Vertebrate Anatomy Morphology Palaeontology 13:98–139
ISSN 2292-1389

# A marginal marine fauna from the upper Dinosaur Park Formation, Canada

Luke E. Nelson[1,*], Joshua A. Doyon[1], Alison M. Murray[1], Donald B. Brinkman[1,2], and Robert B. Holmes[3]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; lenelson@ualberta.ca; jdoyon@ualberta.ca; ammurray@ualberta.ca
[2]Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0Y 0Y0, Canada; don.brinkman@gov.ab.ca
[3]Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; holmes19501950@gmail.com

**Abstract:** During the Late Cretaceous, the coastline of the epicontinental Western Interior Seaway in North America fluctuated in position, temporarily replacing some terrestrial ecosystems with shallow marine habitats. In southeastern Alberta, the uppermost portion of the Dinosaur Park Formation (Belly River Group, late Campanian) preserves one of these transgression–regression cycles in a marine wedge named here as the Johnson Unit. We report the stratigraphy of the unit based on nine stratigraphic sections over several kilometres of exposure. We describe a diverse assemblage of marine vertebrates from the Johnson Unit, represented by microfossils from a surface collecting survey. Our sample includes 1431 specimens, which we assign to 40 taxa. We identify eight new actinopterygians from the unit: *Belonostomus longirostris*, Amiidae indet., Elopiformes indet., *Horseshoeichthys* sp., *Enchodus gladiolus*, *Dercetis* cf. *D. magnificus*, Acanthomorpha indet., and teleost indet. type O. The acanthomorph specimens, which include isolated spines and centra, represent the second marine Cretaceous acanthomorph reported from Alberta, and the highly ornamented spines are unlike any previously described. We revise several chondrichthyan identifications from previous authors and describe partial tooth plates from the chimaeriform *Ischyodus bifurcatus* for the first time in Canada. Compared to earlier samples from the same unit that were collected using screen-washing, our sample has a higher diversity of actinopterygians and tetrapods. We identify several taxa to lower taxonomic levels using more complete specimens. These differences are attributed to our use of surface collection; this method allowed novel biogeographic and taxonomic insights.

## INTRODUCTION

The Western Interior Seaway (WIS) was an epicontinental sea which covered much of central North America for long periods of time during the Cretaceous (Smith et al. 1994). Over the course of its history, the coastline of the WIS underwent a series of transgressions and regressions (Kauffman and Caldwell 1993). In parts of western Canada, this resulted in a series of paralic deposits from local transitions between terrestrial and marine environments. These local environmental changes affected the corresponding faunal assemblages within the areas now surrounding Dinosaur Provincial Park, Alberta, which are documented by vertebrate microfossil assemblages (Brinkman 1987, 1990; Oreska and Cerrano 2019).

The Belly River Group of southern Alberta and Saskatchewan (equivalent to the Judith River and Two Medicine formations of Montana) is a wedge-shaped unit of eastward-thinning clastic rock (Eberth 2024). The wedge is bounded by marine formations: the Pakowki (Lea Park) Formation lies below it (Cullen et al. 2016), and the Bearpaw Formation lies above (Eberth and Hamblin 1993). Within the Belly River Group, the Dinosaur Park Formation (DPFm) is a primarily fluvial deposit that is notable for its high quality of preservation of vertebrate fossils (Eberth and Hamblin 1993). The DPFm is the uppermost portion of the Belly River wedge in Alberta and Saskatchewan, and was deposited in coastal floodplains along the west coast of the WIS (Eberth 2005).

Published December 22, 2025
submitted July 15, 2025; revisions received December 1, 2025; accepted December 5, 2025.
*corresponding author. Handling editor: Jordan Mallon. DOI 10.18435/vamp29410

At the top of the DPFm in Southern Alberta lies a distinct coal layer, known as the Lethbridge Coal, which was formed from extensive wetlands along the margin of the transgressing Western Interior Seaway (Koster et al. 1987; Eberth 2005). The section of the DPFm including and above this coal layer is known as the Lethbridge Coal Zone (LCZ; Eberth and Hamblin 1993). Since the seaway underwent multiple higher-order sea-level cycles during deposition of this zone, both marine and fluvial deposits alternate within the LCZ (Eberth 1996; Brinkman et al. 2005). Some of the fine-grained marine deposits were formed from mud-filled incised valleys (MFIVs; Eberth 1996, 2005). These formed after the seaway flooded areas with existing incised fluvial channels, which were then filled with fine-grained sediments from the brackish or marine waters. Although the LCZ contains fully marine beds, these are not grouped within the overlying marine Bearpaw Formation because the uppermost layer of the LCZ is non-marine; the top of the Dinosaur Park Formation is identified as the last non-marine bed (Eberth and Hamblin 1993).

In the area immediately to the east of Dinosaur Provincial Park, in the Red Deer River valley, a 6 m mudstone unit within the LCZ contains a high abundance of microfossils (Brinkman et al. 2005). Dinoflagellate diversity from this unit indicates a marine depositional environment (Brinkman et al. 2005). This unit lacked a name in previous works, so here we name this layer the Johnson Unit. We detail the geology of this section below. This name is in recognition of the Johnson ranch, which includes most of the study area. Several generations of the Johnson family have encouraged palaeontological research in the area; family members assisted the Sternbergs with their research in the region in the early part of the 20th century. The Johnson Unit is equivalent to the 6 m marine layer which Brinkman et al. (2005:fig. 26.1) figured as "Vertebrate Bearing Shales". Microfossil screen-washed samples from a layer near the bottom of the unit were described by Beavan and Russell (1999) from locality BB96, and Brinkman et al. (2005) from locality L2377. The unit was deposited under shallow marine conditions (Beavan and Russell 1999) and thus offers an opportunity to compare its fauna with the terrestrial environments in the older layers of the DPFm and the open marine environments of the younger Bearpaw Formation. Near-contemporaneous coastal assemