740, and UFHNNH 20741 represent four partial vertebral centra of amiids (Fig. 2, A-D). These large vertebrae can confidently be assigned to this family by being wider than tall, featuring hourglass-shaped neural arch pits, and a distinctive well-ossified and vascular bone texture (Brinkman et al., 2013). Though incomplete, these vertebrae would have measured roughly 28 to 30 mm in diameter. Bryant (1988) referred several vertebrae to this genus and described *Melvius* as having distinctive trunk vertebrae with ventrolaterally concave surfaces.

Discussion: *Melvius* was a large amiid present across Laramidia from the Turonian to the Maastrichtian (Winkler et al., 1990; Bryant, 1988). There are currently two named species of this fish; *M. thompsoni* from the Maastrichtian of Montana, North Dakota, South Dakota, and Wyoming, and *M. chauliodous* from the Campanian of New Mexico and Utah (Bryant, 1988; Hall and Wolberg, 1989; Sullivan et al., 2011). Both of these species were described from cranial

material, but the genus is often diagnosed by its distinctive vertebrae, which are large, ovular in silhouette, and have deeply excavated ventrolateral surfaces between the basapophyses and aortal facets (Bryant, 1988). Teeth and vertebrae that have been referred to *Melvius* are particularly prolific across the American Southwest from the Turonian to the Campanian, but it is largely absent from Canada during the Cretaceous. Isolated teeth, in the Williams Fork Formation, similar to those at ReBecca's Hollow, were referred to this fish by Brand et al. (2022) and a vertebra and dentary were reported by Hunt-Foster et al. (2023). This is the third report of teeth and the second report of vertebrae that match this taxon in the Williams Fork Formation. *M. chauliodous* is among the characteristic taxa of the Kirtlandian fauna of the Late Campanian San Juan Basin of New Mexico and *M. thompsoni* appears to only be present in the Lancian ecosystems of the Williston Basin, Powder River Basin, and Rock Springs Uplift of Montana, Wyoming, and the Dakotas (Sullivan & Lucas, 2006). It is unclear which species of *Melvius* these teeth represent (if they are from this genus, rather than another vidalamiine). This fish appears to be a warm-water taxa, as it is not present in the contemporary Horseshoe Canyon and St. Mary River Formations of Alberta. Bryant (1988) reported a *Melvius* vertebra from the Judith River Formation of Montana, and this seems to be the northernmost occurrence of this genus during the Campanian. It is not until the warmer climate of the late Maastrichtian that *Melvius* reemerges in Montana and the Dakotas. The presence of this fish in the Williams Fork Formation, and its absence in Canadian units at the same time provide further evidence of distinctive climatic/faunal zones across North America during the Campanian/Maastrichtian boundary.

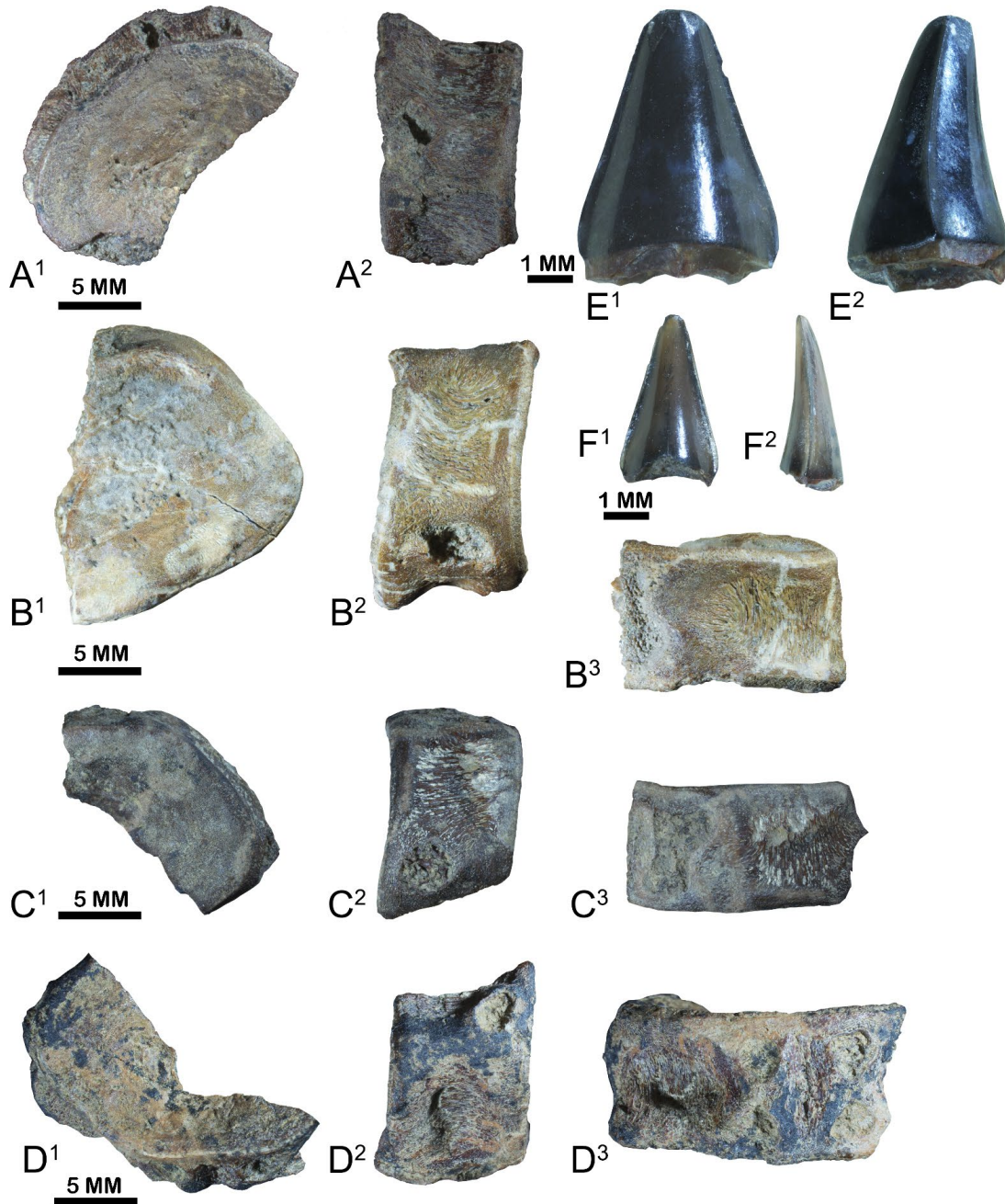


FIGURE 7. cf. *Melvius* sp. specimens from ReBecca’s Hollow (SCP 2019-2). (A) UFMNH 20740, partial vertebral centrum in (A¹) anterior view and (A²) right lateral view. (B) UFMNH20742, partial vertebral centrum in (B¹) anterior view, (B²) left lateral view, and (B³) dorsal view. UFMNH 20741, partial vertebral centrum in (C¹) posterior view, (C²) right lateral view, and (C³) dorsal view. UFMNH 20739, partial vertebral centrum in (D¹) posterior view, (D²) left lateral view and (D³) ventral view. (E) UFMNH 19273, marginal tooth crown in (E¹) lingual and (E²) mesiodistal views. (F) UFMNH 20187, marginal tooth crown in (F¹) lingual and (F²) mesiodistal views.

Subfamily AMIINAE Grande and Bemis, 1998

Cyclurus Agassiz, 1844cf. *Cyclurus* sp.**Fig. 8, I-J**

Referred Specimens and Locality: UFHNH 19292, 9 partial palatal elements with teeth from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Cyclurus*: Aguja Formation, Texas (Campanian), Belly River Group, Montana and Alberta (Campanian); Fruitland Formation, Utah (Campanian); Kirtland Formation, Utah (Campanian); Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Meeteetse Formation, Wyoming (Maastrichtian); St. Mary River Formation, Alberta (Maastrichtian); Lance Creek Formation, Wyoming (Maastrichtian); Hell Creek Formation, Montana & South Dakota (Maastrichtian), Ferris Formation, Wyoming (Maastrichtian), Scollard Formation, Alberta (Maastrichtian)

Description: UFHNH 19292 represents 7 fragmentary palatal elements with tall styliform teeth, measuring ~ 0.5 to 1.4 mm in height and up to 1.5 mm in diameter (Fig. 8, I-J). These elements are too fragmentary to assign to a skull bone, but the presence of this tall, blunt, and conical tooth morphotype means that they are likely either vomers or coronoids (Gaudant, 1992; Grande & Bemis, 1998; Wink & Brink, 2022). These elements are similar to those figured in Estes (1964) (Fig. 17), Estes (1969) (Fig. 8), Grande & Bemis (1998) (Fig. 134), and Wink & Brink (2022) (Fig. 3) all of which were referred to this genus. This genus is differentiated from *Amia* on the basis of possessing tall styliform coronoid and vomer teeth, rather than being conical, pointed, and slightly recurved.

Discussion: *Cyclurus* has been subject to a complex taxonomic history. Originally described by Agassiz in 1839 from articulated specimens from the Paleocene of France, this fish is a relatively common occurrence in Lancian microvertebrate sites in the Hell Creek Formation of Montana, Lance Creek Formation of Wyoming, and the Scollard Formation of Alberta (Estes, 1964; Gaudant, 1992). Unlike *Melvius*, which is mostly restricted to warm climates, *Cyclurus* seems to have been able to tolerate cooler temperatures (Larson et al., 2010). Because dozens of fragmentary specimens of *Cyclurus fragosus* (the best-known Laramidian form) were historically referred to as the genera *Amia*, *Kindleia*, and *Stylomyleodon* without much analysis, it is unknown how widespread this genus was in the Late Cretaceous. Some of these referred specimens may be examples of *Melvius* or new species of amiid. Archibald (1987) included *Amia* sp. in his Williams Fork Formation faunal list but did not assign a specimen number, element, or reason for this designation. UFHNH 19292 represents the first well-documented occurrence of this genus in the Williams Fork Formation. *Cyclurus* appears to have inhabited freshwater ecosystems of both Colorado and Alberta during the “Edmontonian”.

Amiidae gen et sp. indet.

Fig. 8, A-H, K-L

Referred Specimens and Locality: UFHNH 20201, dentary; UFHNH 20200, dozens of scales; UFHNH 20182, dentary; UFHNH 20732, skull elements; UFMNH uncataloged, palatal tooth; UFHNH uncataloged, 22 tooth-bearing elements, UFHNH 20185, 9 vertebral centra; UFHNH 19274, 15 vertebral centra; UFHNH 20712; 2 palatal elements; UFHNH 19293, tooth-bearing element from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Amiids are a common occurrence at ReBecca's Hollow with numerous skull and vertebrae elements having been collected (Fig. 8, A, C, D, E, F, G). Palatal elements with smaller and more numerous teeth than referred specimens of *Cyclurus* are possibly those different taxa (Fig. 8, K-L). Brinkman et al. (2014) reported similarly diminutive amiid elements from the Hell Creek Formation of Montana. Striated amiiform scales, similar to those from the Cretaceous Las Hoyas Formation of Spain figured in Martín-Abad (2017) are a frequent occurrence in ReBecca's Hollow (Fig. 2, B). UFHNH 19293 is a single fragmentary palatine element (possibly a vomer of dermopalatine) with at least five short styliform teeth (Fig. 9, G). The teeth are circular in cross-section and terminate in a distinctive blunt enamel cap. The morphology of UFHNH 19293 is nearly identical to a fish palate from the Bug Creek Anthills of Montana, which Estes (1969a) referred to as *Palaeolabrus montanensis*. In his description, Estes referred to this genus as the sole member of a new family Palaeolabridae, which he placed in Amiiiformes. Similar fragmentary palatal elements from the Aguja Formation of Texas were referred to as cf. *Cyclurus* sp. by Wink & Brink (2022). Because amiids such as *Cyclurus* can have styliform palatal teeth with enamel caps, I refer UFHNH 19293 as an indeterminate amiid, rather than this proposed genus.

Discussion: Most of these elements are too fragmentary to assign to a genus, but the frequency of bones and dermal elements from this site suggests that these fish were a keystone family in freshwater ecology. More material needs to be collected in order to gauge how many species of amiids are present in this unit, but Donald Brinkman suggested that there are likely three taxa given the size discrepancy between the referred *Cyclurus* material and other amiid palatal material (personal communication in August of 2024).

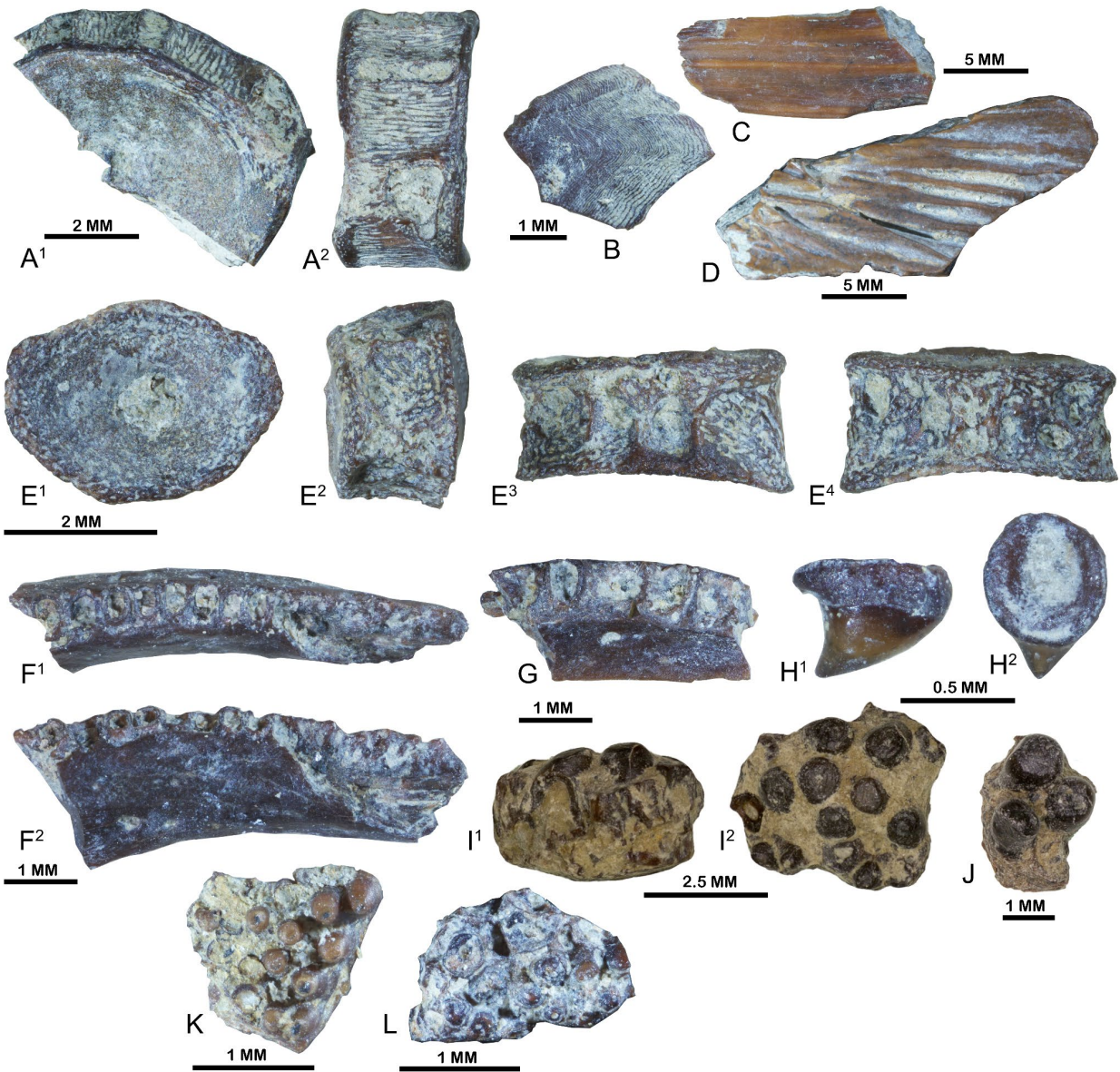


FIGURE 8. Amiinae specimens from ReBecca's Hollow (SCP 2019-2). (A) UFHNSH 19274, partial vertebral centrum in (A¹) anterior view and (A²) left lateral view. (B) UFHNSH 20200, amiiform scale in lateral view. (C-D) UFHNSH 20732, skull elements in dorsal or lateral views. (E) UFHNSH 20185, vertebral centrum in (E¹) anterior view, (E²) left lateral view, (E³) dorsal view, and (E⁴) ventral view. (F) UFHNSH 20128, left dentary in (F¹) occlusal view and (F²) lingual view. (G) UFHNSH 20201, jaw element in occlusal view. (H) UFHNSH uncataloged, recurved palatal tooth in (H¹) linguolabial and (H²) dorsal views. (I-J) UFHNSH 19292, cf. *Cyclurus* sp. coronoid or vomer fragments in (I¹) linguolabial view, (I²) occlusal view, and (J) occlusal view. (K) UFHNSH uncataloged, small amiine coronoid or vomer fragment in occlusal view. (L) UFHNSH 20712, small amiine coronoid or vomer fragment in occlusal view.

Infraclass TELEOSTEOMORPHA Arratia, 2001
Order ASPIDORHYNCHIFORMES Bleeker, 1859
Family ASPIDORHYNCHIDAE Bleeker, 1859

Belonostomus Agassiz 1834

Belonostomus sp.

Fig. 9, A

Referred Specimen and Locality: UFHNH 20177, a fragmentary rostrum from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Belonostomus*: Tokio Formation, Texas (Cenomanian); Carlile Shale, Kansas (Turonian); Kaskapau Formation, Alberta (Turonian); Milk River Formation, Alberta (Santonian); Eutaw Formation, Mississippi (Santonian–Campanian); Belly River Group, Montana and Alberta (Campanian); Mesaverde Formation, Wyoming (Campanian); St. Mary River Formation, Alberta (Maastrichtian); Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Fox Hills Formation, North Dakota (Maastrichtian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, South Dakota, North Dakota, and Montana (Maastrichtian).

Description: *Belonostomus* is likely represented by an anterior fragment of fused premaxillae, approximately 2.5 mm in length (Fig. 9, A) The rostrum is identifiable by its narrow conical shape, simple and tightly spaced marginal teeth, flattened oval cross-section, slight dorsal keel, and external pores running laterally above the tooth row (all of which are consistent with Estes' 1964 description of this fish). This jaw fragment is weathered at the anterior tip, but given its slight upward curve, it likely comes from the anterior of the rostrum. The left side of the jaw

preserves at least ten teeth and tooth sockets, while the right side only preserves 5 visible teeth and sockets. The teeth are simple, blunt, and slightly recurved in shape. UFHNNH 20177 lacks the ganoid surface and distinctive ridging seen in more complete specimens, but this may be because the nutrient pores are present (a feature that Estes points out in his 1964 description). The morphology of UFHNNH 20177 is consistent with known examples of *Belonostomus*, but this specimen is too incomplete to be assigned to the species level.

Discussion: Aspidorhynchids are well known from marine and brackish water facies across the globe during the Jurassic and Cretaceous Periods. *Belonostomus* is best known from complete body fossils from the Jurassic of Germany, but fragmentary remains (usually jaw elements and scales) of this fish are known from microvertebrate sites across the Late Cretaceous of Laramidia (Estes, 1964). UFHNNH 20177 is the first occurrence of *Belonostomus* in the Williams Fork Formation. The presence of this taxon in this unit is not surprising as it is known from earlier Campanian and later Maastrichtian localities, as well as the contemporary Horseshoe Canyon Formation and St. Mary River Formation of Alberta, Canada (Larson et al., 2010; Langston, 1975).

Division TELEOSTEI Müller, 1845

Order ELOPIFORMES Sauvage, 1875

Family ALBULIDAE Bleeker, 1859

Subfamily PHYLODONTINAE Estes and Hiatt, 1978

Paralbula Blake, 1940

Paralbula casei Estes, 1969

Figure 9 J

Referred Specimen and Locality: UFHNH 19296 teeth; UFHNH 20186 teeth from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian Stage, Late Cretaceous).

Known Distribution of *Paralbula*: Wahweap Formation, Utah (Campanian); Menefee Formation, New Mexico (Campanian); Black Creek Formation, North Carolina (Campanian); Blufftown Formation, Georgia (Campanian); Aguja Formation, Texas (Campanian); Demopolis Formation, Mississippi (Campanian); Belly River Group, Montana and Alberta (Campanian); Mesaverde Formation, Wyoming (Campanian); Fruitland Formation, New Mexico (Campanian); Kaiparowits Formation, Utah (Campanian); Williams Fork Formation, Colorado (Campanian-Maastrichtian); St. Mary River Formation, Alberta (Maastrichtian); Ripley Formation, Mississippi (Maastrichtian); Navesink Formation, New Jersey (Maastrichtian); Fox Hills Formation, Colorado (Maastrichtian); Hornerstown Formation, New Jersey (Maastrichtian); Lance Creek Formation, Wyoming (Maastrichtian); Hell Creek Formation, North Dakota and Montana (Maastrichtian); Ferris Formation, Wyoming (Maastrichtian).

Description: UFHNH 19296 and UFHNH 20186 are a series of rounded button-shaped teeth with lightly ornamented enamel that radiates from the center of the tooth, toward its margins (Fig. 9, J). The root of the tooth is constricted, and the center of the root is surrounded by a series of banded enamel folds which run around the center of the base.

Discussion: *Paralbula casei* is an enigmatic taxon that occurs throughout the Cretaceous of Laramidia and Appalachia. This genus was originally described by Blake (1940) from the Eocene of Maryland, it is widespread and common in freshwater and brackish coastal plain environments and ranges (Hoganson et al., 2022). *P. casei* is among the most common osteichthyans present in the Williams Fork Formation, with hundreds of teeth repositied in the

collections of the University of Colorado Museum of Natural History. Despite being common across North America from the Campanian to the Late Maastrichtian, *P. casei* is seemingly absent from the Horseshoe Canyon Formation of Alberta and has yet to be reported from the St. Mary River Formation (Langston, 1975; Larson et al., 2010). The absence of this fish in Northern latitudes during the “Edmontonian”, and its proliferation in water environments provides further evidence of distinctive faunal zones between northern and southern regions of Laramidia during this part of the Cretaceous.

Cohort OSTEOGLOSSOMORPHA Greenwood, Rosen, Weitzman & Myers, 1966

Coriops Estes, 1969

Coriops sp.

Fig. 9, B-C

Referred Specimens and Locality: UFHNH 19296, 2 palatal elements with teeth; UFHNH 20186, palatal element with teeth from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Coriops*: Trinity Group?, Arkansas (Albian-Aptian); Belly River Group, Montana and Alberta (Campanian); Mesaverde Formation, Wyoming (Campanian), Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Lance Creek Formation, Wyoming (Maastrichtian); Hell Creek Formation, Montana and North Dakota (Maastrichtian)

Description: UFHNH 19296 and UFHNH 20186 represent 3 partial jaw elements, (the former possibly parasphenoids or basibranchials) (Fig. 9, B-C). UFHNH 19296 sports short, evenly spaced styliform teeth. These elements are too incomplete to assign to individual skull bones.

However, the dorsal side of these elements have the distinctive vascular cancellous bone seen in examples of *Coriops* (Peng et al., 2001). UFHNNH 20186 is missing all but one tooth but features large open pulp cavities with thick margins perforated by small foramina which are characteristic of this fish (Estes, 1969; Peng et al., 2001). The jaw anatomy of UFHNNH 19296 and UFHNNH 20186 is consistent with known examples of *Coriops*, but I regard them as too incomplete to assign to the species level.

Discussion: *Coriops* is a relatively common teleost genus in the freshwater Judithian ecosystems of Alberta (Brinkman & Neuman, 2002; Brinkman, 2005), where it is known from numerous vertebral and jaw elements. *Coriops* is far less common in Lancian environments, where its fossils are greatly outnumbered by those of durophagous amiids like *Cyclurus* (Brinkman et al., 2014). At ReBecca's Hollow, *Coriops* elements are far rarer than those of amiids, suggesting that the composition of this ecosystem is closer to that of Lancian examples, than earlier Judithian deposits. This hypothesis requires further analysis, but the similarity in morphology between these two distant lineages of fish implies that they would have competed for resources. *Coriops* fossils have been reported from the roughly contemporaneous Horseshoe Canyon Formation of Alberta (Larson et al., 2010).

Order HIODONTIFORMES Taverne, 1979

Family HIODONTIDAE Cuvier & Valenciennes, 1846

Hiodontidae gen et sp. indet.

Figure 9 K

Referred Specimen and Locality: UFHNNH 19270, atlas vertebra from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFHNNH 19270 is a single fragmentary vertebral centra, which is split in half along its central axis (Fig. 3, K). The vertebra has a damaged quadrapartite anterior articular surface, large neural arch articular pits, a single convex articular posterior surface, and developed rib articular pits along its lateral side. The vertebrae feature a highly woven bone texture across its lateral surface. This morphology is consistent with the teleost atlas vertebrae referred to as Morphoserries IIB-1 from the Dinosaur Park Formation, featured in Brinkman & Neumann (2002), which were referred to as hiodontids.

Discussion: Hiodontids were not recognized in Cretaceous microvertebrate sites until Brinkman & Neuman (2002) described a series of vertebrae which matched the morphology of the extant *Hiodon*. Cretaceous Laramidian hiodontid vertebrae have since been identified from the Hell Creek Formation of Montana (Brinkman et al., 2014), Aguja Formation of Texas (Wink & Brink, 2022), and Dakota Group, Straight Cliffs, and Kaiparowits Formations of Utah (Brinkman et al., 2013). UFHNNH 19270 represents the first report of this family of teleost in the Williams Fork Formation of Colorado.

Superorder OSTARIOPHYSI Sagemehl, 1885 (sensu Fink and Fink, 1996)

Series OTOPHYSI Garstang, 1931 (sensu Rosen and Greenwood, 1970)

Gen. et sp. indet. (U-3/BvD Morphotypes)

Figure 9 M

Referred Specimen and Locality: UFHNNH 19279, 4 vertebral centra (2 anterior and 2 posterior) from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFHNNH 19279 represents a batch of osteichthyan centra, which are consistent with those described by Brinkman et al. (2013) from the Straight Cliffs Formation of Utah, Eaton et al. (2014) from the Iron Springs Formation of Utah, Eaton et al. (2014) from the Hell Creek Formation of Montana, Brinkman et al. (2017) from the Milk River Formation of Alberta, Brinkman (2017) from the Belly River group of Alberta, and Wick & Brink (2022) from the Aguja Formation of Texas. Two of the vertebrae (the U-3 morphotype) feature a posterior articular surface that is notably more concave than that of the anterior end (Fig. 9, M). These centra are equal or slightly wider than they are tall, laterally shortened, and oval in silhouette from the posterior/anterior view. The bone texture is fibrous, with small vascular pits along the sides. The dorsal side of these vertebrae features paired circular pits at the neural arch and a rounded bar of bone that separates them. The ventral side has one large pit along the midline of the vertebrae. These vertebrae have been interpreted as being the anterior-most vertebrae on the Weberian apparatus. The second two vertebrae are longer in lateral view than the U-3 examples, feature a more pneumatic bone texture, a sub-rectangular shape, and are more or less equally concave on both articular ends of the centra. The vertebrae (while incomplete) seemingly lack the fused neural arches seen in true examples of the BvD morphotype and are similar to the more posterior U-3 vertebrae figured in Brinkman et al. (2017) (Fig 17. C), which are thought to be vertebrae that are distal to but still connected to the Weberian apparatus.

Discussion: These enigmatic vertebrae have been suggested to be from a Weberian apparatus (a structure that is diagnostic of otophysans) (Brinkman et al. 2013). These authors suggested that

this fish may be closely related to Siluriformes, perhaps slightly basal to this group. Brinkman et al. (2017) later suggested that these fish are likely more basal to this group, given the presence of autogenous parapophyses with significant parapophyseal pits, which are seen in Cypriniformes and other basal otophysans. These vertebrae represent the first known occurrence of this vertebral morphotype in the Williams Fork Formation, and by proxy, the first known otophysans in this unit. The Laramidian fossil record of this group has been expanded with the discovery of vertebrae and dentaries in a variety of microvertebrate sites across Western North America (Brinkman et al. 2013; Eaton et al. 2014; Brinkman et al. 2014; Brinkman et al. 2017; Brinkman 2019; Wick & Brink 2022). These vertebrae are generally found in warm water Laramidian environments and are seemingly absent from the contemporaneous St. Mary River and Horseshoe Canyon Formations. The presence of these fish in the Williams Fork could be used to argue for separate climatic zones across North America during the “Edmontonian”.

Superorder PROTACANTHOPTERYGII Greenwood et al. 1966

Order ESOCIFORMES Bleeker, 1859

Family ESOCIDAE Cuvier, 1817

Estesesox Wilson et al., 1992

Estesesox foxi Wilson et al. 1992

Figure 9 D-F

Referred Specimen and Locality: UFHNH 19285, 3 partial right dentaries from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Known Distribution of *Estesesox*: Milk River Formation, Alberta (Santonian); Belly River Group, Alberta (Campanian); Kaiparowits Formation, Utah (Campanian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, Montana (Maastrichtian)

Description: UFHNH 19285 represents three short crescent-shaped dentaries with two to three rows of small C-shaped tooth sockets (Fig. 9, D-F). These teeth become more numerous towards the anterior end of the dentary. All of these specimens are from the anterior end of the dentary, and the wedge-shaped symphysis is present in one specimen. These features are consistent with descriptions of this species by Wilson et al. (1992), Peng et al. (2001) and Brinkman (2005).

Discussion: These specimens represent the first examples of *Estesesox foxi* from the Williams Fork Formation and the southern-most occurrence of this genus. Specimens of this fish from the Hell Creek and Lance Formations have been known since at least the 1960s but were referred to as dentaries of the perciform *Platacodon nannus* (Estes, 1964; Bryant, 1989). It was not until Wilson et al. (1992) described these jaw elements as those of basal esocids, that the taxonomic identity of these fossils was properly understood. *Estesesox foxi* is known from the contemporary Horseshoe Canyon Formation of Alberta, and thus its presence in the Williams Fork Formation is not surprising (Larson et al., 2010).

Teleostei indet. (Morphotype A)

Figure 9 I

Referred Specimen and Locality: UFHNH 20176, partial left dentary from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFHNH 20176 is a partial left osteichthyan dentary, approximately 10 mm in length. The jaw is long and low and features a series of faint ridges running from the posterior to the anterior of the bone on the exterior side (Fig. 9, I). UFHNH 20176 sports a deep meckel's groove. The dentary preserves at least 7 tooth sockets, all of which are circular, uniform in size, feature striated bases, and are arranged in linear orientations along the top of the dentary. This dentary is similar in size and morphology to a fish that Neuman & Brinkman (2005) refers to as actinopterygian indeterminate #1, and later in Brinkman's 2022 guidebook as Teleost indet. SSTR.

Discussion: This incomplete jaw is distinctive from other fish at ReBecca's Hollow in that it has a single row of uniformly sized teeth like that of an amiid, but the shape of the dentary does not feature the downward turned anterior tip, rough and pitted bone texture, and it is much longer and straighter than an amiid. The tooth bases resemble those of a lepisosteid in size and spacing, but they lack infolded dentine, and they do not feature the smaller second row of marginal teeth. Additionally, the external bone does not feature the enamel ornamentation seen in fossil and extant examples of lepisosteids. In his 2022 guide, Brinkman states that Alison Murray said in personal communication, that the shape of the dentary resembles an enchodontoid. Unlike some enchodontoids, this jaw and the similar examples seen in the Belly River Group of Alberta do not feature larger anterior teeth. UFHNH 20176 is the first report of this jaw morphotype seen in the Williams Fork Formation, the first record of this jaw morphotype outside of the Dinosaur Park Formation, and potentially the first enchodontoid reported from the unit. Enchodontoids are generally regarded as marine fish and thus this jaw could represent an example of a taxa from the Western Interior Seaway.

Teleostei indet.

Figure 9 N, O

Referred Specimen and Locality: UFHNH 19275, dozens of partial vertebrae; UFHNH 20188, 5 partial vertebrae; UFHNH 20718, 6 partial skull elements from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFHNH 19275 and UFHNH 20188 represent numerous partial osteichthyan vertebral centra which range from complete centra that are only 1 mm in width to partial centra, which would have exceeded 5 mm in width. These elements are too fragmentary to assign to a more specific group of fish, but the amphicoelous condition of the articular surfaces and pneumatic texture of the bone is consistent with examples of fossil teleosts figures in Brinkman & Neuman (2002), Neuman & Brinkman (2005), Brinkman et al. (2013, 2014, 2017), Brinkman (2019), and Brinkman (2020). In addition to vertebral fragments, a collection of isolated skull elements (UFHNH 20718) has been recovered from this site (Fig. 9, N-O). These fragmentary bones are each over 2 mm in length and feature a variety of finely ornamented and serrated surfaces. Several teleost groups such as Perciformes and Carangiformes possess several serrated bones on their skulls. The incomplete nature of these elements makes them difficult to assign to any teleost group or individual skull bones, but their unique morphology and ornamentation are consistent with Teleostei.

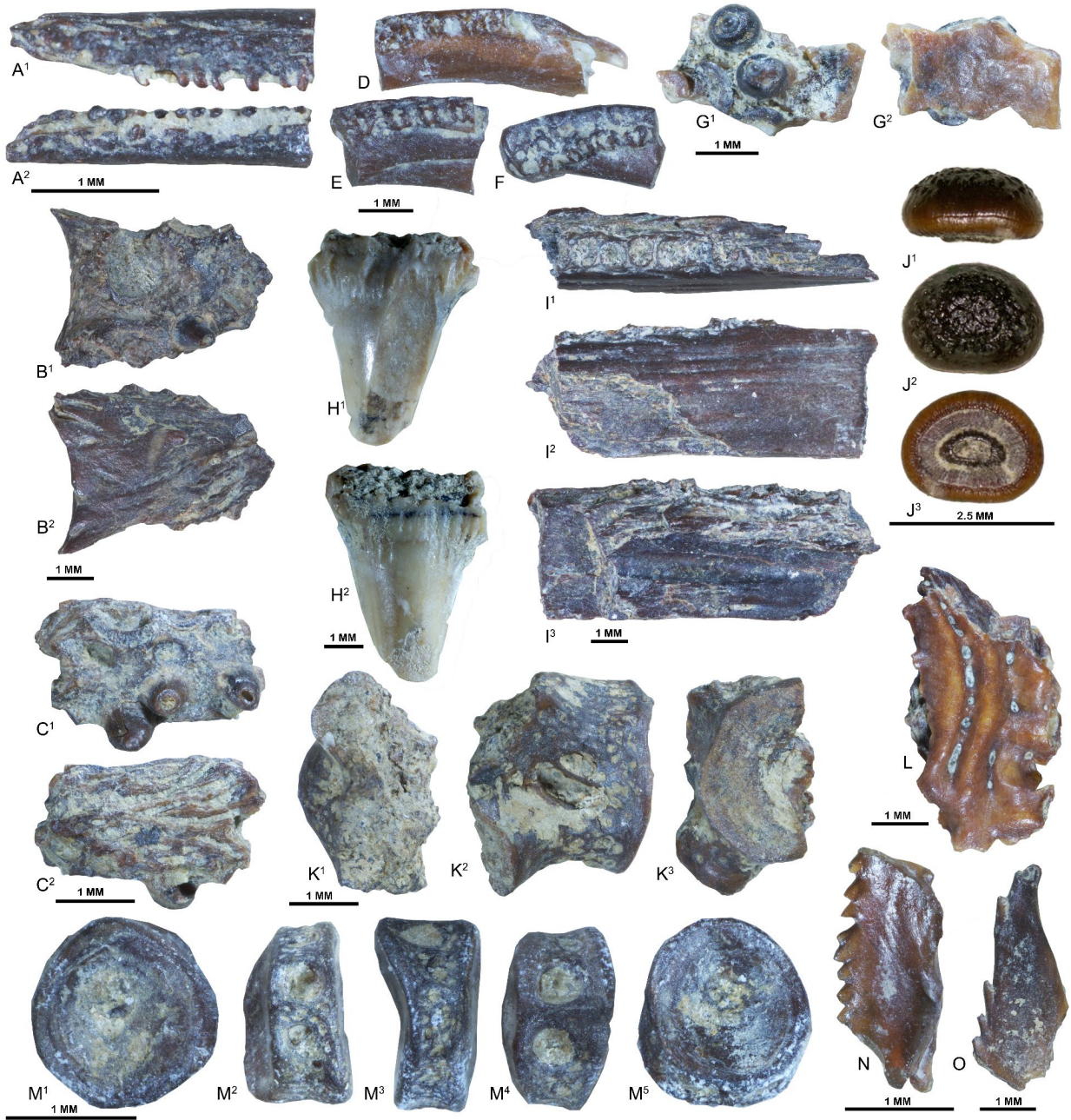


FIGURE 9. Chondrichthyan, chondrosteian, amiid, and teleosteomorph specimens from ReBecca's Hollow (SCP 2019-2). (A) UFHNNH 20177, cf. *Belonostomus* sp. premaxillae in (A¹) left lateral and (A²) occlusal view. (B) UFHNNH 20186, cf. *Coriops* sp. palatal element in (B¹) occlusal view and (B²) dorsal view. (C) UFHNNH 19296, cf. *Coriops* sp. palatal element in (C¹) occlusal view and (C²) dorsal view. (D-F) UFHNNH 19285, *Estesesox foxi* partial right dentaries in (D-E) medial view and (F) occlusal view. (G) UFHNNH 19293, amiid palatal element in (G¹) occlusal view and (G²) dorsal view. (H) UFHNNH 19295, cf. *Meristodonoides* sp. tooth in (H¹) labial view and (H²) lingual view. (I) UFHNNH 20176, teleost (Morph A/?SSTR Morph) partial left dentary in (I¹) occlusal view, (I²) labial view, and (I³) lingual view. (J) UFHNNH 19296, *Paralbula casei* tooth in (J¹) medial view, (J²) occlusal view, and (J³) dorsal view. (K) UFHNNH 19270, hiodontid partial atlas vertebra in (K¹) anterior view, (K²) left lateral view, and (K³) posterior view. (L) UFHNNH 19284, ?acipenserid dermal bone in dorsal view. (M) UFHNNH 19279, otophysan (U-3/BvD Morphotype) vertebra in (M¹) anterior view, (M²) ventral view, (M³) left lateral view, (M⁴) dorsal view, and (M⁵) posterior view. (N-O) UFHNNH 20718, teleost indet. Serrated skull elements in lateral view.

Class REPTILIA Linnaeus, 1758

Subclass DIAPSIDA Osborn, 1903

Clade ARCHELOSAURIA Crawford et al., 2015

Clade TESTUDINATA Klein, 1760

Suborder CRYPTODIRA Cope 1868

Family BAENIDAE Cope, 1882

Baenidae gen. et sp. indet.

Figure 10 Q

Referred Specimen and Locality: UFHNH 19307, 3 fragmentary shell elements; UFHNH 20734, 6 fragmentary shell elements from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian Stage).

Description: Baenids are represented by a number of fragmentary shell elements at ReBecca's Hollow. These shell elements are thick and feature a distinctive rough exterior bone texture that is not like that of trionychids, chelydrids, or *Adocus*. UFHNH 19307 and UFHNH 20734 represent isolated bits of shell from this group, but none of these bones are complete enough to refer them to a specific region of the shell (Fig. 4, Q). One fragment in UFHNH 19307 has a distinctive series of sulci that resemble that of a *Boremys* peripheral series figured in Brinkman's 2022 guide to vertebrate fossils of the Dinosaur Park Formation of Alberta (Page 99, Fig. 4), but the fragment is too incomplete to assign to a genus confidently. Additionally, two of the fragments in UFHNH 20734 feature a uniquely smooth texture and nodular bumps along the exterior surface of the bone. These elements are consistent with *Boremys pulchra* specimens from the Dinosaur Park Formation. This genus is distinguished from other baenids by the

morphology of the carapace (Brinkman & Nicholls, 1991, Brinkman, 2005). Because these bones are too incomplete to assign even to the region of the shell, I hesitate to refer them to this genus.

Discussion: Baenids (specifically *Boremys* sp.) have been previously reported from the Williams Fork Formation by Archibald (1987). Although Archibald did not give a specimen number, locality, or describe what element he referred to this genus, the University of Colorado Museum of Natural History has several well-preserved specimens of this family. It is therefore no surprise that ReBecca's Hollow has yielded examples of this family of turtles. Baenids are a relatively primitive group of cryptodire turtles that serve an important predatory role in the freshwater Laramidia (Estes, 1970; Brinkman, 2005). Baenids have been reported from the contemporary St. Mary River Formation of Alberta but are curiously absent from the Horseshoe Canyon Formation of the same province (Langston, 1975; Brinkman & Eberth, 2006; Larson et al., 2010). The relative abundance of this group in Colorado, and their absence in colder The Horseshoe Canyon Formation is further evidence of discrete faunal/climatic zones existing during the Edmontonian stage of the Late Cretaceous Period.

Superfamily TRIONYCHOIDEA Fitzinger, 1826

Family NANHSIUNGCHELYIDAE Yeh, 1966

Basilemys Cope, 1876

Basilemys sp.

Figure 10 O

Referred Specimen and Locality: UFHNH 19308, two associated fragmentary shell elements from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Basilemys*: Milk River Formation, Alberta (Santonian); Straight Cliffs Formation, Utah (Turonian-Campanian); Aguja Formation, Texas (Campanian); Wahweap Formation, Utah (Campanian); Belly River Group, Montana and Alberta (Campanian); Kirtland Formation, Kaiparowits Formation, Utah (Campanian); New Mexico (Campanian); Fruitland Formation, New Mexico (Campanian); Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Fox Hills Formation, North Dakota (Maastrichtian); Ojo Alamo Formation, New Mexico (Maastrichtian); Meeteetse Formation, Wyoming (Maastrichtian); Laramie Formation, Colorado (Maastrichtian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, South Dakota, North Dakota, and Montana (Maastrichtian); Denver Formation, Colorado (Maastrichtian); Ferris Formation, Wyoming (Maastrichtian); Frenchman Formation, Alberta (Maastrichtian); Ojo Alamo Formation, New Mexico (Maastrichtian)

Description: UFHNH 19308 are two fragmentary shell elements that are 2 cm at their thickest regions. These shell elements have a distinctive deeply pitted texture with diamond-shaped indentations, surrounded by raised net-like reticulations (Fig. 10 O). These elements are heavily worn, but characteristic of *Basilemys* (Brinkman, 2005). These elements are too fragmentary to refer to a specific shell region or a species of *Basilemys*.

Discussion: *Basilemys* is among the largest turtles from Laramidia's coastal plain ecosystems, with a shell length of about a meter (Mallon & Brinkman, 2018). This genus is generally regarded as a mostly terrestrial turtle, and thus its rarity at ReBecca's Hollow may be attributable to this lifestyle (Mallon & Brinkman, 2018). This animal is prevalent from the start of the Campanian to the end of the Maastrichtian. UFHNH 19308 is the first reported example of this turtle in the Williams Fork Formation. This genus is known from the contemporary Horseshoe

Canyon Formation of Alberta, but it has yet to be described from the St. Mary River Formation (Larson et al., 2010; Brinkman & Eberth, 2006; Langston, 1975)

Family ADOCIDAE Cope, 1869

Subfamily ADOCINAE Cope, 1869

Adocus Cope, 1868

Adocus sp.

Referred Specimen and Locality: UFHNH 19309, 51 fragmentary shell elements; UFHNH 20725, 37 fragmentary shell elements from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Adocus*: Willow Tank Formation, Nevada (Cenomanian); Milk River Formation, Alberta (Santonian); Coachman Formation, South Carolina (Campanian); Cerro Del Pueblo Formation, Coahuila (Campanian); Black Creek Group, North Carolina and South Carolina (Campanian); Blufftown Formation, Georgia (Campanian); Belly River Group, Montana and Alberta (Campanian); Fort Crittenden Formation, Arizona (Campanian); Fruitland Formation, New Mexico, (Campanian); Kirtland Formation, New Mexico (Campanian); Kaiparowits Formation, New Mexico (Campanian); Mesaverde Formation, Wyoming (Campanian); Williams Fork Formation, Colorado (Campanian-Maastrichtian), Monmouth Group, New Jersey (Campanian-Maastrichtian); Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Meeteetse Formation, Wyoming (Maastrichtian); Laramie Formation, Colorado (Maastrichtian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, South Dakota, North Dakota, and Montana

(Maastrichtian); Hornerstown formation, New Jersey (Maastrichtian); Ferris Formation, Wyoming (Maastrichtian); Frenchman Formation, Saskatchewan (Maastrichtian); Scollard Formation, Alberta (Maastrichtian)

Description: *Adocus* is by far the most common turtle at ReBecca's Hollow, being represented by numerous fragmentary shell elements (Fig. 10 S). These pieces of shell are thick, feature prominent sutural margins, and exhibit the distinctive glossy bone texture and fine sub-triangular pitting that characterizes this genus (Bryant, 1989; Brinkman, 2005). Most of these shell elements are too fragmentary to assign to a region of the shell. The largest *Adocus* shell fragments at Rebecca's Hollow are at about 1.5 CM in thickness. These specimens are too fragmentary to be referred to the species level.

Discussion: *Adocus* sp. was reported by Archibald (1987) from the Willims Fork Formation, but like the other turtle taxa in this publication, no specimen numbers, localities, or fossil elements were referred to. Despite the lack of information in this publication, *Adocus* specimens are common in the Williams Fork Formation, with many partial specimens represented in the collections of the University of Colorado Museum of Natural History (personal research). This taxon is frequently recovered from Laramidian freshwater environments and is thought to be largely restricted to warm water environments (Brinkman & Eberth, 2006). *Adocus* is known from the Horseshoe Canyon Formation of Alberta but appears to be restricted to warm intervals of Edmontonian (Brinkman & Eberth, 2006; Larson et al., 2010). Additionally, this taxon is not known from the contemporary St. Mary River Formation of Alberta (Langston, 1975).

Family TRIONYCHIDAE Gray, 1825

Trionychidae gen. et sp. indet.

Figure 10 R

Referred Specimen and Locality: UFHNH 19307, 8 fragmentary shell elements; UFHNH 20724, 8 fragmentary shell elements from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFHNH 19307 and UFHNH 20724 represent a large trionyhid turtle taxon with shell fragments up to 2.5 CM in thickness. These shell fragments feature a series of large shallow circular pitting across their exterior surfacing, which is distinctive from that of plastomenines (Fig. 10, R). The fragmentary nature of these shell elements and the intraspecific variability of trionyhid shells make identification to the generic level difficult.

Discussion: Archibald (1987) reported “*Trionyx* sp.”, but failed to provide specimen numbers, localities, or fossil elements to this taxon. *Trionyx* has been historically treated as a wastebasket taxon, and it is currently thought that this genus is restricted to the Cenozoic (Georgalis & Joyce, 2017). Similar examples of these specimens from the Williams Fork formation are present in the collections of the University of Colorado Museum of Natural History and may provide greater insight into the identity of this turtle with future research.

Subfamily PLASTOMENINAE Hay, 1902

Plastomeninae gen. et sp. indet.

Figure 10 P

Referred Specimen and Locality: UFHNH 19305, 16 fragmentary shell elements; UFHNH 20723, 10 fragmentary shell elements from UFHNH locality SCP 2019-2, Williams Fork

Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian Stage, Late Cretaceous).

Description: Plastomenine turtles are represented at ReBecca's Hollow by numerous fragmentary shell elements. Most of these bones are too incomplete to be referred to a region of the animal's body, but both UFHNH 19305 and UFHNH 20723 feature examples of costals, and UFHNH 19305 features a possible eroded marginal element. This subfamily features a distinctive finely sculpted exterior shell texture. Both UFHNH 19305 and UFHNH 20723 have fragments with minute subcircular pits along the exterior of the shell (Fig. 10 P). This morphology is similar to examples of *Aspideretoides* (DeMar & Breithaupt, 2006, Brinkman, 2005). Other examples of both UFHNH 19305 and UFHNH 20723 demonstrate a pattern of raised reticulations across the shell, which appear similar to that of *Gilmoremey's* (Joyce et al., 2016) (Fig. 4). Despite these similarities, this material is too incomplete to confidently assign to a genus and thus I will only assign it to the subfamily.

Discussion: The subfamily Plastomeninae has only recently been well understood in terms of its phylogenetic history, and paleogeography (Jasinski et al., 2022). This is the first report of this subfamily in the Williams Fork Formation, although other Trionychids have been reported by Archibald (1987) and they have likely been recovered for decades without proper identification. These turtles are widespread across Laramidian freshwater environments and were an important group in the ecology of this region. Plastomenines have yet to be reported from both contemporary St. Mary River and Horseshoe Canyon Formations of Alberta and appear to prefer warm water freshwater environments (Langston, 1975; Larson et al., 2010). The presence of these turtles in the Williams Fork Formation at this time is further evidence of discrete climatic/faunal zones during the Edmontonian Stage of the Late Cretaceous.

Family CHELYDRIDAE Gray, 1831

Chelydridae gen. et sp. indet.

Figure 10 T

Referred Specimen and Locality: UFHNH 20727, 18 fragmentary shell elements; UFHNH 20726, 3 shell fragmentary elements from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Chelydrid turtles are represented at ReBecca's Hollow by numerous thin fragmentary shell elements with a rough vascular exterior bone texture and deep angular sulci (DeMar & Breithaupt, 2006; Brinkman personal communication). UFHNH 20727 features at least one partial costal (Fig. 10 T). These elements are consistent with that of other fragmentary chelydrids figured in Brinkman (2005) (Fig. 11.3). No other shell elements assigned to these specimen numbers are referable to a region of the shell and are not referable to a genus or species of this family.

Discussion: Despite being a relatively common occurrence across Laramidian freshwater ecosystems chelydrids have yet to be reported from the Williams Fork Formation, and thus UFHNH 20727 and UFHNH 20726 represent the first examples of this family from this unit. This family does not seem to be as climatically restricted as other turtles of the Late Cretaceous Period. This family is known from the Horseshoe Canyon Formation of Alberta but has seemingly yet to be reported from the St. Mary River Formation (Brinkman & Eberth, 2006; Larson et al., 2010; Langston, 1975).

Clade ARCHOSAUIROMORPHA von Huene, 1946

Clade ARCHOSAURIFORMES Gauthier, 1986

Clade ARCHOSAURIA Cope, 1869

Order CROCODILIA Owen, 1842

Crocodylia gen. et sp. indet.

Figure 10 G-N

Referred Specimen and Locality: UFHNH 19302, osteoderms; UFHNH 20184, osteoderms; UFHNH 20721, ectopterygoid(?); UFHNH uncataloged, mandible(?) element; UFHNH 19277, 3 skull elements; UFHNH 20722, vertebral centrum from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Indeterminate crocodylians are a common occurrence at ReBecca's Hollow and are represented by numerous osteoderms, skull elements, and a few fragmentary procoelous vertebral elements (Fig. 4 G- N). Most of these bones are far too incomplete to assign to a lower taxonomic designation, but it's possible that they are from alligatoroids, as their teeth are commonly found at ReBecca's Hollow. These skull elements are identifiable via their rugose and pitted exterior texture, paired with the presence of sutural regions. The texture of these osteoderms and skull bones may aid in further identification in the future. UFHNH 20721 has an uncanny resemblance to a right ectopterygoid of an adult *Alligator mississippiensis* skull, but because it was not found in association with a definitive skull element, this assignment is tentative (Fig. 4, I).

Discussion: Crocodylians are among the most common vertebrate fossils in the Williams Fork Formation. Archibald (1987) reported specimens of *Leidyosuchus* sp. and *Brachychampsia* sp.

but did not designate the specimen numbers, fossil elements, or state the museum in which the fossils were repositied. Given the taxonomic revision of *Leidyosuchus* by Wu et al. (2001), the report of this genus in the Williams Fork Formation by Archibald (1987) can no longer be accepted. Foster & Hunt-Foster (2015) reported a giant eusuchian which may be an example of *Deinosuchus*, a goniopholid, or a pholidosaur. Brand et al. (2022) reported teeth from indeterminate alligatoroids that resemble *Brachychampsa*, and Eberle et al. (2024) reported occurrences of crocodylians throughout the unit. There are currently at least two known taxa of crocodylians in the Williams Fork Formation (a durophagous alligatoriod and a large unknown taxon) It is not clear if any of the crocodylian skeletal elements at ReBecca's Hollow are referable to either of these taxa.

Superfamily ALLIGATOROIDEA Gray, 1844

Alligatoroidea gen. et sp. indet.

Figure 10 A-F

Referred Specimen and Locality: UFHNH 19276, tooth crowns; UFHNH 20180, tooth crowns from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Alligatoriods are represented by numerous molariform and incisiform teeth (Fig. 10, A-F). Most of these teeth are small and likely represent juvenile individuals at 1-5 mm in crown height. Most morphotypes of teeth feature thick folds and striations of enamel which runs vertically from the base of the tooth crown to the tooth. The molariform teeth resemble those of both *Brachychampsa* from the Hell Creek, Lance, and Menefee formations, and *Strangerochampsia* from the Horseshoe Canyon Formation of Alberta.

Discussion: Alligatoroid teeth are a common occurrence in microvertebrate sites across the Williams Fork Formation. The incomplete nature of these teeth and the similarity of tooth morphology across the alligatoroid lineage make the identification of these elements difficult. Brand et al. (2022) reported teeth from an alligatoroid that resembles *Brachychampsa* at the J&M site. Because these teeth are isolated, and the contemporary *Stangerochampsia* of the Horseshoe Canyon Formation has similar blunt durophagous teeth, I hesitate to assign these specimens to the genus level (Wu et al., 1996). Modern alligators and caimans are strictly freshwater taxa, and thus the presence of these teeth, paired with trionychiod turtles, lissamphibians, and a lack of chondrichthyans provides further evidence that ReBecca's Hollow is a freshwater environment. Alligatoroids are rare in the Horseshoe Canyon Formation, and completely absent in certain members, indicating periods of cool climate (Larson et al., 2010). The prominence of these teeth throughout the Williams Fork Formation provides further evidence of a warm climate zone distinct from Alberta at this time in the Cretaceous Period.

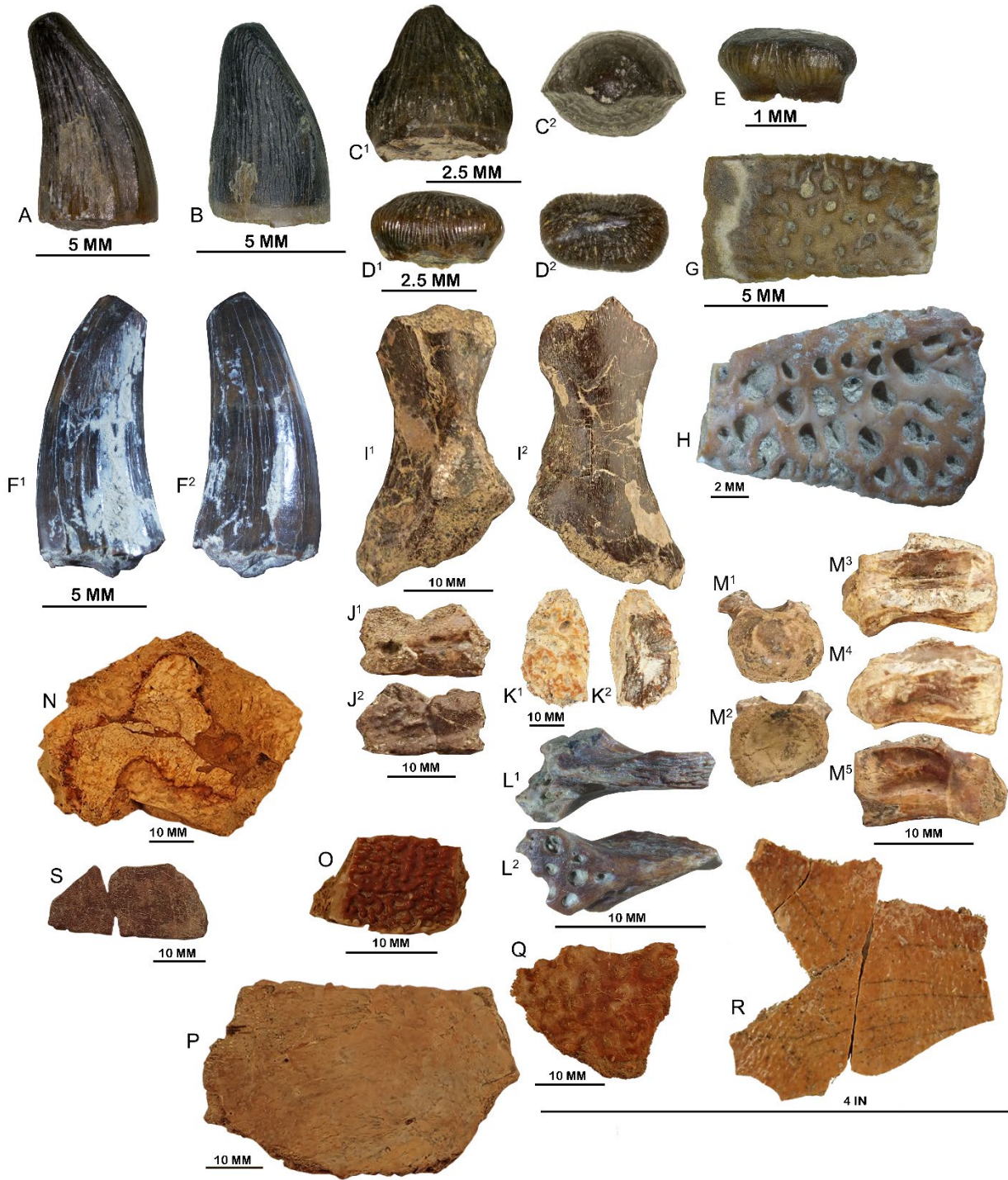


FIGURE 10. Crocodylian and testudine specimens from ReBecca's Hollow (SCP 2019-2). (A) UFHNNH 19276A, alligatoriod tooth (caniniform morph) in medial view. (B) UFHNNH 19276B, alligatoriod tooth (caniniform morph) in distal view. (C) UFHNNH 19276C, alligatoriod tooth (molariform morph) in (C¹) distal view and (C²) occlusal view. (D) UFHNNH 19276D, alligatoriod tooth (molariform morph) in (D¹) distal view and (D²) occlusal view. (E) UFHNNH 19276E, alligatoriod tooth (molariform morph) in lateral view. (F) UFHNNH 20180, alligatoroid tooth in (F¹-F²) lateral views. (G) UFHNNH 19302A, crocodylian osteoderm in dorsal view. (H) UFHNNH 19302B, crocodylian osteoderm in dorsal view. (I) UFHNNH 20721, crocodylian(?) right ectopterygoid(?) in (I¹) right lateral view and (I²) medial view. (J) UFHNNH uncataloged, crocodylian mandible(?) element in (J¹) lateral view and (J²) medial view. (K) UFHNNH 19277A, crocodylian dermal bone in (K¹) dorsal view and (K²) and ventral view. (L) UFHNNH 19277B, crocodylian skull element in (L¹) medial view and (L²) exterior view. UFHNNH JC14, crocodylian vertebral centrum in (M¹) anterior view and (M²) posterior view, (M³) dorsal view, (M⁴) right lateral view, (M⁵) left lateral view. (N) UFHNNH 19308, *Basilemys* sp. carapace fragment in dorsal view. (O) UFHNNH 19305, plastomenine carapace fragment in dorsal view. (P) UFHNNH 19307, baenid shell fragment in exterior view. (Q) UFHNNH 19307, trionychid carapace fragment in dorsal view. (R) UFHNNH 19309, *Adocus* sp. carapace fragment in dorsal view. (S) UFHNNH 20727, chelydrid costal fragment in dorsal view.

Clade DINOSAURIA Owen, 1842

Clade SAURISCHIA Seeley, 1888

Clade THEROPODA Marsh, 1881

Clade TETANURAE Gauthier, 1986

Clade COELUROSAURIA von Huene, 1914

Family Indeterminate

Richardoestesia Currie, Rigby & Sloan, 1990

cf. *Richardoestesia* sp.

Figure 11 L, M

Referred Specimen and Locality: UFMNH 20190, complete cheek tooth crown; UFHNNH uncataloged, distal end of tooth fragment from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Richardoestesia*: Cedar Mountain Formation, Utah (Berriasian-Cenomanian); Naturita Formation, Utah (Cenomanian); Holly Creek Formation, Arkansas (Aptian-Albian); Woodbine Group, Texas (Cenomanian); Milk River Formation, Alberta (Santonian); Aguja Formation, Texas (Campanian); Cerro Del Pueblo Formation, Coahuila (Campanian); Belly River Group, Montana and Alberta (Campanian); Fruitland Formation, New Mexico (Campanian); Kirtland Formation, New Mexico (Campanian); Kaiparowits Formation, Utah (Campanian); Mesaverde Formation, Wyoming (Campanian); Williams Fork Formation, Colorado (Campanian-Maastrichtian); Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, South Dakota, North Dakota, and Montana (Maastrichtian); Ferris Formation,

Wyoming (Maastrichtian); Frenchman Formation, Saskatchewan; (Maastrichtian); Ojo Alamo Formation, New Mexico (Maastrichtian); Scollard Formation, Alberta (Maastrichtian)

Description: Two theropod teeth from ReBecca's Hollow fit the description for the enigmatic tooth genus *Richardoestesia*, which was erected by Currie et al. (1990) based on a pair of partial dentaries with distinctive finely serrated teeth from the Dinosaur Park Formation of Alberta.

UFMNH 20190 is a nearly complete tooth crown, approximately 6.5 mm from the base to the tip of the crown (Fig. 5, L). The tooth is recurved, laterally compressed, and features a slight restriction of the base. The base of the crown is suboval in cross-section. This tooth features short, rounded denticles on both the anterior and posterior sides of the tooth. The posterior denticles are approximately 0.1mm in width at the base of the tooth and 0.08 mm in width at the tip. The denticles on the posterior side are fairly uniform in shape, slowly grading into the tooth at its very distal tip. The anterior denticles are less pronounced, than those on the posterior size and are generally around 0.09 mm in width. These denticles stretch from the very tip of the tooth and grade back into the tooth at around 1 mm above the base of the crown. The tooth averages 7 denticles per millimeter. According to Currie et al. (1990), this relatively tall silhouette of this tooth could indicate it is an anterior dentary tooth. The morphology of this tooth is similar to examples of *Richardoestesia gilmorei* teeth figured in Currie et al. (1990) (Fig 8.4: J)

“*Richardoestesia gilmorei*” from the Lance Formation of Wyoming figured in Longrich (2008) (Fig 9.9 A) and *Richardoestesia* sp. from the Fruitland Formation of New Mexico (Fig 8 E-J).

Because of the incomplete nature of the type material and frequent assignment to this genus, I hesitate to refer to this specimen as *R. gilmorei*.

UFMNH uncataloged is a distal fragment of a broken tooth, approximately 1 mm in length (Fig. 5, M). The fragment is relatively circular in cross-section and preserves 8 denticles

along its posterior side. The denticles are proportionally taller than that of UFMNH 20190 but are similarly bunt. The high denticle count and relatively thick conical shape of the tooth are consistent with his tooth being too incomplete to assign to a species of *Richardoestesia*, but it resembles specimen MWC 8865 from the J&M locality, which was assigned to this genus by Brand et al. (2022) (Fig. 7, A).

Discussion: *Richardoestesia* is a somewhat problematic tooth genus of theropod dinosaur that is frequently encountered in Late Cretaceous Laramidian deposits. There are two recognized species of this dinosaur, *R. gilmorei* (which features recurved and laterally compressed teeth with minute denticles) and *R. isosceles* (which has taller and straighter teeth) (Sankey, 2001). Neither of these taxa is well understood or known from anything more than teeth (or dentary fragments in the case of *R. gilmorei*), and thus taxonomic identification of these two tooth morphs has been difficult. Complicating the matter is the fact that many theropod teeth are tentatively assigned to this genus but are not assigned to either *R. gilmorei* or *R. isosceles*. Diem (1999) assigned theropod from the Williams Fork Formation to *Richardoestesia gilmorei*, *Richardoestesia* sp., cf. *Richardoestesia* sp. and Brand et al. (2022) assigned a theropod tooth from the J&M site to *Richardoestesia* sp. Because of the morphological disparity between the examples from the Williams Fork Formation, referred examples of this genus could represent two or more taxa. Additionally, because no certain examples of maxillary or premaxillary teeth are known from this genus, these teeth could represent heterodonty or tooth ontogeny in a single taxon of animal. Examples of a theropod tooth genus turning out to be an unknown heterodont condition in a known taxon have been observed in *Saurornitholestes langstoni*, and tyrannosaurids (Currie & Evans, 2020; Holtz, 2001). Additionally, theropod tooth morphology changing with ontogeny has been proposed in examples such as *Tyrannosaurus rex* (Carr, 2020).

Family TYRANNOSAURIDAE OSBORN, 1905

Tyrannosauridae gen. et sp. indet.

Figure 11 I-K

Referred Specimen and Locality: UFMNH 19272, 2 tooth fragments; UFMNH 20178, tooth fragment from UFHMH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Tyrannosaurids are represented by fragments of robust teeth with large chisel-like denticles (Fig 11 I-K). The fragmentary nature of these specimens does not allow identification down to the genus level, but the large size of these teeth and the prominent bulbous denticles are consistent with that of more complete tyrannosaurid teeth.

Discussion: Tyrannosaurids in the Williams Fork Formation are known from isolated teeth and a single pedal phalanx (Diem, 1999; Yun, 2023). Identifying these elements has proven difficult due to their fragmentary nature, but Diem assigned material to Tyrannosauridae indet. and aff. *Aublysodon*. Brand et al. (2022) referred to aff. *Albertosaurus* and aff. *Daspletosaurus* as examples of previous taxonomic assignments to fossils in the Williams Fork Formation but did not designate what specimens or publications those were from. The tyrannosaurid material from this unit is contemporary with the Horseshoe Canyon and St. Mary River Formations of Alberta, both of which yield fossils of *Albertosaurus sarcophagus* (Weishampel, et al., 2004; Larson et al., 2010). Additionally, this unit was deposited at the same time as the Prince Creek Formation of Alaska, which yields fossils of the polar tyrannosaurid *Nanuqsaurus hoglundi* (Fiorillo & Tykoski, 2012; Fiorillo & Tykoski, 2014). Because *Nanuqsaurus hoglundi* is only known from high latitude deposits, I find it unlikely that the tyrannosaurid specimens at ReBecca's Hollow belong to this genus. UCM 87636, an isolated tyrannosaurid pedal phalanx from the Williams

Fork Formation described by Yun (2023) was referred to as more similar to Campanian *Gorgosaurus* specimens of Alberta and Montana than contemporary Campanian southwestern tyrannosaurs such as *Bistahieversor*. *Gorgosaurus* and *Albertosaurus* have consistently been placed in a subfamily called Albertosaurinae (Currie et al, 2003; Fiorillo & Tykoski, 2014; Zheng et al., 2024) and were likely sister taxa or held an anagenic relationship, thus it is possible that tyrannosaurid material from the Williams Fork Formation is from an albertosaurine.

Clade MANIRAPTORA Gauthier, 1986

Clade PARAVES Sereno, 1997

Family DROMAEOSAURIDAE Colbert and Russell, 1969

Subfamily SAURORNITHOLESTINAE Longrich & Currie, 2009

Saurornitholestinae gen et. sp. indet.

Figure 11 H

Referred Specimen and Locality: UFMNH 19289, a fragmentary dentary or maxillary tooth from UFHNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of Saurornitholestinae: Milk River Formation, Alberta (Santonian); Mooreville Chalk Formation, Alabama (Campanian); Coachman Formation, South Carolina (Campanian); Black Creek Group, South Carolina (Campanian); Menefee Formation, New Mexico (Campanian); Aguja Formation, Texas (Campanian); Belly River Group, Montana and Alberta (Campanian); Cerro Del Pueblo Formation, Coahuila (Campanian); El Gallo Formation, Baja California (Campanian); Fort Crittenden Formation, Arizona (Campanian); Kirkland Formation, New Mexico (Campanian); Mesaverde Formation, Wyoming

(Campanian); Wapiti Formation, Alberta (Campanian); Williams Fork Formation, Colorado (Campanian-Maastrichtian); Prince Creek Formation, Alaska (Campanian-Maastrichtian); Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Fox Hills Formation, North Dakota (Maastrichtian); Meeteetse Formation, Wyoming (Maastrichtian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, South Dakota, North Dakota, and Montana (Maastrichtian); Ferris Formation, Wyoming (Maastrichtian); Frenchman Formation, Saskatchewan (Maastrichtian); Scollard Formation, Alberta (Maastrichtian).

Description: UFMNH 19289 is an incomplete lingual-labially compressed and recurved theropod tooth that is suboval cross-section (Fig. 11, H). This specimen features large rounded denticles on the posterior side of the tooth and minute serrations on the anterior side. Only around the proximal two-thirds of this tooth are preserved, and thus the precise proportions of this specimen are lost. The significant recurvature, large posterior denticles, and disparity in size between the posterior and anterior denticles of the tooth are consistent with that of the dromaeosaurids *Saurornitholestes* and *Atrociraptor* (both of which are members of the subfamily Saurornitholestinae). The denticles of the tooth are rounded in outline, rather than pointed and flaring up away from the base of the crown (the morphology traditionally cited as being diagnostic of the Judithian *Saurornitholestes langstoni* of the Belly River Group of Montana and Alberta) (Currie et al., 1990). Despite UFMNH 19289 having blunt denticles, it overlaps in morphology with examples of both *Saurornitholestes* and *Atrociraptor* (personal communication with Don Brinkman in February of 2025). This tooth also resembles examples of cf. *Saurornitholestes* teeth from the Campanian Aguja Formation and Maastrichtian Tornilla Group of Texas (Sankey et al., 2005). Because UFMNH 19289 resembles the teeth of both *Saurornitholestes* and *Atrociraptor*, I hesitate to assign it to the genus level.

Discussion: Though *Saurornitholestes* is known from well-preserved cranial and postcranial material, it has functioned as a tooth genus of dinosaur since Currie et al. (1990) described teeth from the Belly River Group of Alberta in detail. Virtually all skeletal material is known from the Campanian of Alberta, but teeth have been reported from Laramidian and Appalachian deposits from the Santonian through the Maastrichtian. If these reports are accurate, this would render this genus one of the most successful dinosaur taxa. Despite the proliferation of this tooth form, (Larson & Currie, 2013) demonstrated that theropod tooth taxa (including specimens assigned to *Saurornitholestes* and related forms) likely do not represent the same animals and differ slightly in morphology across time and geologic formations. Diem (1999) reported a tooth of *Saurornitholestes langstoni* from the Williams Fork Formation. This specimen (UCM 57477) does resemble Judithian examples of this theropod in the pointed and outwardly flaring denticle shape. The best known “Edmontonian” dromaeosaurid is another saurornitholestine, *Atrociraptor marshalli* from the Horseshoe Canyon Formation of Alberta. Though *Saurornitholestes* specimens had been recognized from this unit, most of this material has been reassigned to *Atrociraptor* (Baszio, 1997; Currie & Varricchio, 2004). It is not known if *Atrociraptor* was present in the Williams Fork Formation of Colorado, and the similarity in tooth form between these two dinosaurs suggests that they may be referred to as *Atrociraptor*. The disparity in denticle shape between the two known Williams Fork examples could suggest that there were two taxa of saurornitholestine theropods present in this unit, or perhaps more likely, that these teeth represent ontogenetic changes in tooth morphology or heterodonty in a singular taxon.

Family TROODONTIDAE(?)

Paronychodon Cope, 1876

Paronychodon sp.**Figure 11 N**

Referred Specimen and Locality: UFMNH 19286, an incomplete tooth from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Cretaceous North American Distribution of *Paronychodon*: Cedar Mountain Formation, Utah (Cenomanian); Naturita Formation, Utah (Cenomanian); Milk River Formation, Alberta (Santonian); Straight Cliffs Formation(?), Utah (Campanian); Aguja Formation, Texas (Campanian), Belly River Group, Montana and Alberta (Campanian); Kaiparowits Formation(?), Utah (Campanian); Fruitland Formation, New Mexico (Campanian), Kirtland Formation, New Mexico (Campanian); Mesaverde Formation, Wyoming (Campanian); Almond Formation, Wyoming (Campanian-Maastrichtian); Horseshoe Canyon Formation, Alberta (Campanian-Maastrichtian); Laramie Formation, Colorado (Maastrichtian); Lance Formation, Wyoming (Maastrichtian); Hell Creek Formation, South Dakota, North Dakota, and Montana (Maastrichtian); Ferris Formation, Wyoming (Maastrichtian); Scollard Formation, Alberta (Maastrichtian)

Description: UFMNH 19286 is the distal end of an unserrated theropod tooth (Fig. 11, N). The tooth is flattened on the lingual side, slightly convex on the labial side, and features a series of smooth apicobasally-oriented ridges running from the base of the crown to the tip on both the lingual and labial sides. As previously mentioned, the tooth features no serrations or significant carinae along its margins. The morphology of UFMNH 19286 is consistent with examples of the *Paronychodon*, a common tooth theropod genus from across Laramidia (Cope, 1876). Because of the fairly robust morphology of the tooth compared to the type species *Paronychodon*

lacustris, and the incomplete nature of the tooth, I hesitate to assign this specimen to a species of *Paronychodon*.

Discussion: *Paronychodon* is a well-known and problematic tooth genus that occurs throughout the Cretaceous of North America. There are a few competing hypotheses regarding the nature of these strange teeth, such as them being pathological dromaeosaurid teeth, a heterodonty of *Richardoessesia*, or a valid tooth taxon of a yet unknown theropod lineage (Longrich, 2008). Although the identity of these teeth has never been confirmed, Hwang (2005) noted the similarity of these teeth to the Asian troodontid *Byronosaurus*. This is the first report of the *Paronychodon* tooth morph in the Williams Fork Formation. If *Paronychodon* is a troodontid, this would make it the second known member of this family in the Williams Fork Formation (Archibald, 1987).

Theropoda indet. (Tooth Morphotype A)

Figure 11 G

Referred Specimen and Locality: UFMNH 19288, unserrated tooth from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFMNH 19288 is an extremely small labiolingually-compressed theropod tooth (Fig. 11, G). This tooth features no serrations along the posterior and anterior carinae and is well-recurved. The tooth is oval in cross-section and features distinctly flattened areas along the center of its lingual and labial sides. This is by far the smallest specimen of a theropod from this site.

Discussion: This tooth does not comfortably match any reported or illustrated theropod specimens in the Laramidian microvertebrate literature. The diminutive size, prominent recurvature, and lack of serrations is not typical of maniraptoran teeth from the Horseshoe Canyon Formation of Alberta or the Williams Fork Formation. This tooth has some similarities in size and morphology to teeth hypothesized by Averianov et al. (2019) to be those of microraptorine theropods from the Early Cretaceous of Siberia. The subfamily Microraptorinae has had a complex taxonomic history over the last two decades, with notable disagreement between authors regarding the placement and validity of this group (Jasinski et al., 2020). Two possible microraptorines have been reported from the Campanian of Laramidia (*Bambiraptor* from the Two Medicine Formation of Montana and *Hesperonychus* from the Dinosaur Park Formation of Alberta) (Longrich & Currie, 2009). Regardless of the validity of this group, or whether this tooth is from a ‘microraptorine’ theropod, this specimen probably represents a new Cretaceous theropod tooth morphology.

Theropoda indet.

Figure 11 O, P

Referred Specimen and Locality: UFMNH 20203, numerous fragments of theropod tooth; UFMNH 20720, a distal fragment of a pedal(?) phalange from UFHNS locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Numerous theropod tooth fragments are present at ReBecca’s Hollow but are far too fragmentary to assign to a family or genus. These elements are referable to theropods based

on their laterally compressed geometry and smooth enamel texture, which differs from the folded enamel seen in alligatoroids (Fig. 11, O).

UFMNH 20720 is a small fragmentary theropod phalange (Fig. 11, P). Only the distal articular end of this bone is preserved. It has the typical smooth glassy bone texture and deep ligament pits seen in examples of coelurosaurian phalanges. The robust nature of the articular surface suggests that this element is a pedal phalange, rather than from the hand, but it is far too incomplete to assign to a region of the foot. This element is within the size range of a large dromaeosaurid, troodontid, oviraptorosaur, or ornithomimosaur, but is probably too gracile to have come from a tyrannosaurid.

Clade ORNITHISCHIA Marsh, 1881

Clade NEOORNITHISCHIA Benton 1985

Family THESCELOSAURIDAE Sternberg 1937

?Thescelosauridae gen. et indet.

Figure 11 E

Referred Specimen and Locality: UFMNH 19290, fragmentary cheek tooth? from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: UFMNH 19290 is a broken crown of what appears to be a heavily worn fan-shaped tooth (Fig. 11, E). This element has a series of well-developed carinae along its margin and what appears to be the margins of a cingulum around the proximal end of the crown. The surface of UFMNH 19290 has a slight rugose ornamentation across its surface. One side of the tooth, the center of the crown preserves a pair of crescent-shaped ridges that run approximately halfway up

the crown and bow inwards towards one another. The extremely incomplete and worn nature of this tooth makes it difficult to confidently call this element a thescelosaurid tooth, or to assign it to a region of the jaws or to decipher which side is lingual or labial. This element is extremely thin and does not perfectly match better-preserved examples in the Cretaceous microvertebrate literature, but Caleb Brown of the Royal Tyrell Museum of Paleontology stated that the UFMNH 19290 resembled examples of thescelosaurid teeth from the Horseshoe Canyon Formation of Alberta (personal communication in February of 2024). UFMNH 19290 bears some resemblance to a polyodontid (paddlefish) denticle, such as those figured in MacAlphin (1947) and Brinkman's 2022 guidebook to microvertebrates from the Dinosaur Park Formation.

Discussion: Thescelosaurids were a prominent family of herbivorous basal neornithischians in Laramidian ecosystems. Bones of these animals are relatively rare, due to the gracile quality of their skeletons, but teeth are a common occurrence in microvertebrate sites (Hudgins et al., 2022). Diem (1999) reported a tooth of *Thescelosaurus neglectus* from the Williams Fork Formation, but because this species was described from a nearly complete skeleton and is only known from Lancian deposits, I find this assignment dubious. UFMNH 19290 resembles a worn thescelosaurid tooth, but because it's its thin cross section and incomplete nature, I cannot confidently assign it to this group. Better examples of thescelosaurid teeth have recently been extracted from ReBecca's Hollow and will be described in an upcoming publication.

Clade CERAPODA Sereno, 1986

Clade ORNITHOPODA

Family HADROSAURIDAE

Hadrosauridae gen et sp. indet.

Figure 11 F

Referred Specimen and Locality: UFMNH 19271, isolated teeth, from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: Several teeth at ReBecca’s Hollow are referred to hadrosaurids based on their lanceolate shape, strong medial carinae, and asymmetrical enamel placement (Fig. 11 F). These teeth sometimes feature minute serrations on the margins of the enamel, and they are taller than wide if complete, and wider than tall if heavily worn. Most of these teeth are too worn to be assigned as dentary or maxillary.

Discussion: Hadrosaurids were a keystone megafaunal herbivore group in Late Cretaceous Laramidian environments. They are known from many isolated teeth in the Williams Fork Formation and a few isolated skeletal remains. Bender et al. (2023) reported a kritosaurine skeleton from this unit, but it has yet to be described as preparation was ongoing at the time of this report. Hadrosaurid teeth and skeletal elements have been reported by Diem (1999), Brand et al. (2022). The hadrosaurid teeth from ReBecca’s Hollow are far too incomplete to assign below the family level.

Clade MARGINOCEPHALIA

Clade CERATOPSIA

Family CERATOPSIDAE

Ceratopsidae gen et sp. indet.

Figure 11 A-D

Referred Specimen and Locality: UFMNH 19287, fragmentary shed teeth; UFMNH 20738, isolated shed teeth, from UFHNNH locality SCP 2019-2, Williams Fork Formation, Douglas Creek Arch, Rio Blanco County, Colorado, USA (Campanian-Maastrichtian).

Description: ReBecca's Hollow preserves numerous incomplete examples of ceratopsid teeth. These teeth are usually reduced to only their crowns and feature the typical asymmetrical morphology of this family of dinosaurs. Enamel is only present on one side of the tooth, and a prominent medial ridge runs vertically down the enamelous area (Fig. 11, A-D). These teeth feature highly ornamented enamel areas in comparison to hadrosaurids.

Description: Ceratopsids are among the best-known dinosaurs in the Williams Fork Formation. A partial skull of a chasmosaurine, sometimes regarded as *Pentaceratops*, was described by Diem (1999), Diem and Archibald (2005), and Lucas et al. (2006). This presence of a *Pentaceratops*-like chasmosaurine in this unit was used to argue that the Williams Fork Formation featured a Kirtlandian dinosaur fauna and a southwestern influence on its dinosaurs, rather than a Canadian influence (Sullivan & Lucas, 2006). The ceratopsid teeth from ReBecca's Hollow are far too incomplete to assign to a genus or subfamily of ceratopsids, but they do provide another data point for the distribution of these dinosaurs in this formation.

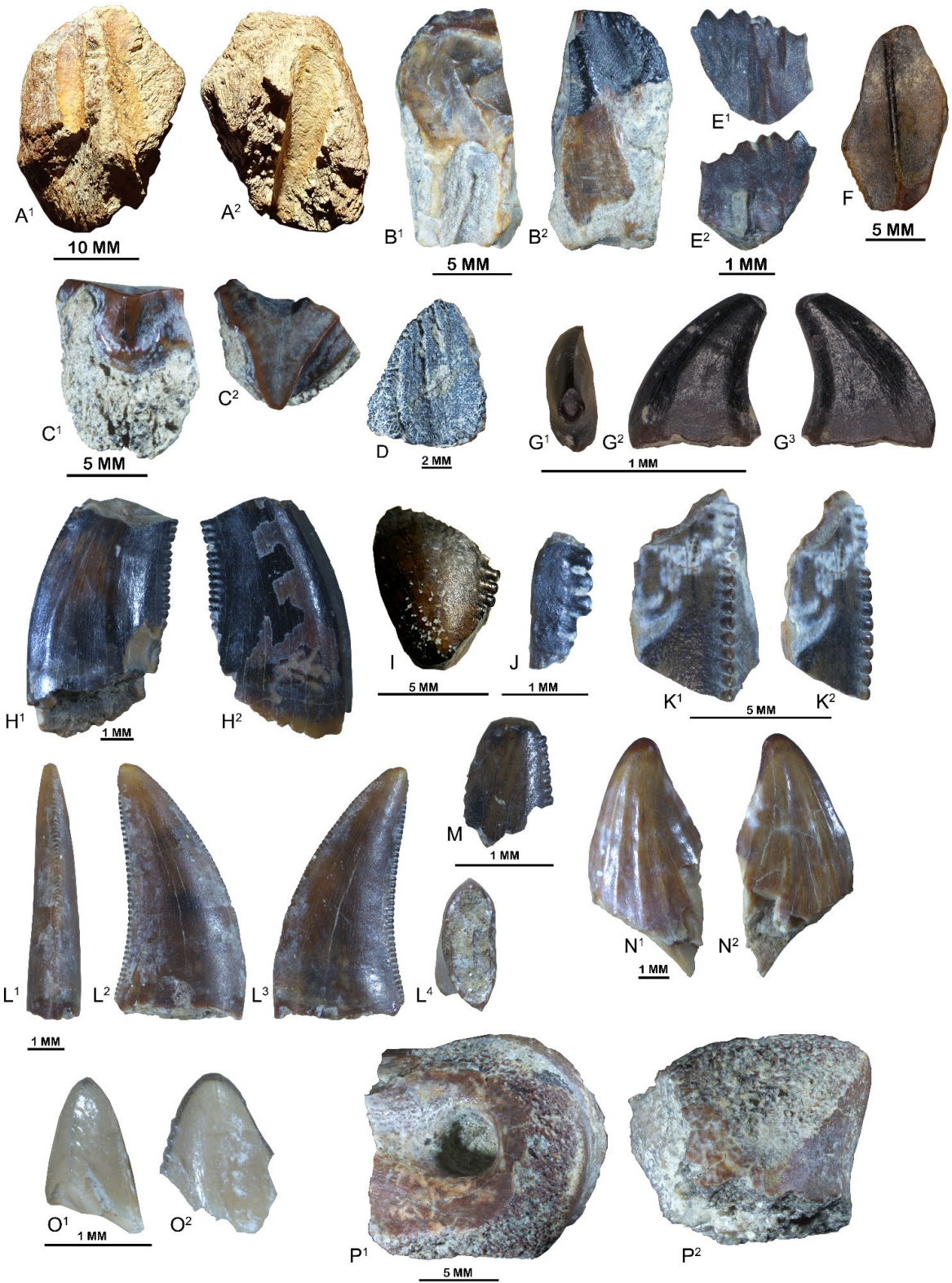


FIGURE 11. Dinosaur specimens from ReBecca's Hollow (SCP 2019-2). (A) UFHNNH 20738A, ceratopid tooth in (A¹) lateral view and (A²) medial view. (B) UFMNH 19287, ceratopid maxillary(?) tooth in (B¹) medial view and (B²) lateral view. (C) UFMNH 19287, worn ceratopsid dentary(?) tooth in (C¹) medial view and (C²) occlusal view. (D) UFHNNH 20738B, ceratopid tooth enamel. (E) UFMNH 19290, thescelosaurid(?) cheek tooth in (E¹-E²) lateral views. (F) UFMNH 19271, hadrosaurid tooth in external view. (G) UFMNH 19288, theropod tooth (Tooth Morphotype A) in (G¹) occlusal view, (G²) labial view, and (G³) lingual view. (H) UFMNH 19289, cf. *Saurornitholestes* sp. tooth in (H¹) lingual view and (H²) labial view. (I) UFMNH 19272A, tyrannosaurid tooth fragment in lateral view. (J) UFMNH 19272B, tyrannosaurid denticles. (K) UFMNH 20178, tyrannosaurid tooth fragment in (K¹) distal view and (K²) lateral view. (L) UFMNH 20190, cf. *Richardoestesia* sp. tooth in (L¹) distal view, (L²) labial view, (L³) lingual view, and (L⁴) basal view. (M) UFMNH JC17 cf. *Richardoestesia* sp. tooth in lateral view. (N) UFMNH 19286, *Paronychodon* sp. tooth in (N¹) labial view and (N²) and lingual view. UFMNH 20203, theropoda indet. Tooth fragment in (O¹) distal view and (O²) lateral view. (P) UFMNH 20720, theropod phalange fragment in (P¹) lateral and (P²) ventral view.

THE PALEOECOLOGY AND A FRESHWATER GUILD ANALYSIS OF REBECCA'S HOLLOW

With dozens of diagnostic fossils, representing at least 37 non-mammalian taxa having been collected from ReBecca's Hollow by Appalachian State University between 2021 and 2022 alone, this locality lends itself to a larger palaeoecological analysis. Following the template of Brinkman's (2008) palaeoecological and freshwater guild analysis of fossil localities in the Campanian Dinosaur Park Formation of Alberta, I will first break down the ecological role of ReBecca's Hollow's fauna, analyze their relative abundance patterns, and then attempt to place the aquatic taxa within Brinkman's guild system. This analysis is preliminary, as hundreds of additional fossils and new occurrences of taxa not mentioned in this thesis have been collected from this site by the University of Colorado Museum of Natural History and the Utah Field House of Natural History State Park Museum.

Overview of Taxa

Chondrichthyans

Chondrichthyans have proven to be among the least common taxa present at this site and are currently represented only by a single worn tooth referable to the hybodont cf. *Meristodonoides* and a *Chiloscyllium* tooth (not featured in the systematic section of this thesis). *Meristodonoides* is well-known from other Upper Cretaceous formations across Laramidia, such as the Dinosaur Park Formation of Alberta and the Kaiparowits Formation of Utah (where it was historically referred to as *Hybodus*) (Larson, et al., 2010; Kirkland et al., 2013). The rhinobatid *Myledaphus bipartitus* and the hybodontid cf. *Lonchidion selachos* are frequent occurrences in other Williams Fork Formation localities. Brand et al. (2022) reported the elasmobranchs *Lonchidion griffisi*, *Cantioscyllium markaguntensis*, *Chiloscyllium* sp., *Cristomylus* sp., *Cristomylus* sp., and

Pseudomyledaphus madseni from the nearby (>500 m away) J&M Site. The worn nature of the cf. *Meristodonoides* specimen at ReBecca's Hollow could be indicative of a reworked tooth, but this is difficult to test at the moment. cf. *Meristodonoides* was likely one of the top predators of the freshwater ReBecca's Hollow community.

Chondrosteans

A single dermal element from ReBecca's Hollow is attributable to a sturgeon. Modern and extinct sturgeons are generally considered durophagous bottom feeders or scavengers, which feed on soft-bodied prey (Brinkman, 2008). Because of the lack of fossils from this group at ReBecca's Hollow and the rest of the Williams Fork Formation, it is difficult to gauge how common or influential they were in these freshwater communities.

Holostean-Grade Fish

Bony scales, skull elements, vertebrae, and teeth of holostean-grade fish are among the most commonly recovered fossils from ReBecca's Hollow. These groups are represented by at least two lepisosteids (*Atractosteus* and a new gar with unique dentition), two or three amiids (cf. *Melvius*, *Cyclurus*, and possibly another small amiid), and the long-snouted aspidorhynchid *Belonostomus* (so far only known from one specimen).

Lepisosteids represent the single most recovered group at ReBecca's Hollow and the Williams Fork Formation. Well over two thousand ganoid scales have been collected from this locality, as well as teeth, jaw fragments, skull bones, vertebral centra, and lepidotrichia. This family is a common occurrence in coastal Laramidian environments, but their potential to be preserved as body fossils is likely much higher than that of other fish species due to their hard bony scales, numerous teeth, and robust skeletons (Estes & Berberian, 1970; Wilson, 2008).

Amiids are by far the second most common fossils at ReBecca's Hollow, with cf. *Melvius* teeth and amiid palatal fragments being among the most numerous elements in the assemblage. The numerous amiid fossils at this site and the occurrence of cf. *Melvius* renders this ecosystem as superficially more similar to the Hell Creek and Lance Formations than that of the Dinosaur Park and Judith River Formations (Brinkman, 2008; Brinkman et al., 2014). It should also be noted that neither *Melvius* nor *Cyclurus* occur in the Dinosaur Park Formation, rarer this unit preserves a distinctive unnamed amiid (Brinkman, 2022). Amiids were seemingly an important predatory species in this ecosystem, and with taphonomic biases accounted for, they were potentially among the most common osteichthyans in the Williams Fork Formation (as they are also common at sites like J&M and Arrowhead).

Belonostomus is currently only known from a single partial specimen at this site and was potentially less common in the Williams Fork Formation than that of the Dinosaur Park, Lance, and Hell Creek Formations.

Teleosts

The Williams Fork Formation's teleost community have received little attention in the paleontological literature but seemingly are represented by a diverse composition of fish from various trophic levels. Outside of ReBecca's Hollow, *Paralbula casei* is among the dominant teleost taxa found in the Williams Fork Formation, as it is a frequent occurrence in the collections of the University of Colorado Museum of Natural History. This fish is only known from five teeth at ReBecca's Hollow, thus making it abnormally uncommon in this locality. This fish is thought to be a close ecological analog to modern durophagous abulids (bonefish) (Brinkman, 2008). Much like the microvertebrate localities of the Dinosaur Park Formation, osteoglossomorphs are represented by *Coriops* (known from a few palatal elements) and an

unnamed hiodontid (known from an incomplete atlas centrum). Much as in the case of upper Lancian ecosystems these fish were probably in direct competition with amiids and their populations were restricted due to their overlapping diets and trophic niches (Brinkman et al., 2014).

Ostophysans are seemingly a common occurrence across the Williams Fork Formation and are known from a few specimens at ReBecca's Hollow. These fish are relatively small and would have probably served as a food source for larger vertebrates in their ecosystem. Esocoids are known from this site in the form of three dentaries, which are referred to *Estesesox foxi*. A single relatively large teleost dentary is possibly referable to the SSTR Morphotype from the Dinosaur Park Formation, which is figured in Brinkman's 2022 Illustrated Guide to the Vertebrate Microfossils from the Dinosaur Park Formation. This fish was likely one of the larger teleost taxa in this ecosystem and its long snout probably means that it occupied a similar ecological niche to lepisosteids and *Belonostomus*. Though they are not mentioned in the systematics section of this thesis, acanthomorphs are known from dorsal spines and an atlas centrum from ReBecca's Hollow.

Amphibians

As previously mentioned, the lissamphibians of ReBecca's Hollow will be described in detail in a series of upcoming publications, but here they will be mentioned briefly regarding their role in the ecology of this site. Salamanders are represented by at least three taxa, including the batrachosauroidids *Opisthotriton* and *Prodesmodon*, and at least one scapherpetontid. These taxa are known from cranial elements and vertebrae. Anurans are known from jaw elements at the site and include at least one toothed variety and the toothless *Theatoni*, which has yet to be

reported from the Williams Fork Formation. The enigmatic albanerpetontids are present at this site in the form of maxillae and a dentary.

Squamates

Though not necessarily part of the aquatic fauna at ReBecca's Hollow, at least three squamate taxa are present at the site, including osteoderms of anguids (similar to *Odaxosaurus*) and helodermatids. Indeterminate squamate vertebrae are rare but present at ReBecca's Hollow, as is the partial vertebra of a snake.

Turtles

Turtle carapace and plastron elements are some of the most common macrofossils present at the site and are represented by several aquatic taxa. The most common turtle at the site is the cryptodire *Adocus*, which is known from more than 81 shell elements. Rarer taxa at the site include indeterminate baenids, chelydrids, and the large terrestrial nanhsiungchelyid *Basilemys*. There are at least two trionychids at the site, one being potentially much larger than the other. Better preserved turtle fossils from the Williams Fork Formation are housed in the collections of the University of Colorado Museum of Natural History and require more in-depth study.

Crocodylians

ReBecca's Hollow yields only one alligatoroid crocodylian, which is known from many osteoderms and teeth, ranging in size from a few millimeters to a few centimeters in crown length. These fossils resemble specimens that were referred to by Brand et al. (2022) as cf. *Brachychampsa*. Though I agree that *Brachychampsa* is a likely candidate, I hesitate to refer these specimens to this genus with such scrappy material. Regardless of the identity of these specimens, the crocodylians of this site were likely some of the apex aquatic predators of ReBecca's Hollow.

Saurischians

Though theropod dinosaurs were terrestrial organisms, they may have played a role in the aquatic community of ReBecca's Hollow. The most common elements from theropods at this site are the fragmentary teeth of tyrannosaurids. A single recurved tooth, possibly referable to *Saurornitholestes*, represents the only definitive representative of a dromaeosaurid at the site. The potentially piscivorous theropods *Paronychodon* and *Richardoestesia* are both present in this locality, and according to some authors, may represent teeth of the same animal (Longrich, 2008). A problematic small well-recurved and unserrated tooth may represent a microraptorine-grade theropod present at ReBecca's Hollow.

Ornithischians

Indeterminate ornithischian teeth are among the most commonly recovered identifiable elements present at this site. These teeth are worn examples of both hadrosaurids and ceratopsians. Both of these dinosaur groups are known from complete or nearly complete examples at this site, with hadrosaurs being only slightly more common than ceratopsians. A single worn element may belong to a thescelosaurid, but it is so incomplete that this identification is very tentative.

Guild Structure of ReBecca's Hollow

Following the guild analysis designed and utilized by Brinkman (2008) for the Dinosaur Park Formation, I will attempt to organize the aquatic taxa of ReBecca's Hollow into a series of freshwater guilds, based on their locomotive systems, feeding styles, and size ranges (Table 2).

Benthic Durophages

Benthic durophagous taxa appear to be one of the least diverse and least prolific guilds at ReBecca's Hollow, with only *Paralbula casei* and a tentative sturgeon being the only

representative species. If there is a sturgeon at this site, it is the only large-bodied taxa in this guild, while *Parabula* falls into the medium-size range. Elsewhere in the Williams Fork Formation, durophages such as *Myledaphus* and *Paralbula* are prolific occurrences

Pelagic Durophages

Like the Dinosaur Park Formation localities analyzed by Brinkman (2008), all of the pelagic durophages at ReBecca's Hollow are tetrapods and include trionychids, baenids, and alligatoroids. These groups are all common occurrences elsewhere in the Williams Fork Formation, and all examples of this guild are comparatively large taxa

Benthic Carnivores

All of the benthic carnivorous taxa which lack durophagous dentition or jaws are lissamphibians (scapherpetontids, *Opisthotriton*, *Prodesmodon*, and albanerpetontids), and fall within the medium to small size range (Brinkman, 2008). Fossils of lissamphibians have been discovered from other sites in the Williams Fork Formation, but their abundance and diversity is not yet understood.

Pelagic Piscivores with Long Jaws

Going off of Brinkman's designations of piscivorous guilds by jaw morphologies, ReBecca's Hollow presents four piscivorous osteichthyan taxa with elongated jaws and conical teeth (*Atractosteus*, *Belonostomus*, *Estesesox*, and an enigmatic teleost that resembles Brinkman's (2022) SSTR Morphotype. These species all fall into the medium to small size range. It should be noted that the theropod *Richardoestesia* may fall into this guild, as its conical teeth and elongated jaws have been interpreted as adaptations for piscivory (Currie et al., 1990; Brinkman, 2008).

Pelagic Generalized Piscivores

By far the most diverse guild preserved at ReBecca's Hollow is that of generalist pelagic piscivores, almost all of which are fish. The only tetrapods in this group are chelydrid turtles, which fall into the large body size range. The other large body-sized taxa are cf. *Melvius* (by far the most common member of this guild) and *Meristodonoides*. Mid-sized members of this group include *Cyclurus*, the much rarer *Coriops*, and possibly the new gar taxon (the teeth of which closely resemble the lower jaw of an undescribed short-faced taxa from the Late Cretaceous of Utah). Small-bodied members of this guild include small amiids (possibly a distinct from *Cyclurus*), hiodontids, otophysans, and acanthomorphs.

Amphibious Insectivores

The various frogs at this site are the only obvious insectivores preserved at this site, and the presence of both toothed and toothless taxa suggests some niche partitioning in this group. As stated by Brinkman (2008), juvenile crocodylians and turtles may have also been part of this guild for part of their lives.

Relative Abundance Patterns in Guilds

Using the relative abundance template developed by Brinkman (2008) for the Dinosaur Park Formation, individual fossil elements from ReBecca's Hollow were divided by elements of similar taphonomic qualities and painstakingly counted (Table 1). Subdivisions include tooth & tooth-like elements, tooth-bearing elements, centra, flat, compact, or enamel-covered bones, flat dermal bones, and bones of complex shape. Brinkman designed this system to evaluate possible taphonomic biases that may render some vertebrate groups easier to fossilize than others, and thus bony elements are sorted by their geometric, osteological, and hydrodynamic properties, allowing these potential biases to be resolved. Brinkman applied his relative abundance data to

each of the aquatic guilds and was able to obtain a sense of which taxa were the dominant members of these guilds, and thus the most prolific at a given locality

If this system is applied to the vertebrate fossils of ReBecca's Hollow, abundance patterns of this site seemingly emerge (Table 2). In the guild of benthic durophages, *Paralbula casei* is by far the most common taxa in this guild, far outnumbering the tentative examples of sturgeon. As previously mentioned, this taxon appears to be uniquely common in the Williams Fork Formation, with hundreds of teeth preserved at other sites.

Of the pelagic durophages, *Adocus* is the most common in terms of dermal elements, followed by alligatoroids, which are represented by many osteoderms, teeth, centra, and a few skull bones. Because alligatoroids have many more osteoderms than *Adocus* and other turtles have shell elements, the dominance of *Adocus* is probably an accurate representation of the ReBecca's Hollow ecosystem. Trionychids of two or more taxa are the third most common dermal element found at the site, with baenids being the rarest member of this guild.

The non-durophagous benthic carnivore guild (like the Dinosaur Park Formation) is dominated by salamanders and the salamander-like albanerpetontids. The batrachosauroidid salamanders are the dominant family at this site, with *Opisthotriton* proving to be the most common taxa in terms of both centra and jaw elements. *Prodesmodon* centra are the second most common salamander vertebrae at the site. Scapherpetodontids are known from a few centra and one skull element, while albanerpetontids are known only from two maxillae.

In the long-snouted pelagic piscivore guild, lepisosteids far outnumber all other taxa. This fish is known from isolated teeth, thousands of scales, and many examples of centra, skull bones, and lepidotrichia. *Estesesox* is known from three dentaries at the site, while the SSTR teleost and *Belonostomus* are each only known from one specimen. The lack of champsosaurs at

this site and much of the rest of the Williams Fork Formation is an interesting component to this ecosystem as they are known from Lancia deposits in Colorado, and in coeval deposits in Alberta (Carpenter, 1979; Larson et al., 2010).

The pelagic generalized carnivores are the most speciose guild and are represented by at least 8 or more taxa. The most common taxa in the larger range of the guild is cf. *Melivius*, which is preserved in the form of many teeth and a few large centra. Chelydrids are the second most common taxa in the larger end of this guild, with a few shell fragments preserved. As stated by Brinkman in his 2008 analysis of the Dinosaur Park Formation, teeth, and shell elements are not analogous and are thus difficult to compare, but cf. *Melivius* is an extremely common taxa in the Williams Fork Formation at other localities. In the medium-sized range of this guild, *Cyclurus* (and possibly another smaller amiid species) dominates the guild with many palatal elements, jaw fragments, and centra. Small amiids (which may be juveniles of *Cyclurus* or a new species) dominate the small-bodied range of this guild. Every size range of this guild is dominated by amiids. The only amphibious insectivores at this locality are frogs, which represent at least two species, but more specimens will need to be collected to gauge the diversity and relative abundance of this guild.

While Brinkman (2008) applied his guild analysis of the Dinosaur Park Formation to two fossil localities, this thesis only regards one (seemingly unusual) example. Though I currently do not have analogous data to compare ReBecca's Hollow to another site in the Williams Fork Formation, the presented data could be easily compared to a site such as J&M, Arrowhead, or another locality. From this preliminary data, pelagic generalized piscivores are the most speciose group in the assemblage, with over seven taxa present. The most common groups at the site are trionychoid turtles (including *Adocus*), alligatoroids, lepisosteids, amiids, and batrachosauroidid

salamanders. This assemblage is in some ways more similar to Lanciaan deposits from Montana, the Dakotas, and Wyoming, rather than that of the contemporaneous Horseshoe Canyon Formation of Alberta, and the earlier Judith River and Dinosaur Park Formations of Montana and Southern Canada (Pearson et al., 2002; Brinkman, 2008; Wilson, 2008, Brinkman; 2022). Alligatoroids, trionychoids, amiids (especially *Melvius*) and batrachosauroidids, seem to thrive in warm humid climatic conditions. Holostean-grade fish seem to have experienced an explosion of relative abundance during the youngest Maastrichtian (Wilson, 2008). The frequency of these taxa in Lanciaan localities is likely further evidence of a warm climate present in Laramidia during the terminal portion of the Mesozoic.

Characteristic	Element	Number of Specimens
Tooth & Tooth-like Elements		
<i>cf. Melvius</i>	Teeth	29
Lepisosteidae indet.	Teeth	31
New Lepisosteid	Teeth	1
<i>Paralbula casei</i>	Teeth	5
<i>Meristodonoides</i>	Teeth	1
Crocodylia	Teeth	41
<i>Paronychodon</i>	Teeth	1
Thescelosauridae(?)	Teeth	1
<i>cf. Sauronitholestes</i>	Teeth	1
Small Theropod (A)	Teeth	1
Tyrannosauridae	Teeth	3
<i>Richardoestesia</i>	Teeth	2
Ceratopsidae	Teeth	11
Ornithischia indet.	Teeth	76
Hadrosauridae	Teeth	12
Theropoda indet.	Teeth	9
Tooth-bearing Element		
<i>Coriops</i>	Palate	3
<i>Belonostomus</i>	Premaxilla	1
Teleost SSTR	Dentary	1
Amiidae indet.	Dentary	1
Amiidae indet.	Jaw Element	1
Amiidae (including <i>Cyclurus</i>)	Palate	39
Lepisosteidae indet.	Jaw Element	5
" <i>Palaeolabrus</i> "	Tooth Plate	1
<i>Estesesox</i>	Dentary	3
Squamata	Maxilla	1
<i>Opisthotriton</i>	Dentary	1

<i>Opisthotriton</i>	Maxilla	1
Anura indet.	Jaw Element	1
<i>Theatoni</i>	Maxilla	1
Lissamphibia indet.	Jaw Element	5
Caudata indet.	Dentary	2
Albanerpetontidae	Maxilla	2
Albanerpetontidae	Dentary	1
Centra		
Teleost U3	Centra	4
Lepisosteidae	Centra	45
Hiodontidae	Centra	1
Osteichthyan indet.	Centra	72
Amiidae indet.	Centra	24
Acanthomorpha	Centra	1
<i>Opisthotriton</i>	Centra	19
Scapherpetontidae	Centra	2
Crocodylia	Centra	2
cf. <i>Melivius</i>	Centra	4
Batrachosauroididae indet.	Centra	1
<i>Prodesmodon</i>	Centra	7
Serpentes	Centra	1
Testudines(?)	Centra	1
Squamata indet.	Centra	2
Flat, Compact, or Enamel-covered Bones		
Amiidae indet.	Scales	69
Lepisosteidae indet.	Lepidotrichia	25
Lepisosteidae indet.	Skull Bones	79
Lepisosteidae indet.	Scales	+2000
Amiidae indet.	Skull Bones	32

Flat Dermal Bones		
Acipenseridae(?)	Dermal Bone	1
Trionychid (A)	Shell Elements	23
Trionychid (B)	Shell Elements	17
<i>Basilemys</i>	Shell Elements	3
Baenidae	Shell Elements	3
<i>Adocus</i>	Shell Elements	81
Chelydridae	Shell Elements	23
Crocodylia	Osteoderms	71
Anguidae	Osteoderms	10
Helodermatidae	Osteoderms	6
Bones of Complex Shape		
Crocodylia	Skull Bones	8
Teleostei indet.	Skull Bone	7
Theropoda	Phalange	1
Squamata	Skull Bone	1
Scapherpetontidae	Skull Bone	1
Small Tetrapod	Phalange	2

TABLE 1. Counts of identifiable elements from ReBecca's Hollow. These elements are grouped in the taphonomic subsets defined by Brinkman (2008).

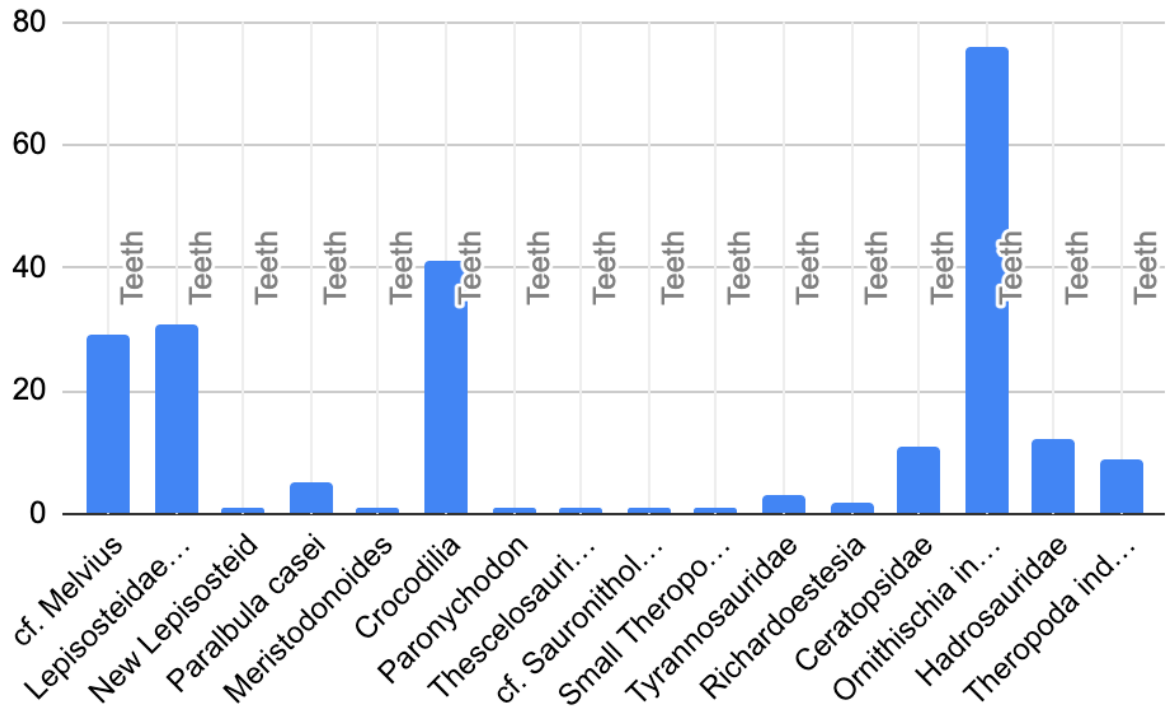


FIGURE 12. Counts of isolated teeth by taxa recovered from ReBecca's Hollow.

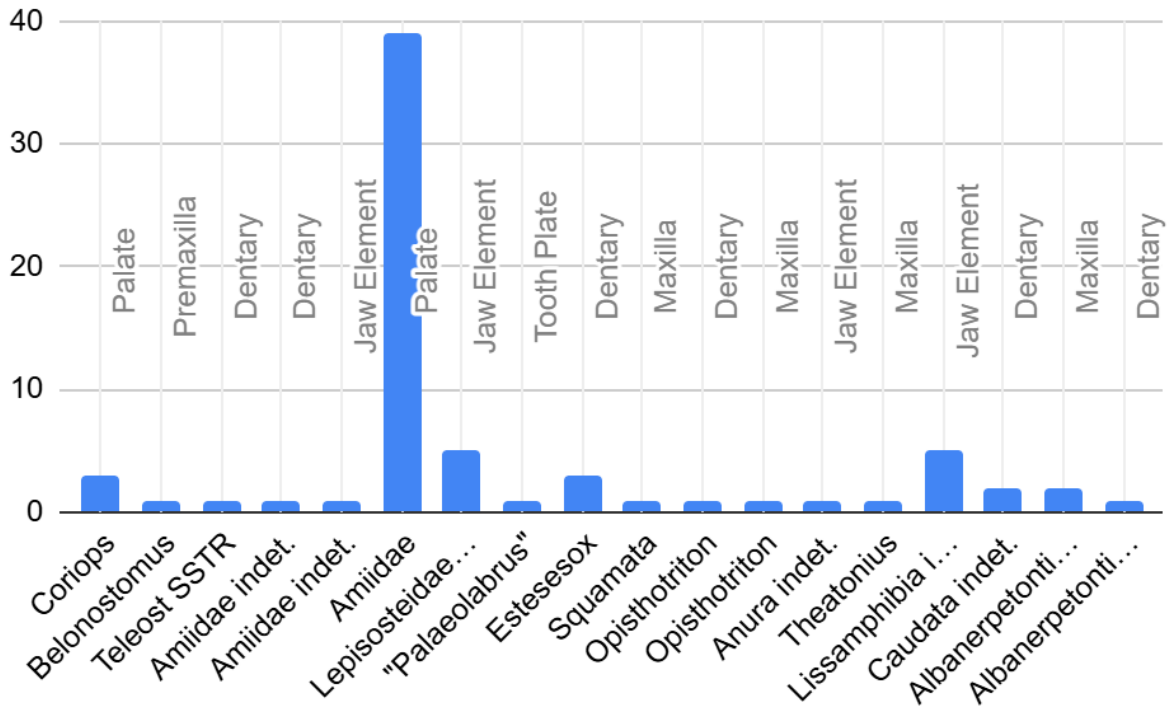


FIGURE 13. Counts of tooth-bearing elements by taxa recovered from ReBecca’s Hollow. It should be noted that *Cyclurus* and indeterminate amiid palatal elements were combined because of the morphological gradation between the two of them.

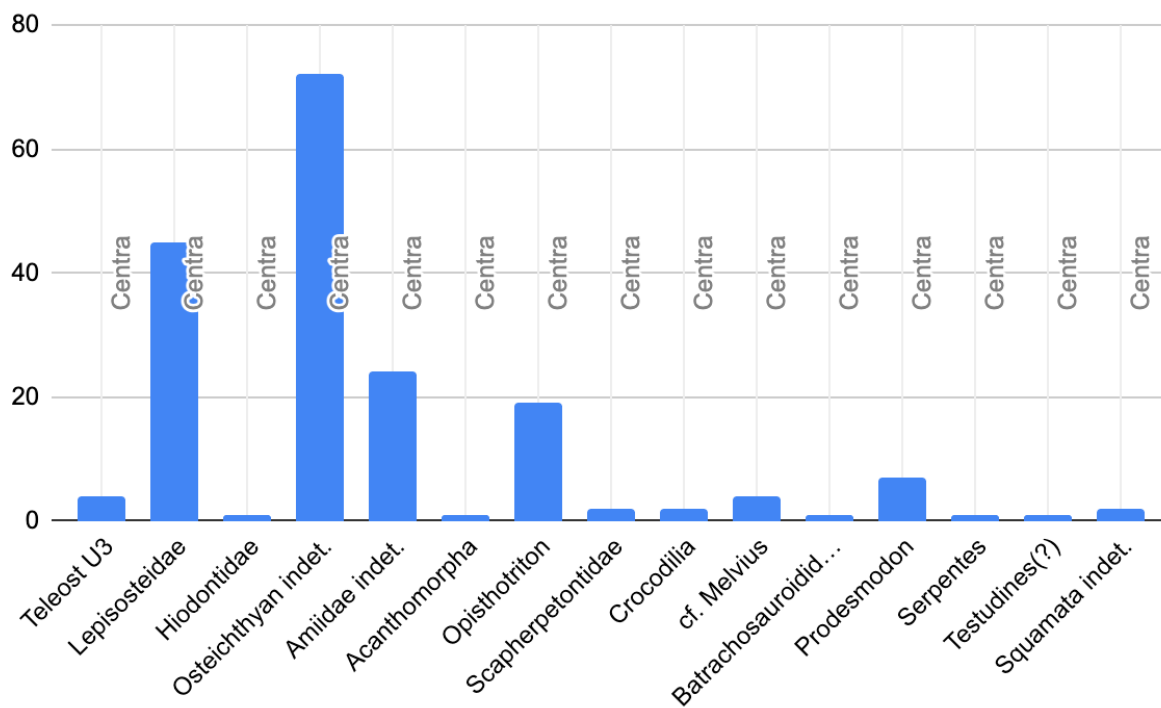


FIGURE 14. Counts of isolated vertebral centra by taxa recovered from ReBecca's Hollow.

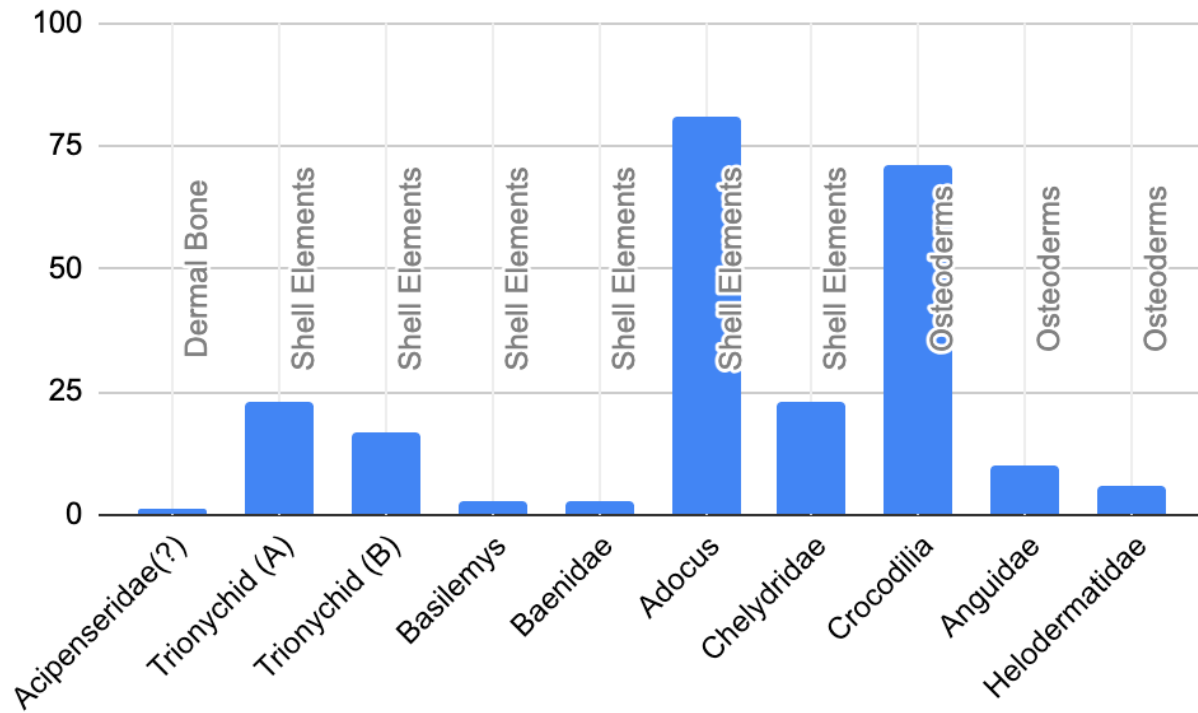


FIGURE 15. Counts of flat dermal elements by taxa recovered from ReBecca’s Hollow.

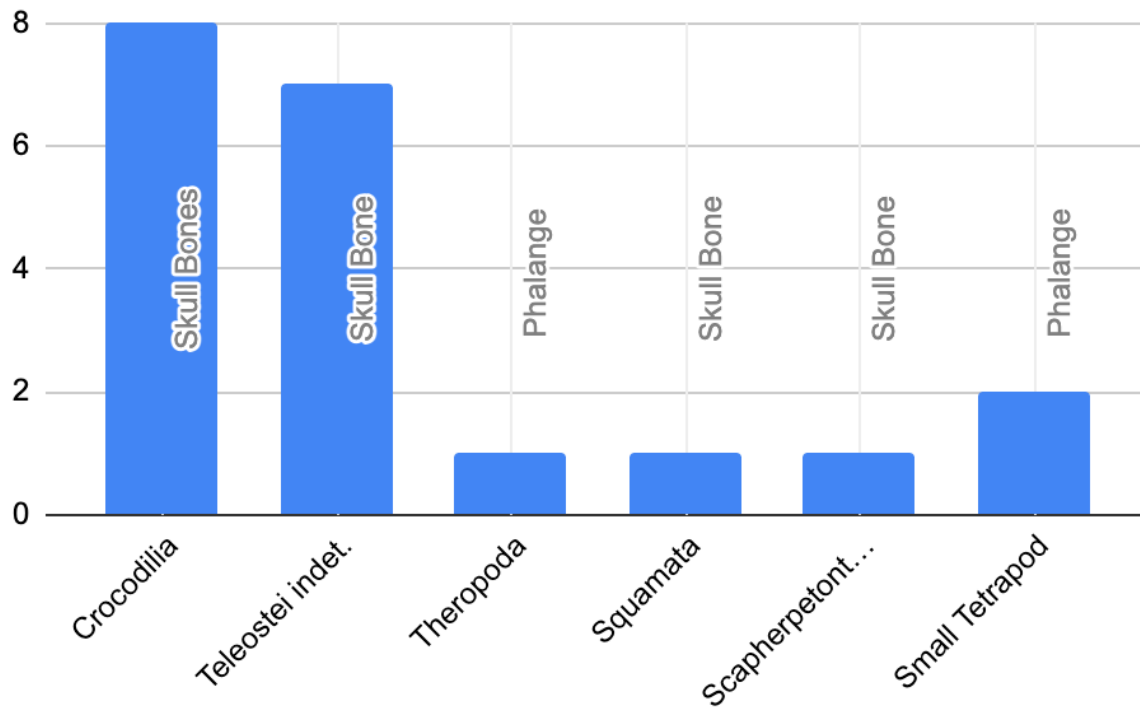


FIGURE 16. Counts of bones of complex shape by taxa recovered from ReBecca's Hollow.

Guild	Large-bodied	Medium-bodied	Small-bodied
Benthic durophages			
	Acipenseridae*	<i>Paralbula</i>	
Pelagic durophages			
	Alligatoroidae		
	Trionychidae		
	Baenidae		
	<i>Adocus</i>		
Benthic carnivores			
		Scapherpetontidae	<i>Opisthotriton</i>
			<i>Prodesmodon</i>
			Albanerpetontidae
Pelagic piscivores		<i>Atractosteus</i>	<i>Belonostomus</i>
			Teleost SSTR
			<i>Estesesox</i>
Pelagic generalized piscivores	<i>Meristodonoides</i>	<i>Cyclurus</i>	Small Amiids
	Chelydridae	<i>Coriops</i>	Acanthomorpha
	<i>Melvius</i>	New Lepisosteid	Teleost U3/BvD
			Hiodontidae
Amphibious insectivores			<i>Theatoniis</i>
			Anura indet.

TABLE 2. Guilds of aquatic communities at UFHNNH locality SCP 2019-2 (ReBecca’s Hollow), as defined by Brinkman (2008).

DISCUSSION & CONCLUSIONS

This thesis builds on other prior studies of the Williams Fork Formation (Archibald, 1987; Diem, 1999; Foster & Hunt-Foster, 2015; Brand et al., 2022; Foster et al., 2023; Eberle et al., 2024) by providing more data regarding the non-mammalian vertebrate and freshwater communities of this formation. To compare ReBecca's Hollow and J&M (described by Brand et al., 2022) to better-known Cretaceous assemblages, Table 3 synthesizes occurrence data from the paleontological literature regarding the Williams Fork, Horseshoe Canyon, St. Mary River, Lance, Hell Creek, Dinosaur Park, and Kaiparowits Formations. As noted above, the Williams Fork Formation appears to have a markedly different fauna than that of the contemporaneous *Albertosaurus* bonebed from the Horseshoe Canyon Formation of Alberta, including a high abundance of turtles, alligatoroids, and lepisosteids. Taxa associated with warm Cretaceous environments like cf. *Melivius*, *Paralbula*, and *Atractosteus* are prominent members of the ReBecca's Hollow vertebrate community but are absent in the *Albertosaurus* bonebed. The *Albertosaurus* bonebed has been dated to c. 70.1 Ma (Eberth & Kamo, 2020) and is correlated with a cold dry period in the "Edmontonian". ReBecca's Hollow is stratigraphically close to the zircon date of 71.7 +/-1.8 Ma, provided by Hunt-Foster et al. (2025), and thus, I will treat this locality as though it is roughly contemporaneous with the better-known Albertan site. The lower Horseshoe Canyon Formation is thought to represent a warm climatic stage and produces fossils of turtles like *Adocus*, *Basilemys*, a chelydrid, a trionychid, and a macrobaenid (Brinkman & Eberth, 2006). The provided zircon date of the Williams Fork Formation correlates with the colder and drier the Tolman Member of The Horseshoe Canyon Formation (Eberth and Kamo, 2022). Eberth

and Kamo (2022) regarded the Scabby Butte locality of the St. Mary River Formation of Alberta as being 72.6–72.2 Ma, making this locality also roughly contemporary with ReBecca’s Hollow. This faunal assemblage displays some similarities with the Williams Fork Formation, such as occurrences of trionychids and alligatoroids. Though Langston (1975) reported lepisosteids from this Scabby Butte, Holostean A was not recognized at the time so the material should be reexamined to confirm that the ganoid scales at this site are those of a lepisosteid rather than Holostean A. The fish and reptiles of this locality have not been significantly studied since Langston’s 1975 description and are likely in need of an updated analysis. The “Edmontonian” El Gallo Formation of Baja California, Mexico appears to preserve a diverse community of dinosaurs, turtles, squamates, osteichthyans, and lissamphibians (López-Conde et al., 2018, Chavarria-Arellano, 2018; Romo de Vivar Martínez, 2016), but because this unit has yielded a zircon date of 74.706 + 0.028 Ma, I will not include it in this discussion as it is likely older than ReBecca’s Hollow (Fastovsky, et al., 2020). Additionally, I will not include the Prince Creek Formation in this analysis, as this unit represents a polar environment that would have been substantially different from that of the Williams Fork Formation and the other contemporary units. A major difference that has been noted between the Prince Creek Formation and other Cretaceous units is that amiids, lepisosteids and ectothermic tetrapods are absent. This is consistent with the kind of latitudinal distribution patterns that would be expected for such a high latitude assemblage.

As suggested by Brand et al., 2022, occurrences of taxa such as cf. *Melvius*, the lizard *Penetius*, and the frog *Theatoniuss* in the Campanian Kaiparowits Formation of Utah, the Campanian-Maastrichtian Williams Fork Formation, and the late Maastrichtian

Hell Creek and Lance Formations suggest that many small Lancian non-mammalian taxa may have originated in southern regions of Laramidia during the Santonian or Campanian and subsequently migrated north during the warm climatic periods of the terminal Maastrichtian. The Williams Fork Formation and its associated vertebrate fossils may prove to be key data points in terms of testing hypotheses and understanding the paleoecological dynamics of the Campanian-Maastrichtian transition.

Taxa	ReBecca's Hollow	J&M	Albertosaurus Quarry (HCF)	Scabby Butte (SMRF)	Lance Fm	Hell Creek Fm	Dinosaur Park Fm	Kaiparowits Fm
<i>Texatrygon</i>			X*		X	X		X
<i>Restesia</i>				X	X	X	X	X*
<i>Myledaphus</i>		X	X	X	X	X	X	X
<i>Pseudomyledaphus</i>		X						
<i>Cantioscyllium</i>		X		X	X	X		X
<i>Chilloscyllium</i>	X	X						X
<i>Cristomylus</i>		X						
<i>Lonchidion</i>		X			X	X		X
<i>Meristodonoides</i>	X*		X				X	X
Acipenseridae	X*		X		X	X	X	
<i>Atractosteus</i>	X	X		X*	X	X		X
New Lepisosteid	X							X*
Holostean A			X			X	X	
Holostean B							X	
<i>Melvius</i>	X*	X			X	X		X
<i>Cyclurus</i>	X		X	X	X	X		
<i>Belonostomus</i>	X		X	X	X	X	X	
<i>Coriops</i>	X		X		X	X	X	
<i>Paralbula casei</i>	X	X		X	X	X	X	
<i>Estesesox foxi</i>	X		X		X	X	X	X

Pycnodontiformes		X*						
Hiodontidae	X				X	X	X	X
Otophysi	X				X	X	X	X
Acanthomorpha	X				X	X	X	X
Teleost SSTR	X						X	
<i>Opisthotriton</i>	X		X		X	X	X	X
<i>Prodesmodon</i>	X		X		X	X		X
Scapherpetontidae	X		X		X	X	X	X
Albanerpetontidae	X				X	X	X	X
Anura indet.	X		X		X	X	X	X
<i>Theatoniuss</i>	X				X			X
Baenidae	X			X	X	X	X	X
<i>Basilemys</i>	X				X	X	X	X
Adocus	X	X			X	X	X	X
Trionychidae	X			X	X	X	X	X
Chelydridae	X		X			X	X	X
<i>Champsosaurus</i>			X	X	X	X		
Alligatoroidea	X	X		X	X	X	X	X
Giant Neosuchian		X						
<i>Richardoestesia</i>	X	X	X		X	X	X	X*
Tyrannosauridae	X		X	X	X	X	X	X
Sauromitholestinae	X		X			X*	X	

Dromaeosauridae		X	X		X	X		X
indet.								
<i>Paronychodon</i>	X		X		X	X	X	X*
Troodontidae			X	X	X	X	X	X
Theropod A	X							
Toothed Birds	X*		X		X	X	X	
Thescelosauridae	X		X		X	X	X	
Hadrosauridae	X	X	X	X	X	X	X	X
Ceratopsidae	X		X	X	X	X	X	X
Ankylosauria			X	X	X	X	X	X

TABLE 3. Occurrences of Late Cretaceous non-mammalian taxa at ReBecca’s Hollow (Williams Fork Formation), J&M (Williams Fork Formation), the *Albertosaurus* Quarry (Horseshoe Canyon Formation), Scabby Butte (St. Mary River Formation), Hell Creek Formation, Lance Formation, Dinosaur Park Formation, and Kaiparowits Formation. X’s indicate occurrences, while a blank space means the taxa are not present at the locality or formation. Tentative or dubious occurrences are marked with an *.

PART II

‘BETWEEN THE DINOSAURS’ TOES: APPROACHES TO EXHIBITING MICROVERTEBRATE FOSSILS IN MUSEUM DISPLAYS

THE MICROVERTEBRATE FOSSIL PROBLEM

Microvertebrate fossil assemblages provide a unique window into the nature of ecosystems, in ways that individual fossil specimens cannot. The *Tyrannosaurus rex* specimen known as “Sue” (FMNH PR 2081) has provided researchers with unprecedented data regarding the osteology, life history, and pathologies of a remarkable individual dinosaur (Brochu, 2003; Cullen, 2020; Hamm et al., 2020), but the matrix around the fossilized bones of this animal yielded a unique assemblage of sharks, which included a new species named *Galagadon nordquistae*, described by Gates et al. in 2019. Despite over a century of fieldwork and analysis, well-studied Mesozoic units such as the Hell Creek, Lance, and Dinosaur Park Formations continue to yield new taxa with important implications regarding the paleoecology, evolution, and extinction patterns of modern and extinct animal groups. Among the perplexing discoveries that have emerged from Cretaceous Laramidian microvertebrate sites over the last 30 years include a possible Cretaceous parrot (Stidham, 1998), tetra fish (Newbrey et al., 2009) (which were never thought to have existed outside of South America), and a possible mutant salamander jaw (Gardner, 2022). Microvertebrate sites (as well as paleobotanical localities) allow paleontologists to flesh out the ancient ecosystems with, at times, stunning attention to detail.

A large dinosaur, marine reptile, or mammoth skeleton may be visually impressive, but it does not provide much information about the world it lived in. This is where where microvertebrate sites like Bushy Tailed Blowout (Late Cretaceous), the Bug Creek Anthills

(earliest Paleocene), and ReBecca's Hollow become crucial to our understanding of the deep past. These sites yield dozens of vertebrates ranging from large dinosaurs to tiny mammals to bizarre toothy fish. Microvertebrate sites provide rich data and paleoecological context that is otherwise challenging to acquire from singular fossils, but several obstacles exist in interpreting (and exhibiting) them to the public. These challenges include (1) microvertebrate fossils are usually so small that they cannot be seen/appreciated without microscopy; (2) these specimens may represent fascinating taxa, but they are only preserved as isolated and abstracted elements; (3) these fossil taxa are often unfamiliar to museum audiences; (4) these specimens and the taxa they represent are perhaps not very attractive to museums in terms of investing resources and space for displays. These problems are difficult to overcome outside of simply displaying microvertebrate fossils with a large magnifying glass or digital microscope (a practice that is utilized in museums like the Gray Fossil Site and Museum). In this chapter, I propose an alternative visual system that explains to museum audiences what these fossil elements are, and who they once belonged. This system includes: (1) enlarged 3D prints of fossil specimens; (2) reconstructions of the completed skeletal element; (3) life reconstructions of the fossil taxa; and (4) a visual depiction of the animal in the context of its environment via a diorama or mural. The following proposed ReBecca's Hollow exhibition and my analysis of contemporary microvertebrate fossil displays are primarily informed by my phenomenological experience in museum spaces and my opinion regarding the aesthetics of natural history museum displays. Because much of this section is my opinion, it should be treated as such by the reader.

EXISTING EXAMPLES IN MUSEUMS

To assess the difficulties and shortcomings of microvertebrate fossil displays, I provide an overview of ways in which existing museums currently attempt to showcase these tiny fossils

and the taxa they represent. The examples I describe below are from museums in the United States and Canada that I have visited and represent the geographical area in which I operate as a researcher and museum specialist. This overview is not meant to critique these museums or their exhibits but is simply an examination of the methods they chose to display microvertebrate fossils and the ethos or philosophical messaging that I perceive from the displays. To organize these museums and microvertebrate displays, I group the museum examples below by their modes of exhibition and utilization of microvertebrate fossils as educational tools. I then evaluate the benefits and shortcomings associated with each display method and what I believe they communicate about ancient ecosystems and our understanding of the deep past.

Microvertebrate Taxa in a Diorama

Perhaps the most visually impressive, immersive, and holistic approach to displaying microvertebrates (specifically life reconstructions of microvertebrate taxa) is that of diorama displays. Some of the most elaborate examples of this style can be seen at the Denver Museum of Nature and Science (DMNS), in Denver, CO. The DMNS' major paleontology exhibit is known as the *Prehistoric Journey* and opened in 1995 under the supervision of Kirk Johnson (Johnson et al., 2013). In addition to the dynamic mounted dinosaur and mammalian skeletons, this exhibition is home to eight hyper-realistic dioramas, which depict the Proterozoic Wilpena Group (Ediacara Hills, Australia), the Silurian Racine Formation (Southeastern Wisconsin), the Devonian Beartooth Butte Formation (Bighorn Basin, Wyoming), the Pennsylvanian Hamilton Formation (Eastern Kansas), the Late Cretaceous Hell Creek Formation (Southwestern North Dakota), the Eocene Wind River Formation (Bighorn Basin, Wyoming), the Miocene Harrison Formation (Agate Fossil Beds National Monument, Nebraska), and the Pliocene of the Afar

Triangle (Ethiopia). These displays vary in size and display style, but each is meticulously rendered with accurate faux plants, invertebrates, sediment, and lighting, and seamlessly blended into their murals (creating a disorienting sense of depth within the display). Each of these dioramas is paired with a small wall panel display, each titled “Evidence of (insert the name of an ancient landscape in the diorama)”. One of the largest of these displays is the Hell Creek Formation diorama, which is paired with a panel display titled “Evidence of a Cretaceous Creekbed” (Fig. 17). This diorama is one of two walk-through diorama ecosystems in the *Prehistoric Journey*, and exists as a rounded room filled with plants, auditory ambiance, flowing water, an artificial breeze, lighting that changes from overcast daylight to purple dusk, and a moon-lit night (a recent addition to the diorama in 2024). The life forms present in the diorama include sparring pachycephalosaurids, small mammals in the underbrush, a rotting *Triceratops* carcass, a trionychoid turtle, and a plethora of angiosperm plants, which create a canopy over the audience. Only a few of these taxa are present in the associated panel display, and technically the only true microvertebrate fossils displayed in the panel are the jaws of the mammals *Cimolodon nitidus* and *Didelphodon vorax* (Fig. 17 A). Despite lacking the incredible diversity of small vertebrates present in the Hell Creek Formation of North Dakota, this display is effective in simulating the atmosphere of the Hell Creek Formation during its heyday. Stepping into this display, the audience gets a sense of the density of the forest, the sticky humid air, and the sandy sediment of the Hell Creek ecosystem. The adjacent panel display serves to tell the visitor the scene they have just witnessed has been informed by fossil discoveries, which range in size from large dinosaurs to tiny mammal fossils, both of which are small parts of the larger Late Cretaceous ecosystem preserved in the Hell Creek Formation (67 Ma).

The Royal Tyrrell Museum of Paleontology (RTMP) in Drumheller, Alberta has a walkthrough diorama at the entrance to the museum's galleries. This display is similar to that of the DMNS, but instead of the Hell Creek Formation, it represents the Late Cretaceous Horseshoe Canyon Formation of Alberta (Fig. 18). This diorama is specifically modeled after the infamous *Albertosaurus* bonebed from Dry Island Buffalo Jump Provincial Park, in Alberta (one of the only known tyrannosaurid bonebeds) (Eberth & Currie, 2010; Larson et al., 2010). In this space, visitors are greeted by a pack of towering *Albertosaurus sarcophagus* emerging out of a forest of conifers and ferns (Fig. 18 A-C). At the feet of the massive theropods is a small faux pond inhabited by a trionychid turtle and an *Opisthotriton* salamander (Fig 18 D, E). Like the DMNS' "Evidence of..." wall panel displays, the wall opposite the entrance to the *Albertosaurus* diorama features a few small window panel displays with real fossils from the *Albertosaurus* bonebed. Amongst the large theropod bones are the fossils of a *Didelphadon coyi* and an *Aspideretes* turtle, both used to further flesh out the 'how we know what we know' about the Late Cretaceous of Alberta (Fig. 18, F, G). Although these animals are technically considered microvertebrate taxa, the smallest of this ecosystem's vertebrates (fish, amphibians, multituberculates, etc., described by Larson et al., 2010) are not displayed. Like the previous example of the DMNS, this impressive diorama largely lacks non-mammalian microvertebrates, and the included small animals are sidelined by the charismatic tyrannosaurids.

The benefit of displaying microvertebrate taxa in dioramas is that they provide visually engaging paleoecological context and life reconstructions of these tiny animals. Unfortunately (as in the case of the *Albertosaurus* display) the actual fossil data that informs what the Earth and its biota would have been like during the Late Cretaceous is lost in the spectacle of larger and more charismatic animals like dinosaurs. Both the DMNS and RTMP have beautiful and

technically impressive exhibitions, but in my opinion the associated fossils displayed alongside the dioramas do not do justice to the plethora of sedimentological, paleobotanical, paleoecological, paleobiological, and paleoclimatic data that went into their construction.



FIGURE 17. Cretaceous Creekbed walkthrough diorama in the *Prehistoric Journey*, Denver Museum of Nature and Science, Denver, CO. (A) “Evidence of a Cretaceous Creekbed” panel display with Hell Creek Formation fossil specimens; (B) Sparring *Stygimoloch spinifer*; (C) Details of *Didelphodon vorax*; (D) Details of trionychoid and rotting *Triceratops* in flowing creek.

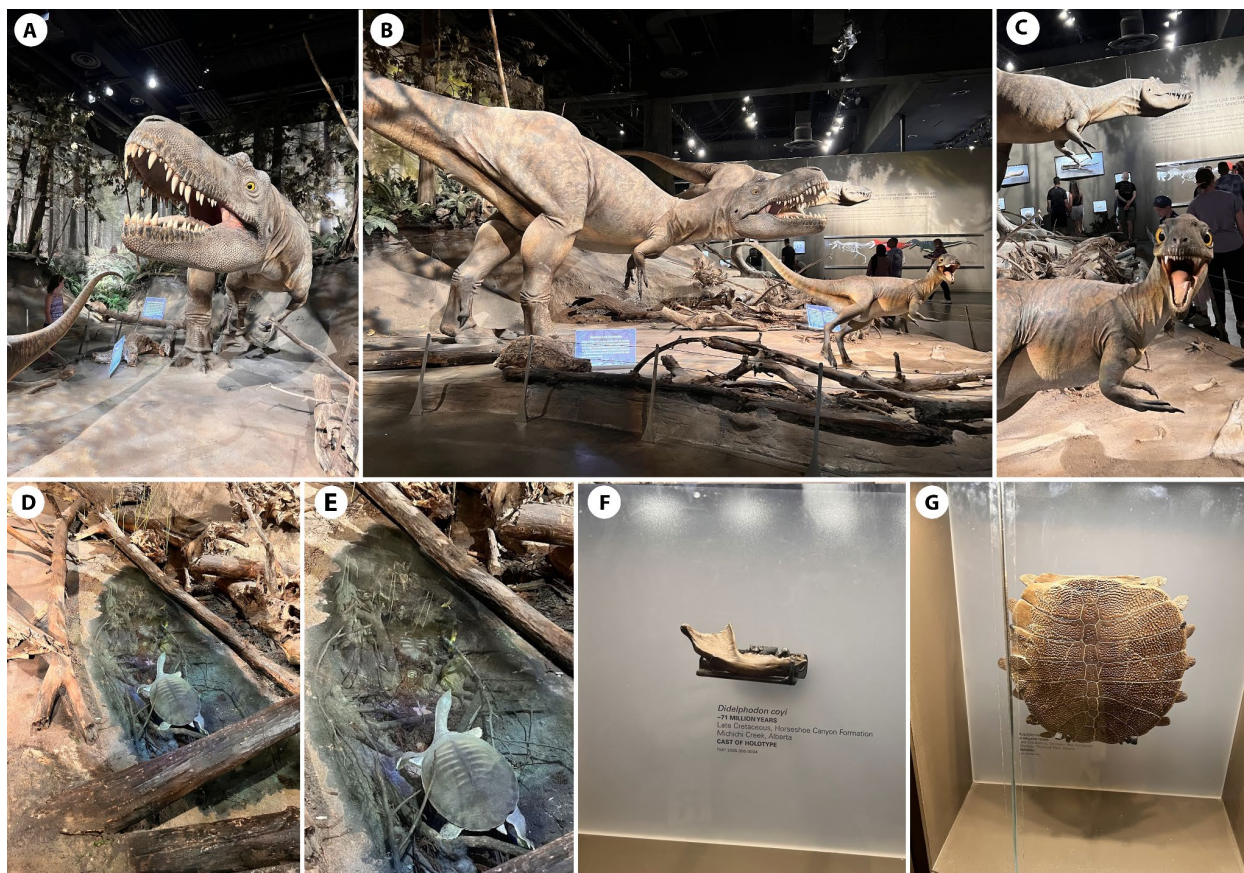


FIGURE 18. *Albertosaurus* walkthrough diorama in the Royal Tyrrell Museum of Paleontology, Drumheller, AB. (A) Adult *Albertosaurus sarcophagus* with forest in the background; (B) Details of *Albertosaurus sarcophagus* ‘pack’; (C) Details of juvenile *Albertosaurus sarcophagus*. (D-E) Faux pond with trionychid turtle and *Opisthotriton kayi*; (F) Mounted cast of *Didelphodon coyi* mandible in an associated panel display; (G) mounted trionychid turtle shell in an associated panel display.

Microvertebrates in Cabinet-style Displays

Perhaps the most common (as well as the least intrusive and technically simplistic) manner of displaying microvertebrates is what I will refer to as cabinet-style displays (Fig. 19). These are simply pedestals or cabinets where fossil specimens are laid directly onto the surface with little mounting or modification. Examples of these displays can be seen in many smaller or regional museums, including the Las Vegas Museum of Natural History (Las Vegas, NV), St. George Dinosaur Discovery Center (St. George, UT), Montana Dinosaur Center (Bynum, MT), H. Earl Clack Museum (Havre, MT), Blaine County Museum (Chinook, MT), Great Plains Dinosaur Museum (Malta, MT), Mesalands Community College Dinosaur Museum (Tucumcari, NM), Virginia Museum of Natural History (Martinsville, VA), Ghost Ranch's Ruth Hall Museum of Paleontology (Abiquiu, NM), Idaho Museum of Natural History (Pocatello, ID), Museums of Western Colorado's Dinosaur Journey (Fruita, CO), and the Canadian Fossil Discovery Center (Morden, MB). These fossils may be accompanied by associated visual or life reconstructions, but all essentially exist in their naked isolated forms. In the case of the Canadian Fossil Discovery Center, a display of microvertebrates is featured on a circular platform with a digital microscope, which projects a live feed of the specimens. This display makes great use of microscopy, but the fossils are displayed essentially in the same form as the previous examples. The benefit of this technique is that it requires very little in terms of exhibit resources, and the fossil specimens are generally in a secure static location, where they are hard to damage. The prominent issues with this method are that it can be harder to make the fossils look visually interesting for visitors, and it can be hard to articulate exactly what the specimens are.



FIGURE 19. Examples of microfossils in raw cabinet-style displays. (A) Virginia Museum of Natural History, Martinsville, VA; (B) Las Vegas Museum of Natural History, Las Vegas, NV; (C) Montana Dinosaur Center, Bynum, MT; (D) Idaho Museum of Natural History, Pocatello, ID.

Elevated Microvertebrates

In a similar vein to the cabinet-style display method, some museums resort to mounting or ‘elevating’ microvertebrate fossils in panel displays (Fig. 20). This display technique is essentially that of microvertebrate fossils suspended on wire mounts. Examples of this can be seen in the Smithsonian’s National Museum of Natural History (Washington, D.C.), Burke Museum of Natural History and Culture (Seattle, WA), Royal Ontario Museum (Toronto, ON), Makoshika State Park’s Visitor Center (Glendive, MT), Carter County Museum (Ekalaka, MT), Old Trail Museum (Choteau, MT), North Dakota Heritage Center and State Museum (Bismark, ND), Gray Fossil Site and Museum (Gray, TN), Museum of the Rockies (Bozeman, MT), Manitoba Museum (Winnipeg, MB), New Mexico Museum of Natural History and Science (Albuquerque, NM) and the Quarry Exhibit Hall at Dinosaur National Monument (Jensen, UT). This method of mounting tiny fossils can make for visually novel displays, which bring the unique form of the fossil specimens into the focus of the museum audience. In some cases, such as the Gray Fossil Site and Museum, these mounted specimens are featured with magnifying glasses, so that the visitor can see them more closely. Some of these examples, such as the Carter County Museum, the National Museum of Natural History, and the New Mexico Museum of Natural History and Science make use of images of life reconstructions of the microvertebrate taxa next to the mounted fossil to further articulate what animal the element once belonged to (Fig. 20 C, D). The benefits of the ‘elevated’ technique are that the individual microfossil is highlighted within the display, and its elevation away from the surfaces of the exhibit can allow for more room for images or text panels. The drawbacks of this method are that this display style takes more resources to meticulously mount the specimens, specimens could be vulnerable to

damage, and they often still lack the visual context of what taxa or anatomical elements they represent.

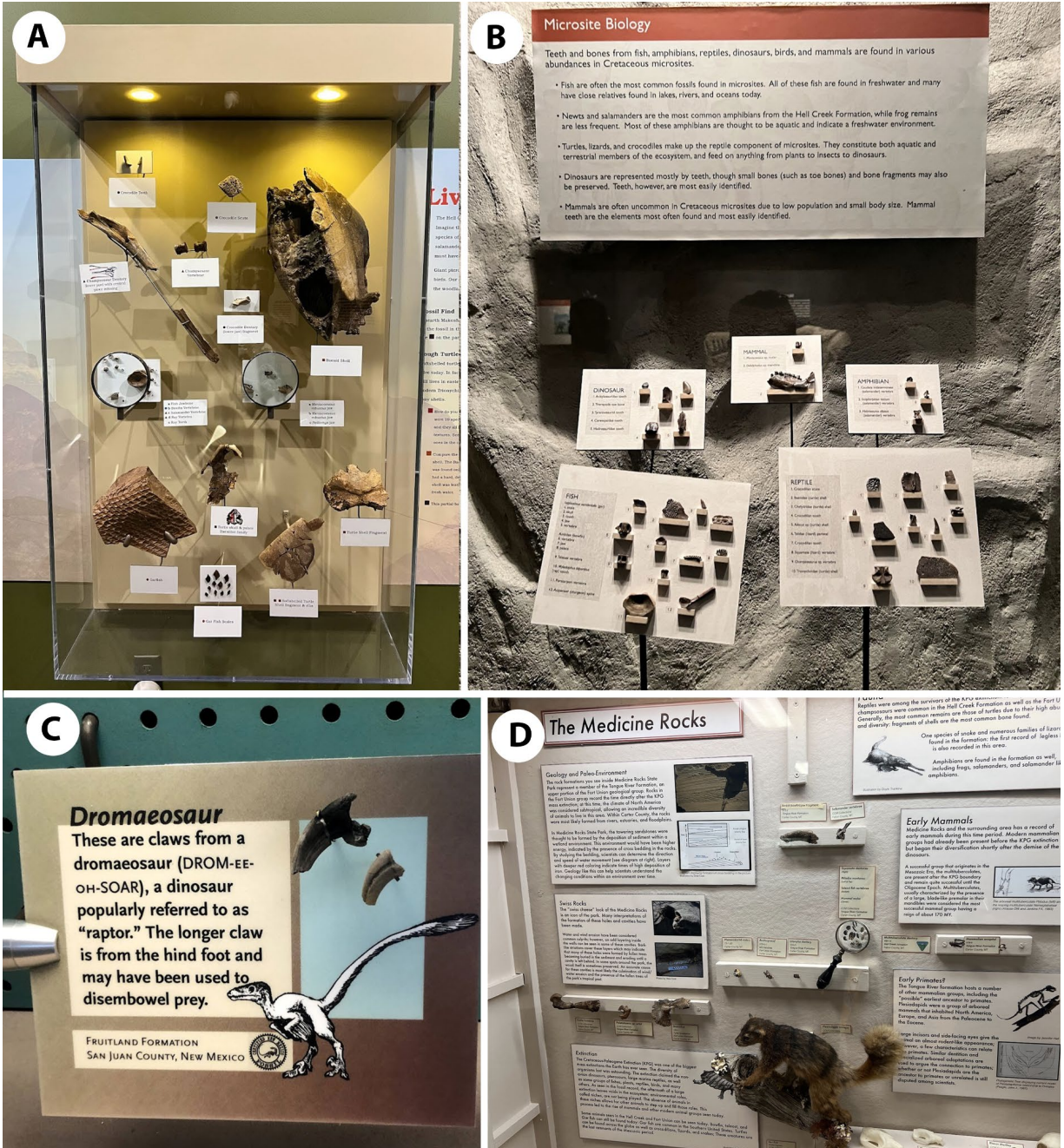


FIGURE 20. Examples of elevated or mounted microvertebrate fossils. (A) Makoshika State Park Visitor Center, Glendive, MT; (B) Museum of the Rockies, Bozeman, MT; (C) New Mexico Museum of Natural History and Science, Albuquerque, NM; (D) Carter County Museum, Ekalaka, MT.

The ‘Ghost Method’

The technique that, in my opinion, best brings out the identity of the microvertebrate is what I refer to as the ‘ghost method’. In this style, the isolated fossil element is mounted or placed onto a surface where the silhouette of the rest of the animal’s body is illuminated, or the specimen is placed in a more dynamic 3D context with a simplified re-creation of the missing elements. This technique has been utilized with large partial fossil specimens (i.e. the 3D-printed *Nanuqsaurus* skull in the Perot Museum of Nature and Science in Dallas, TX (Fig. 21 F)), and its application to microvertebrates has seen interesting results. Perhaps the best examples of this technique with microvertebrates can be seen at the Sternberg Museum of Natural History’s display of fish fossils from the Cretaceous Western Interior Seaway (Fig. 21 A-E). This large panel-style display houses many fragmentary fossils of the menagerie of fish from the Late Cretaceous Niobrara Chalk (c. 80 Ma). Where the fish is not preserved, the rest of the body is illustrated with a large stylized wooden silhouette. Whereas many of these fish such as *Xiphactinus*, *Gillicus*, and *Protosphyraena*, maybe represented by nearly complete elements, the bottom of the display features the isolated teeth of the sharks *Onchopristis* and *Pseudomyledaphus*, which would be nearly invisible if not for the looming blue-green cardboard fantoms of the rest of their bodies (Fig. 21, B-D). This display makes clear to the audience the fact that these tiny fossils once belonged to hulking fish that a modern fisherman would dream of landing. The benefit of this method is that it illuminates the lost form of the fossil taxa, however, the silhouette of the animal may or may not take up quite a lot of horizontal or vertical space in the exhibition.

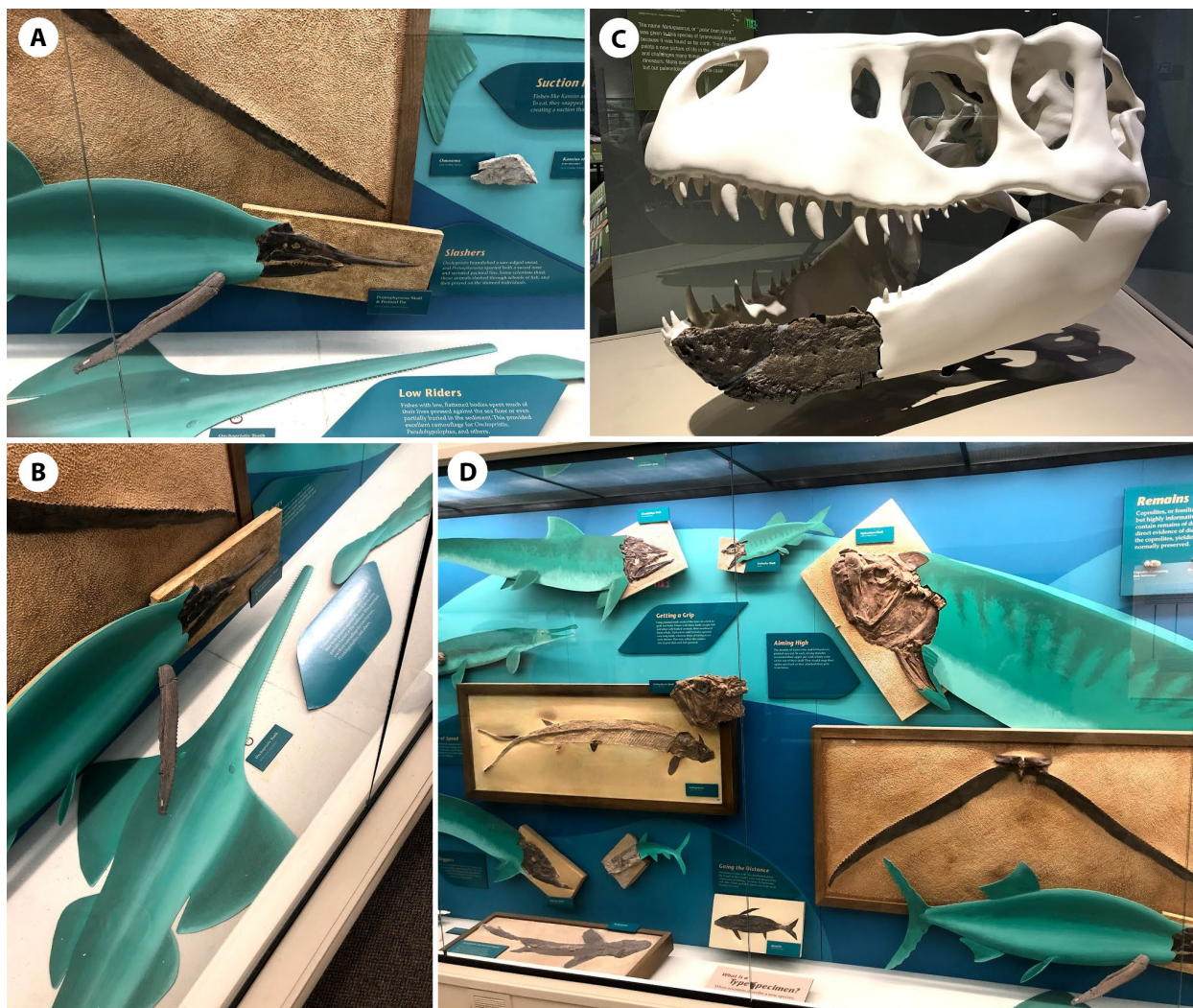


FIGURE 21. Examples of the vertebrate fossils displayed with the ‘ghost method’. (A, B, D) Sternberg Museum of Natural History, Hays, KS. (C) *Nanuqsaurus hoglundi* skull at the Perot Museum of Nature and Science, Dallas, TX (photo by Jonathan Cutrer).

THE ETHOS OF EXISTING DISPLAYS

Having examined these examples of microvertebrate fossils in museum galleries, I think it is worth considering what these displays communicate as they present these small specimens to the public. Generally, microvertebrates are used within paleontological museum exhibitions to supplement the displays dominated by larger and more charismatic fossil species. The thematic throughline of these exhibitions, is that these taxa are marginal organisms in their environment, eking out a living between the toes, hooves, and flippers of large dinosaurs, mammals, and marine reptiles. I think the two displays that best communicate just how marginalized these small and successful animals are in the museum landscape, can be seen at the North Dakota Heritage Center and State Museum and the Smithsonian's National Museum of Natural History. The North Dakota Heritage Center and State Museum's fossil hall (known as "Adaptation Gallery: Geologic Time") features the mounted skeleton casts of a *Triceratops* (a cast of the AMNH's composite skeleton) and a *Tyrannosaurus* (a cast of MOR 555/USNM 555000) elevated on platforms and facing off against one another (Fig. 22 A, B). On the sides of these elevated platforms (at the feet of these huge dinosaurs) are a series of isolated vertebrate, invertebrate, and plant fossils from the Hell Creek Formation of North Dakota in plexiglass displays (Fig. 22 C, E). These specimens include dinosaur, crocodylian, fish, and turtle bits which would be considered examples of microvertebrates. These specimens are mounted and elevated in their displays but given very little textual or visual context and they get visually lost in the cases amongst the larger dinosaur bones). At the feet of the mounted *Tyrannosaurus* is a small mounted skeleton replica of a *Didelphodon*, posed in a crouching position under the massive theropod (Fig. 22 D). The dominance of *Tyrannosaurus* and *Triceratops* in the exhibit, the obscurity of the microvertebrates in their displays, and the inclusion of the *Didelphodon*

covering at the feet of the *Tyrannosaurus* communicate to the museum visitor that the latest Cretaceous of North Dakota was a time solely dominated by large dinosaurs. Any smaller animals that might have inhabited the earth with them, existed helplessly at their feet, and the fossil record is dominated by large bones of *Triceratops* and *Tyrannosaurus*. Conversely, a similar visual paradigm can be seen at the Smithsonian's recently renovated "David H. Koch Hall of Fossils - *Deep Time*". The star attraction of this exhibition is the original skeleton of MOR 555/USNM 555000, this time posed decapitating another composite *Triceratops* cast (the "Hatcher" skeleton or USNM 4842) (Fig. 23 A). Next to the feeding theropod, a separate wing of the same platform stands a mounted skeleton cast of a large *Edmontosaurus*, which shares its enclosure with a sprinting *Thescelosaurus* and a sprawling *Champsosaurus* (Fig. 23 B). Next to the *Tyrannosaurus* is another mounted replica skeleton of *Didelphodon*, seemingly oblivious to the enormous predator gorging itself only a few feet away. While *Thescelosaurus*, *Champsosaurus*, and *Didelphodon* are all taxa that regularly appear in microvertebrate localities, the main microvertebrate display featured in this exhibit appears along the base of the platform on which these animals stand. A small window display houses an assortment of mounted and elevated microvertebrates from the Hell Creek Formation, each of which is annotated and depicted with a small line drawing of the animal they once belonged to (Fig. 23 D). To the left of the fossils are two textual planes. The first titles the display "Tiny Fossils Fill in Pieces of the Past" and explains the inclusion of these specimens with the following text "Small as they are, these microfossils from the Hell Creek Formation (66 million years ago) are packed with information about how animals lived and died in this ancient ecosystem. Fossils like these are so plentiful that paleontologists sometimes learn more from them than from larger or more complete skeletons." The second textual panel in the window is an excerpt written by the

Smithsonian's Curator of Dinosauria Dr. Mathew Carrano, "To learn about dinosaurs and their environments, I often head to the Judith River Formation in Montana. This rock layer records the lush floodplains that bordered an inland sea 80 to 74 million years ago. I work with geologists and other paleontologists to study the rocks and collect fossils. I'm especially interested in finding small fossils from many different species, so I can understand more about the whole ecosystem. With each trip, we learn something new." This display is among the most effective I have observed in terms of communicating the importance of microvertebrate fossils in our understanding of ancient ecology, but the specimens remain abstract, visually hard to appreciate, and the enormity of the dinosaurs on the platform above obscures the importance of these specimens. In the "Adaptation Gallery: Geologic Time", *Deep Time*, the *Prehistoric Journey*, and the *Albertosaurus* diorama of the RTMP, *Didelphodon* serves as the exemplary microvertebrate taxon: a small marginalized mammal, clawing out a meager existence between the dinosaur's toes.

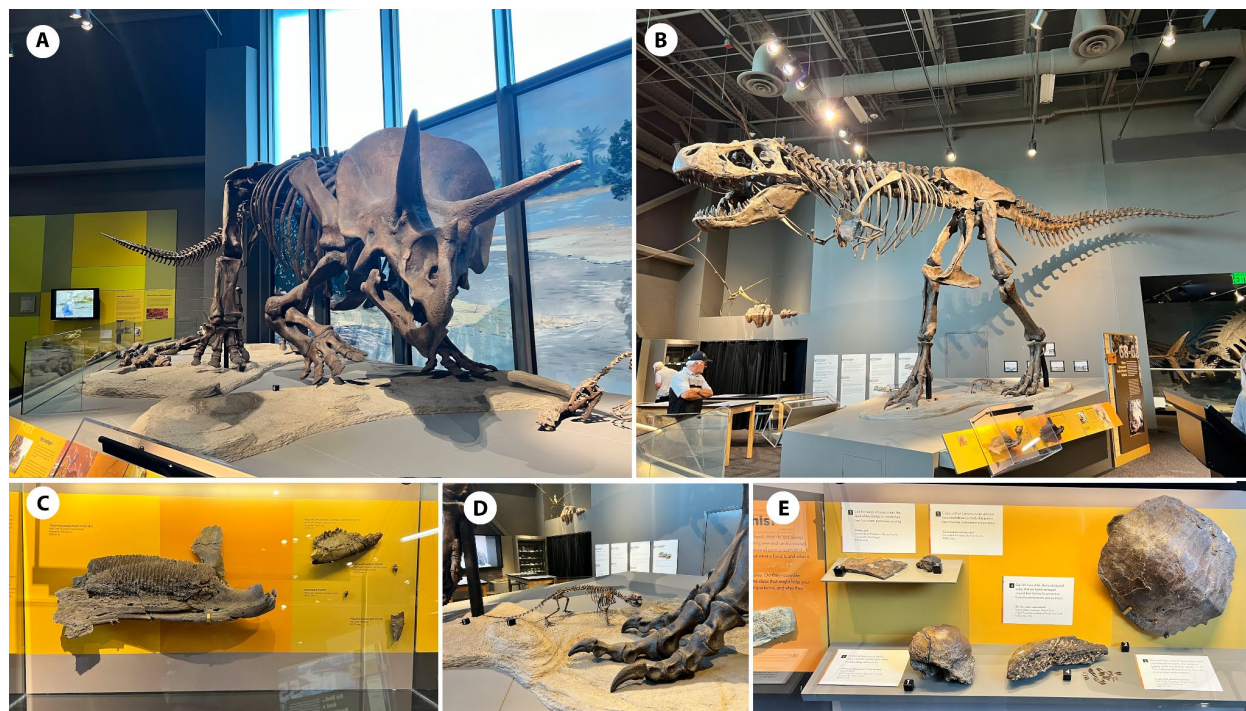


FIGURE 22. Hell Creek Formation displays at the “Adaptation Gallery: Geologic Time” in the North Dakota Heritage Center and State Museum, Bismarck, ND. (A) Mounted AMNH *Triceratops* cast. (B) Mounted cast of *Tyrannosaurus rex*. (C) Details of microvertebrate and isolated macrovertebrate fossils in plexiglass display under the mounted *Tyrannosaurus rex*. (D) Mounted replica skeleton of *Didelphodon vorax* under the mounted *Tyrannosaurus rex*. (E) Additional microvertebrate and isolated macrovertebrate fossils in plexiglass display under the mounted *Tyrannosaurus rex*.

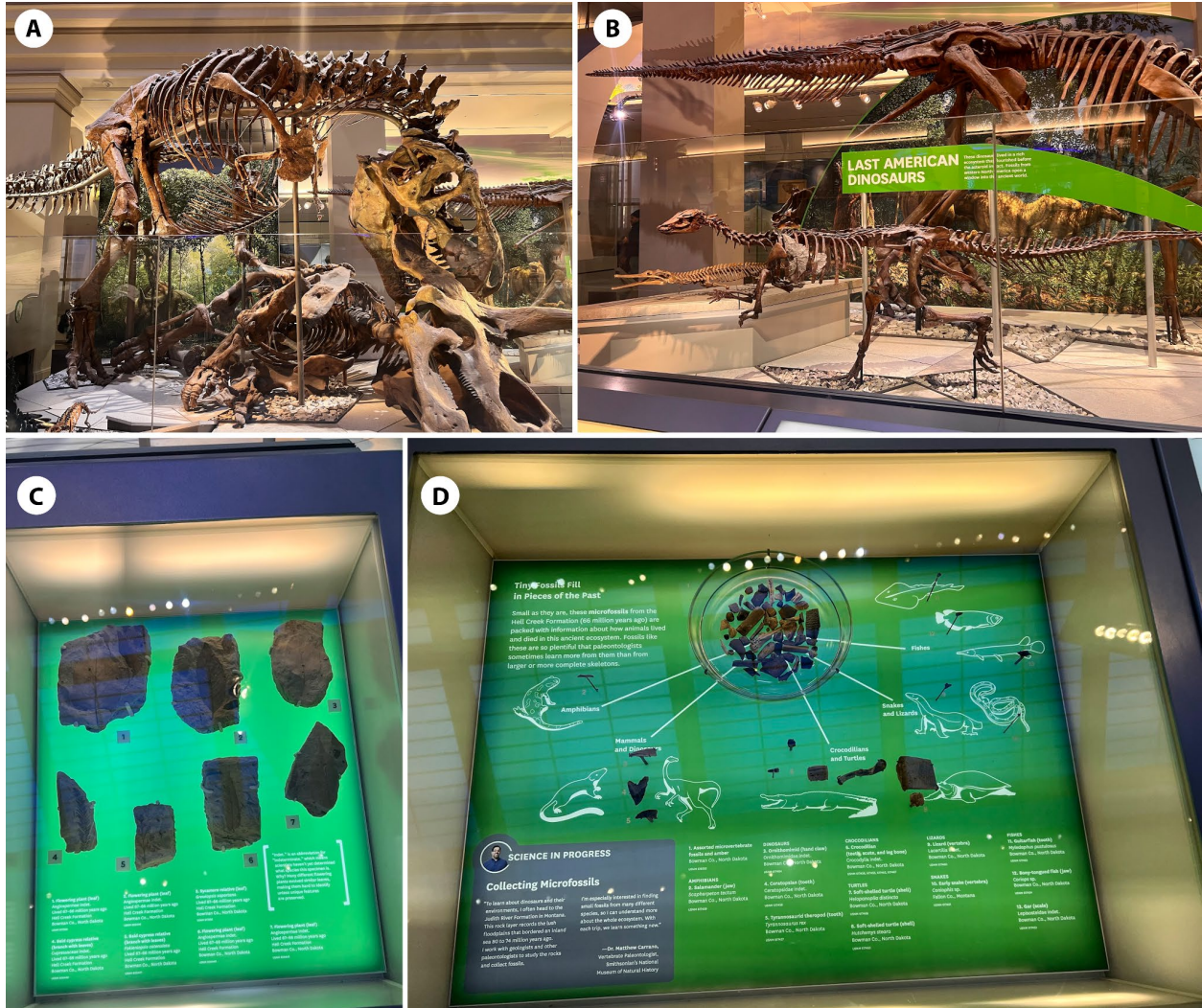


FIGURE 23. Hell Creek Formation display at the David H. Koch Hall of Fossils - *Deep Time* in the Smithsonian’s National Museum of Natural History, Washington, D. C. (A) mounted original *Tyrannosaurus rex* and replica *Triceratops horridus* skeletons. (B) Mounted casts of *Thescelosaurus neglectus*, *Champsosaurus laramiensis*, and *Edmontosaurus annectens*. (C) Associated display of planet fossils. (D) Associated display of microvertebrate fossils.

HOBBITS, HARKONNENS, & MEOW WOLVES: A MEDITATION ON WORLDBUILDING AS AN EXHIBITION APPROACH

Having come from a background in art and production design, I am inclined to ‘solve’ the ‘microvertebrate fossil problem’ and free these obscure taxa from the thematic tyranny of the large dinosaurs through the means of a visual and diegetic language, rather than one that exists primarily through textual interpretation. Like everything else in the material world, fossils are first known to us (humans) as visual objects, before they are conceptual entities that exist within the epistemological frameworks of science, deep time, geology, biology, paleontology, etc. Just as a trained art historian instantly recognizes the works of Van Gogh, Picasso, or Matisse, a paleontologist instantly recognizes the tooth of a mammoth, the vertebra of a champsosaur, or the scale of a gar via reflex and intuition, before the invocation of the geological periods which they are from. That being said, in my opinion these objects are essentially meaningless without the context of their broader ecosystems and geological periods. It is from this point, that I think the best way to credit microvertebrate fossils with the incredible data that they provide is to visually bring them back to life, and then return them to their lost world, within the gallery of the museum. Moving away from the raw scientific, I evoke three unlikely sources for lessons in constructing an intricate world with many nearly invisible details (which is essentially what any extinct ecosystem is). These perhaps unlikely sources are the writings of J. R. R. Tolkien and Frank Herbert and the installations of the American Arts company Meow Wolf (Fig. 24).

Within the fields of science fiction and fantasy writing, there exists a concept known as worldbuilding. According to the Merriam-Webster Dictionary, worldbuilding is defined as “the creation of a fictional world (especially within the science fiction and fantasy genres) that is believable and consistent within the context of the story”. This concept has been embraced by

authors, filmmakers, and roleplaying game enthusiasts as a technique for making a fictional setting more intricate and immersive for the reader, audience, or player. This definition is technically what museums do when rendering mounted dinosaur skeletons, dioramas, and life reconstructions of extinct organisms, in that exhibitions represent not the world as it existed millions of years ago, but rather it is a vision of what the earth and its ancient inhabitants might have been like as surmised from biological and geological data and imagined by human beings. As I stated in my undergraduate honors thesis ‘the dinosaur (as a modern piece of iconography) began and remains an artistic creation on the part of a bizarre species of bipedal primates that began their domination of the earth some 66 million years after the last non-avian dinosaur disappeared’. Worldbuilding, as it is usually thought of today, is largely an aesthetic or stylistic practice, but in the case of two prominent 20th-century fiction authors, this practice was crucial to the ethos and philosophies of their stories. In the museological literature, there is one study conducted by Burke & Tattersdill (2022), that analyzes paleontological museum exhibits from the perspective of science fiction and fantasy worldbuilding. The major difference between this study and my analysis regarding the use of worldbuilding lies in the fact that Burke & Tattersdill directed their analyses at exhibitions that are not based on or consistent with mainstream science, while mine sticks to the mainstream of paleontological sciences.

Museum Exhibitions as ‘Subcreations’

Though it might be strange to invoke the works of author and philologist J. R. R. Tolkien in the context of science and paleontology, I think that his approach to worldbuilding might be useful in regard to imagining a holistic museum exhibition, in two ways. (1) natural history museum exhibitions are ‘subcreations’ that are inspired by, but do not represent the ‘real world’. (2) The meticulous details of a work can be imperative to the immersion and ethos of a story if

utilized properly. Tolkien is perhaps best known for his fantasy works such as *The Hobbit* (1937) and *The Lord of the Rings* (1954-1955). These works, along with many other unpublished stories, take place on the fictional continent of Middle Earth in a world called Arda. This world is, to this day, considered one of the most intricate and well-realized fictional settings ever imagined. Tolkien populated Arda and Middle Earth with hundreds of languages, myths, species, characters, bloodlines, and an intricate cosmological origin. While this world and its characters are technically fictional, Tolkien did not write these stories as artificial entities, but rather an abstracted and mixed mythology of pre-Norman England (Hostetter & Smith, 1992). Middle Earth, its history, languages, and the larger cosmology of Arda, were not written as a plain creative exercise or as a theological allegory, but rather as a lost English mythology, fixed not within a traceable historical period, but rather existing “at a different stage in human imagination”, as Tolkien stated in a 1965 BBC interview with Denys Gueroult. Tolkien crafted his stories within the framework of himself as a sub-creator (a sort of curator of a pre-established creation) (Del Rincón Yohn, 2021). In a way, paleontological museum exhibits do the inverse of this style of worldbuilding. Prehistoric life in the museum gallery is presented as an attempt to render the world as it existed, through the perspective of the modern human mind. Though this style is true to the nature of science, any depiction of Earth’s deep past is simply a guess. This fact is not anything for museums and their staff to be ashamed of, but it is the reality of any exhibition. Drawing from Tolkien’s notions of the nature of art, I think that a good museum exhibition about microvertebrate fossils and the information that they provide to scientists should make clear in both its displays and signage, that what the museum visitors see before them is a ‘best guess’ or hypothesis of what the inhabitants of the ancient earth and their ecosystems were like, based on fossil evidence and comparative zoology, rather than a definitive rendering. This

may take the form of displays regarding comparative anatomy, uniformitarianism, or a visual progression of how inferences about the ancient earth can be made from our knowledge of the modern world. The deductive process must be shown to make it clear how we modern humans know what we know about periods that are lost to us, and how science is a process rather than a body of knowledge. Additionally, drawing from Tolkien's incredible pension for details, any museum exhibition that is devoted to microvertebrate fossils must be obsessive about the details of the display. Rather than side-characters in the story of the mammals and dinosaurs, these taxa must be communicated as important species with rich evolutionary histories, ecological interactions, and connections to our present ecosystems. In short, microvertebrates, their homes, and the important scientific data they represent must be treated like the cultures, histories, and characters of Tolkien's beloved Middle Earth.

A Process Cannot Be Understood by Stopping It

In a similar vein of highly detailed worldbuilding inspired by external scholarship, Frank Herbert's 1965 novel *Dune* was inspired not by a need to predict a future for humanity, but rather as a kind of excuse to explore the role of ecology in the shaping of human cultures. Herbert's inspiration for *Dune* came not from an obvious source such as the Space Race or Islamic history, but rather from his fascination with and study of sand dunes (Scharping, 2024; Gaspar De Freitas). Within the story of *Dune*, the planet Arrakis and its inhabitants work as metaphors for the ways that nature shapes the sensibilities, politics, and spirituality of human cultures. Perhaps the single most poignant quote from this novel, and the one that best exemplifies Herbert's notions about the fluid nature of life, evolution, and the relationship of human beings to the rest of the universe can be found with the First Law of Mentat (a kind of human-computer in Hebert's fictional universe). As stated on page 50 of the 2010 Ace Premium Edition "A process

cannot be understood by stopping it. Understanding must move with the flow of the process, must join it and flow with it.” This law is emblematic of the ethos of *Dune*, and I think that this sentiment applies to both a fictional story set in 10191 AG (approximately 20000 AD) and a hypothetical artistic recreation of an ecosystem from 72000000 BC. Like Tolkien, Herbert filled *Dune* with a vast attention to detail regarding the history, cultures, politics, and conflicts of the fictional Imperium for the sake of the reader’s immersion, but this obsessive detail is, in a way, the point of the story. Herbert’s themes of life as a fluid entity, which cannot be understood by rendering it static, are perfectly applicable to our understanding of geology, paleoecology, and evolution. A good microvertebrate fossil exhibit should make it clear that the fossils and the taxa they represent do not and did not exist in a void, but rather were fluid and ever-evolving elements in an equally fluid environment. Microvertebrate taxa like fish, turtles, and crocodylians can be used to track environmental changes over time, and mammals are key taxa in the biostratigraphic record of terrestrial ecosystems. Taking a page from the philosophy of Herbert and his science fiction epic, to best represent microvertebrates and the information that they yield to paleontologists, the dynamic nature of these taxa and the environments they lived in must be represented.

Contextual Learning at *Convergence Station*

Within the field of modern museum education, the prevailing educational model that has been embraced by museum professionals is that of contextual learning. The museological contextual learning model was pioneered by Falk and Dierking in their 2000 work *Learning from Museums: Visitor Experiences and the Making of Meaning*. The contextual learning model asserts that museum audiences learn via stimuli that resonate with them at physical, sociocultural, and personal levels. The museum exhibition or educator must engage their

audience from the orientation of one or more of these contexts, that way the audience member may resonate with the museum's interpretation from a phenomenological level. Falk and Dierking's philosophy behind this model is derived from constructivist notions of epistemology, which assert that learners construct knowledge from experience, rather than passively take it in (Yager, 1991).

Though I see the utility of this method and the need to create a sense of relatability for museum audiences in an exhibition, the contextual learning model is a difficult thing to utilize in the face of paleontological displays. Dinosaurs (and related subject matter) are inherently alien to us modern humans. No person today has ever laid eyes on a living non-avian dinosaur, nor could they as they existed many millions of years before modern humans. Additionally, paleontology is such an interdisciplinary subject matter, that it is nearly impossible to invoke fossils in a museum setting, without providing some context via geology, biology, or the complex history of the science. It is for this very reason that I, personally, hesitate to encourage the utilization of paleontology in K12 curricula because an understanding of paleontology requires an understanding of so many other topics. These topics may not be relevant to the average person's life, and the sheer amount of time separating a museum visitor's life and a given fossil specimen is usually a number that their mind literally cannot comprehend. In short, dinosaurs (and other extinct animals) often do not fit into the context of our lives and are perhaps too alien to fit into the contextual learning model. In the face of this challenge, perhaps the familiar should be rejected in favor of the alien. In the case of art, the novel or alien can be just as compelling (if not at times more so) as the familiar. The appeal of artists like Salvador Dalí, René Magritte, H. R. Giger, and C. M. Koseman is their invocation of the surreal, the uncomfortable, and the unknown. One of the most interesting examples of surrealist art installation, with a massive

following and cultural appeal, is that of the American entertainment company Meow Wolf. Meow Wolf stands as a unique kind of commercialized art experience, in that it appeals to younger visitors, but it presents a vibrant and at times, uncomfortably alien immersive gallery experience (so much so that Meow Wolf provides sensory guides and supplies for visitors who are subject to overstimulation). The largest of Meow Wolf's five galleries is *Convergence Station* in Denver, CO. This 90,000-square-foot facility is styled as a sort of interdimensional train station, in which visitors can move in between portals to four different alien worlds (Brando, 2022). There is a considerable amount of worldbuilding at play at *Convergence Station*, with detailed settings completed with fictional languages, advertisements for extraterrestrial products, and several cryptic mythological motifs across the installation. The creatives behind *Convergence Station* wrote an in-universe backstory to the display, which can be read in three guidebooks available at the *Convergence Station* gift shop. These guidebooks, titled *The Quantum Transportation Department: Celebrating 50,000 Years of Travel*, *Me'ekap's Myths of Convergence*, and the *Tome of Forgetting* provide the visitor with the backstory to the locations, alien cultures, and symbolism seen throughout the neon-lit landscapes, but these are supplementary materials that must be purchased, rather than part of the experience of Meow Wolf's galleries. Entering with little mental preparation, the visitor is greeted with a barrage of bizarre visuals and sounds. The novelty of Meow Wolf is just how alien its galleries are, and how little it prepares its visitors for such an experience. Should the visitor demand to understand what is being presented in front of them, they can research *Convergence Station* and its alien worlds, but to be immersed in the surrealist landscapes and simply accept that one does not understand what they are seeing is perhaps the best way to experience Meow Wolf.

My takeaway from the immersion and surrealism of Meow Wolf and its *Convergence Station* is not that paleontological museums should limit the context of their displays for the sake of novelty, but rather that museums should lean into the alien when presenting alien subject matter in the face of a lack of relatability to the lives of modern humans. Animals such as those of the Ediacaran biota (Proterozoic Era), Chengjiang biota (Cambrian Period), Burgess Shale (Cambrian Period), and even the modern deep oceans are far weirder than any of the imaginary creations seen in Meow Wolf's galleries. Organisms like *Anomalocaris* (a marine arthropod with segmented arms on its head from the Cambrian Period), *Tullymonstrum* (a mysterious animal with stalked eyes and a proboscis from the Pennsylvanian Period), and *Vetulicola* (an eye-less filter-feeding chordate from the Cambrian) are difficult to explain to museum audiences and difficult to imagine being real inhabitants of our own Earth. In this regard, I think an idealized microvertebrate fossil display could take a page from Meow Wolf and display the weird and wonderful lifeforms and landscapes of the creatures without explaining everything to the audience at first blush (this can always be done later in the sequence of the display via signage or other forms of interpretation). There is something to be said about explaining that Colorado was once lush, humid and partially covered in an inland sea during the end of the Cretaceous Period via text and diagrams, but it is another thing to address the audience with a statement like "here is your backyard...68 million years ago" and reveal a scene of a dense *Taxodium* (bald cypress) swamp, populated by sharks with horns, coffee table-sized turtles, 6ft-long carnivorous lizards, dragon-like pachycephalosaurids, and pterosaurs as tall as a modern giraffe. Regardless of how this scene resonates with audiences on a physical, sociocultural, or personal level, this is what the world was like when ReBecca's Hollow was deposited. The explanation for how we can reconstruct this scene could come later in the sequence of the display, but it should be clear to

the visitors of the exhibit, that the Mesozoic Era, while intricately part of our earth and connected to our own lives, would have been alien to any human time traveler. It is this weirdness and this rejection of a need for immediate context, that I would embrace in a microvertebrate fossil display.



FIGURE 24. Diagram of lessons learned from examples of wordbuilding in popular media. Tolkien’s notion of ‘subcreation’ (lower left), Herbert’s notion of fluid systems (lower right), and Meow Wolf’s utilization of a lack of context (upper center) converge on a hypothetical ReBecca’s Hollow exhibition (center). The throughline of these examples is a utilization of obsessive detail, which is imperative for selling the realism and immersion of a ‘sub-created’ world.

REBECCA'S HOLLOW FROM THE GROUND (OR TEETH) UP

Using these lessons from what I consider to be extremely interesting examples of worldbuilding from popular media, I propose a hypothetical museum exhibition about ReBecca's Hollow and its vertebrate life that will utilize the following lessons from Tolkien, Herbert, and Meow Wolf. (1) This work will regard itself as a subcreation and will be explained as a 'best guess' about what the Williams Fork Formation was like using available geological, paleontological, and paleoclimatic data. (2) ReBecca's Hollow (like any other paleontological site) is not a monolith, but a fluid ecosystem, full of relationships between lifeforms, deep evolutionary histories, and the ever-changing surface of the earth. (3) The bizarreness of the organisms and the fact that they are represented by nearly microscopic fragments will be embraced and put first before too much explanation or interpretation. (4) obsessive detail is imperative to both the immersion and the narrative of the exhibition (Fig. 24). Now that these rules have been established, it is essential to find a way to do justice to the microvertebrate fossils in the display. To solve this issue, I propose a five-step visual solution that would act as a kind of resurrection of each microvertebrate taxa presented in the display (Fig. 25). For the sake of simplicity, and space, let us imagine that the representative animals in the display are *Melivius* (a bony fish), *Adocus* (a turtle), *Opisthotriton* (a salamander), an alligatoroid, a multituberculate mammal, *Saurornitholestes* (a theropod dinosaur), and *Meristodonoides* (a shark). Each taxon would be featured in a display case (these animals could share a large case or be featured in their own separate vitrines). The display would feature a tiny mounted example of a real fossil from the animal (perhaps a tooth or bone). This example of mounted microvertebrates could incorporate microscopy, if needed, to allow the specimens to be better seen by the audience. Next to the tiny specimen in the display would be an enlarged 3D-printed version of the same

specimen. This larger copy would allow the unique geometry and texture of the fossil to be better seen by the museum visitors. Next to the enlarged fossil replica, would be a 1:1 scale replica of the completed fossil element from which the real fossil originates. This completed element could be a skull, vertebrae, or shell, depending on the vertebrate. The region of the completed replica, which the original fossil specimen represents, would be colored or highlighted using the 'ghost method'. Finally, the display would feature a highly detailed and hyper-realistic life reconstruction of the animal next to all of these elements. This life reconstruction would have to be included elsewhere in the context of its ancient environment, rendered as a large mural or diorama of the swampy ReBecca's Hollow (Fig. 26). In this visual system, the fossil is quite literally explained before the audience's eyes in terms of what it is, what it once belonged to, and why that animal is important in terms of human understanding of life on Earth. This display would utilize a directionality, in which the eye of the visitors moves from the fossil element to the life reconstruction of the organism in that sequence, or vice versa. These displays would either surround, or gesture to the scene of the entire ecosystem of ReBecca's Hollow, filled with swimming fish, crawling lizards, and large dinosaurs looming in the distance (Fig. 27). The ecological relationships of the various vertebrates would be depicted via their position in the scene or their physical interaction with one another. For instance, the inclusion of a toothy *Melvius* snatching a smaller fish, or even a tetrapod, would clearly articulate that this species is among the top aquatic predators in this ecosystem. Regardless of the larger display being rendered in the form of a three-dimensional diorama or a large mural, the texture and atmosphere of the environment would need to be communicated visually. The humidity of the Williams Fork swamp, the age and girth of the trees, the texture of the mud around the water, and the sliminess of the fish would need to pop to sell the fact that ReBecca's Hollow was a real living ecosystem.

The signage and textual content around the scene and the reconstructed microvertebrates would make it clear that this intricate and vibrant image in front of the audience is entirely informed from the tiny remains of bizarre swamp-dwelling organisms, rather than giant dinosaur bones. This method utilizes the immersion and environmental context of dioramas and life reconstructions, the visual novelty and attention to the fossil specimen seen in ‘elevated’ microvertebrate displays, and finally the anatomical context of the ‘ghost method’ to fully flesh out the microvertebrate taxa and brief artistic life back into these 72-million-year-old specimens. Using this system, a fragmentary tooth can be returned to the toothy meter-long *Melvius* (complete with flaring gills and vacant glassy eyes), the adorable wiggly *Opisthotriton*, and the fearsome bird-like *Saurornitholestes*. A simplified version of this display method, which took the form of a series of outreach kits was adapted by the University of Colorado Museum of Natural History in Spring of 2022. This project is discussed and figured in the Appendix of this thesis and could serve as a kind of trial run for this display method once the museum obtains frontend data from its educational performance.

This hypothetical ReBecca’s Hollow display makes use of what works with existing examples in natural history and science museums and the lessons I provided from my meditation on the use of worldbuilding in this context. This exhibit is proud to call itself a ‘subcreation’, it denotes a network of fluid geological and biological systems, it embraces its alien inhabitants, and it is detail-obsessed to articulate how tiny unassuming fossils like those at ReBecca’s Hollow allow humans to peer into versions of our earth that we will never get to visit. The material costs and logistics of this exhibition will not be calculated in this thesis for the sake of brevity. The museological landscape features hundreds of examples of large dinosaur skeletons posed in a sort of void of space and time. This matter of context is exactly the issue that this proposed

exhibition tries to avoid. Though *Melvius*, *Adocus*, and *Opisthotriton* will never be able to compete with *Tyrannosaurus rex* in terms of popularity or museum exhibition real estate, in my humble opinion, they are absolutely more valuable than their larger contemporary in informing scientists about the nature of the ancient Earth, and it is with this proposed exhibit that I hope they finally receive their just rewards.

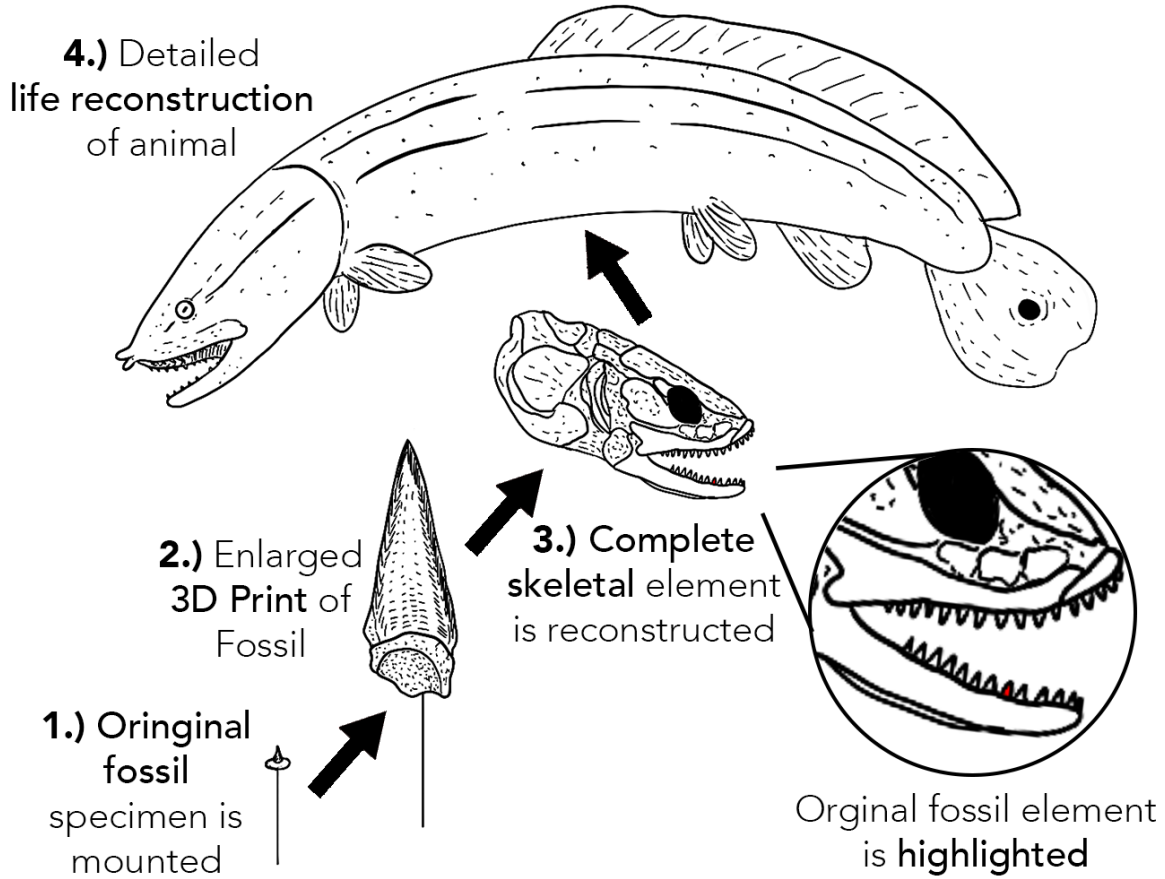


FIGURE 25. Proposed model of representing microvertebrate taxa in ReBecca’s Hollow exhibition with a *Melvius* fish. This visual method features a mounted original fossil, an enlarged 3D-printed replica of the fossil, a reconstruction of a complete skeletal element (the area that the fossil represents is highlighted), and a life reconstruction of the fossil taxa.



FIGURE 26. Proposed mural or diorama of ReBecca's Hollow ecosystem. Featured on poster presented at the Society of Vertebrate Paleontology's annual meeting by Crothers et al. (2024).

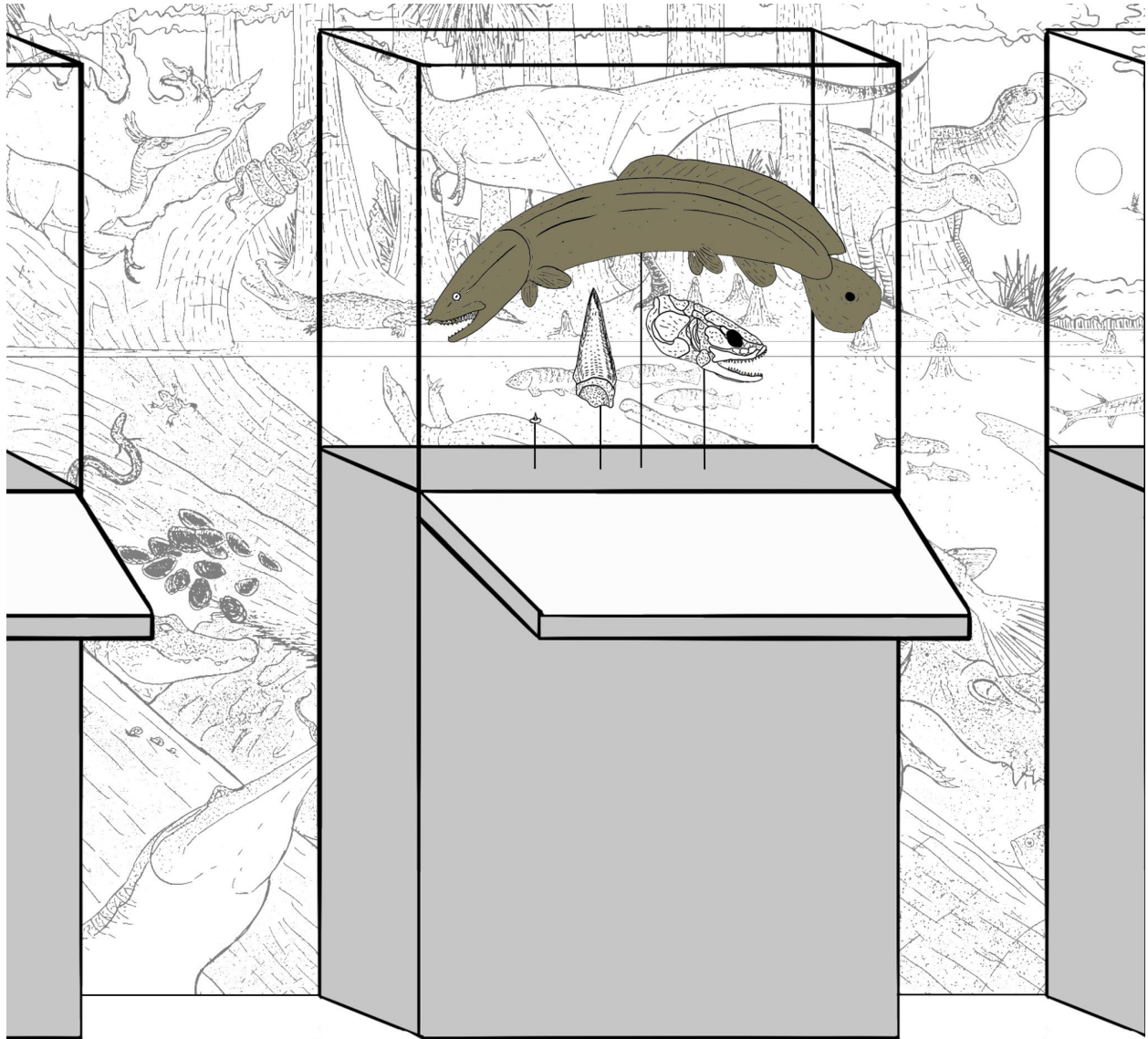


FIGURE 27. Proposed vitrine display of microvertebrate taxa at ReBecca's Hollow display, surrounding or backdropped by the mural or diorama of the ecosystem.

CONCLUDING REMARKS

As the science of vertebrate paleontology progresses, and the social and material landscape of museums adjusts to changes in human societies, paleontological exhibitions will be forced to reinvent themselves at a pace that is slower than both of these forces. One of the reasons why I embrace Tolkien's subcreation notion regarding paleoart, museum exhibits, and the associated text around these media forms, is because they will ultimately become outdated as more discoveries are made and analytic techniques are developed. Science is not a body of knowledge, but rather a process by which we make inferences about our very ancient world. Within this series of shifting landscapes, there remains a comforting constant: even the smallest and most unassuming sources of information will continue to yield groundbreaking discoveries. Microvertebrate fossil assemblages remain one of our most robust tethers to the Mesozoic Era, and they continue to provide tantalizing insight into the origins of the modern world as we know it today. I hope that by providing this thought experiment of an exhibition that is solely devoted to these important little bones and the information they provide paleontologists, perhaps they will receive more attention from the museological community. Though dinosaurs will continue to remain the star attractions in museum displays, it is between their toes that the answers to many of our questions regarding deep time lie.

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APPENDICES

APPENDIX A:

PALEOCLIMATE KITS

During the fall semester of 2024 and the spring semester of 2025, the University of Colorado Museum of Natural History's Education Section designed and constructed a series of outreach kits for K12 classrooms, which utilized some of the exhibit methods proposed in the second part of this thesis. This project was titled *Journey Through Time: A Paleoclimate Investigation*, and these kits were given to 18 K12 schools in the San Luis Valley of Southern Colorado in February of 2025. These kits were designed for and given to 6th through 11th grade classrooms and were meant to introduce students to various facets of paleoclimate data and the ways that sciences make inferences about the Earth's past from the field of geology. One of the components of these kits was a series of enlarged 3D prints of microvertebrate fossils specimens from the collections of the Colorado Museum of Natural History.

The ethos behind this component of the kits was for students to adopt a sense of comparative anatomy and uniformitarianism (comparisons of modern animals and environments with those preserved in the rock record). This activity was oriented towards the "hothouse" conditions that North America endured during the late Mesozoic and early Cenozoic Eras. In the kits was a collection of replica fossil specimens from the Rocky Mountain region, which represented relatives of organisms that are relegated to warm and humid areas of the US in the present day. These fossils were paired with images and additional replicas of modern animal skulls, which are close cousins of the fossil taxa. The students would first be introduced to the modern counterparts of these fossils, the areas and climatic conditions in which they live today and then would be asked to make inferences about the nature of the American interior as it existed during

the Cretaceous and Paleogene Periods. The logical inference that should be made about the Rocky Mountain Region (which is currently arid and seasonally volatile) is that it was once wet and humid, as it preserves fossils of aquatic warm water animals like alligators and siren salamanders. Like the proposed ReBecca's Hollow exhibit, the modern skeletal elements were painted in a manner that would highlight the region of the body that the fossils counterpart represented.

For this project, I 3D surface scanned a lachrymomaxilla bone of a lepisosteid (UCM 43534) from the Cretaceous/Paleocene Bug Creek Anthills of Montana, a *Habrosaurus dilatus* trunk vertebra (UCM 43428) from the Cretaceous/Paleocene Bug Creek Anthills of Montana, and a crocodylian articular bone (UCM 63350) from the Paleocene Denver Formation of Colorado. In addition to these fossil specimens, a modern juvenile alligator (*Alligator mississippiensis*) skull and lower jaw and a modern gar (*Lepisosteus* sp.) skull and lower jaw were scanned with the same methods. These scans were exported as OBJ files and sent to the University of Colorado College of Engineering and Applied Sciences' "Idea Forge" workshop, where they were 3D printed with PLA (Polylactic Acid) filament on Prusa MK4 3D Printers. The finished prints were freed of their supports, painted with acrylic paints, and primed with a clear spray-on polyurethane coating.

These specimens were scanned using the Abound-3D Scanner (formerly Metascan) software on an iPhone 13 Pro Max. Abound utilizes the built-in LiDAR hardware in iPhones, starting with the 13th generation onwards, and efficiently combines it with photogrammetric information to quickly render a 3D mesh within a few minutes. The scanning of the smaller of these specimens was aided with a clip-on Apexal Macrolens, which was attached to the iPhone's camera. The 3D

data from these scans will be available upon request at the University of Colorado Museum of Natural History's MorphoSource page upon the publication of this thesis.

Frontend evaluation data on the success of these kits in a classroom setting is still pending, as they were sent to their classrooms only a few weeks before the completion of this thesis, but their effectiveness will likely provide important data on the educational success or shortcomings of the methods which I propose in my imagined ReBecca's Hollow exhibit. Below, I provide the list of materials that were used in this project and the cost of each of these tools for the use and benefit of other institutions.

APPENDIX TABLE I

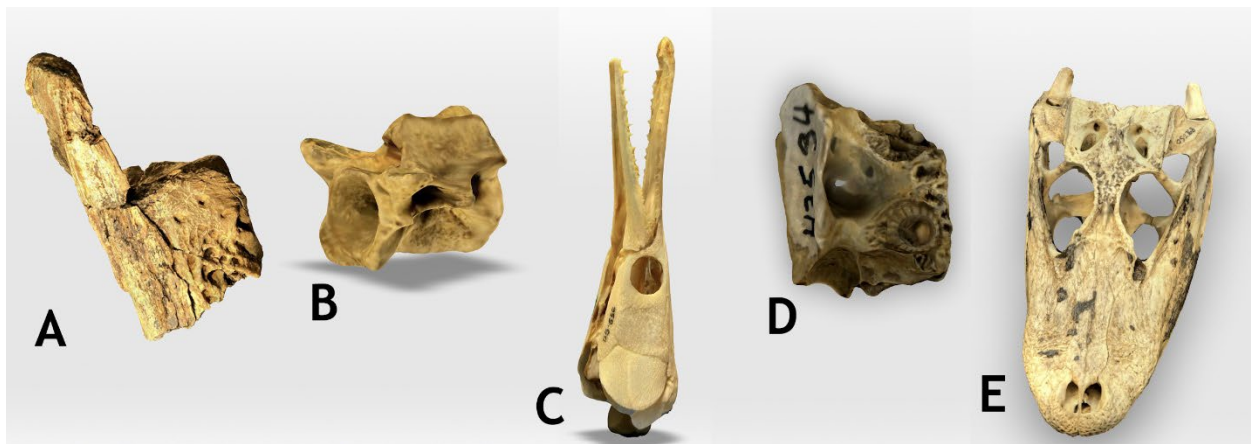
LIST OF MATERIALS FOR PALEOCLIMATE KITS

Materials	Cost
iPhone 13 (or later generation)	\$300-\$1200
Apexel Macrolens	\$37.98
Ringlight (clip-on)	\$9.99
Rotating Swivel Stand	\$11.99
Abound-3D Scanning Pro Subscription	\$6.67 a month
Original Prusa MK4S 3D Printer	\$999
OVERTURE PLA Filament 1.75mm (1kg)	\$16.99 (\$0.48 an ounce)

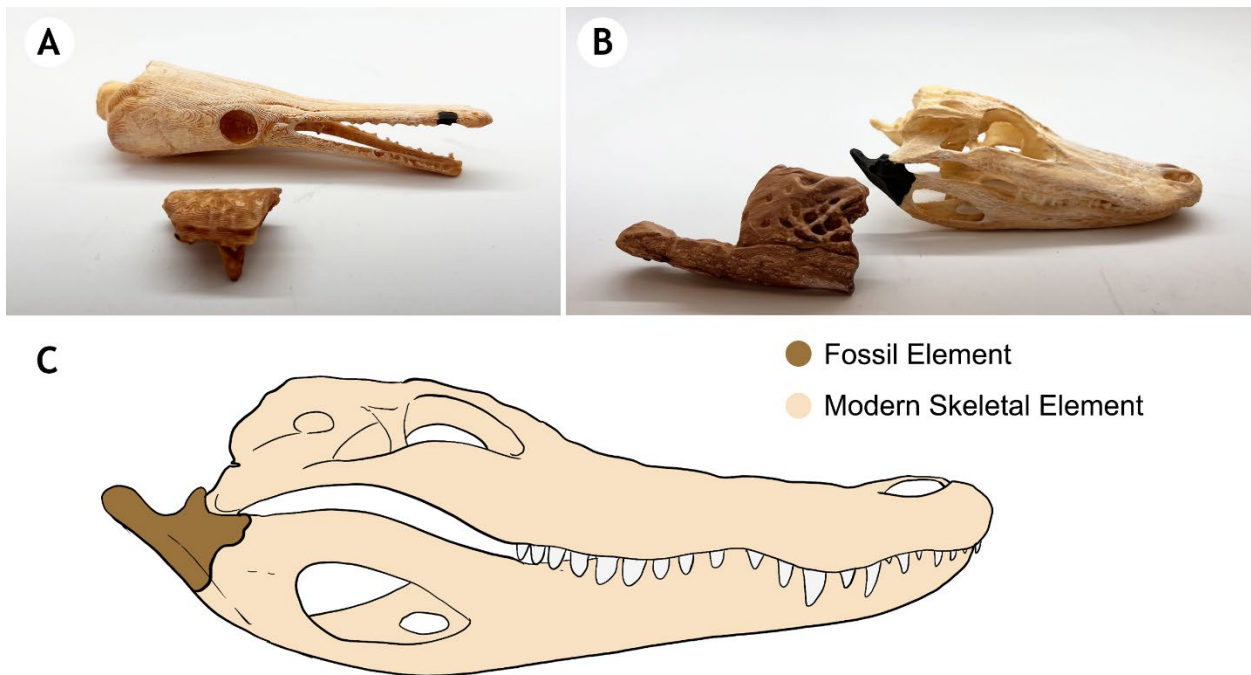
FIGURES OF PALEOCLIMATE KITS



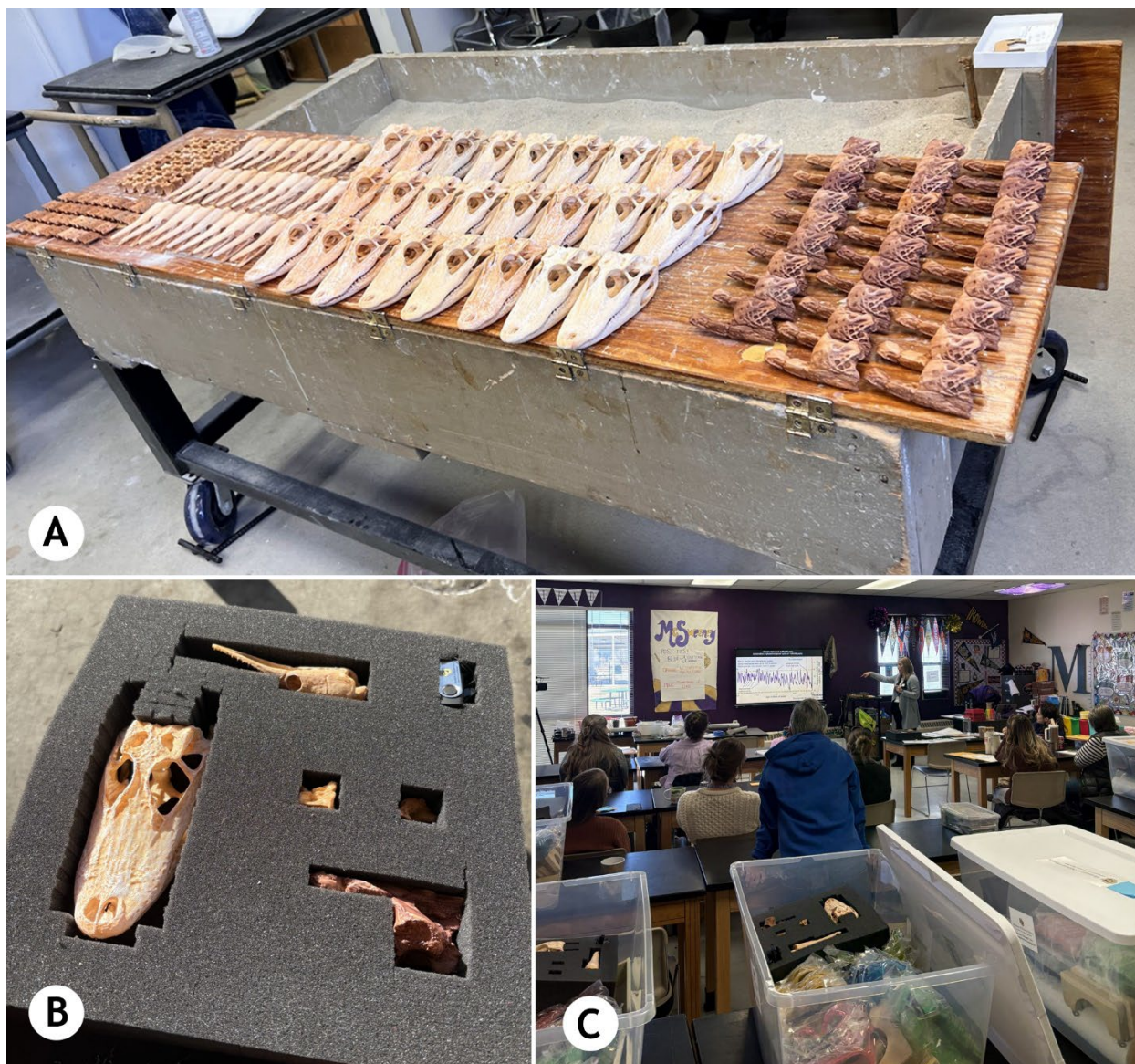
APPENDIX FIGURE 1. Fossils specimens that were 3D scanned for *A Journey Through Time: A Paleoclimate Investigation*. (A) UCM 43534, a lachrymomaxilla bone of a lepisosteid. (B) UCM 43428, a trunk vertebra of *Habrosaurus dilates*. (C) UCM 63350, a crocodylian articular bone. (D) UCM TC I-5, a modern *Lepisosteus* sp. skull. (E) UCM OS 2768, a modern juvenile *Alligator mississippiensis* skull. Scale bar in centimeters.



APPENDIX FIGURE 2. 3D scans of fossil specimens (captured via Abound-3D Scanning on an iPhone 13 Pro Max). (A) UCM 63350. (B) UCM 43428. (C) UCM TC I-5. (D) UCM 43534. (E) UCM OS 2768.



APPENDIX FIGURE 3. Completed 3D prints for Paleoclimate kits. (A) Associated gar skull bones. (B) Associated alligator skull bones. (C) Diagram of where the fossil element is highlighted on the completed skull print.



APPENDIX FIGURE 4. Completed fossil kits. (A) Finished 3D prints after painting and priming. (B) Storage container for paleoclimate kits. (C) Completed paleoclimate kits with 3D printed fossils and modern bones in a Colorado classroom.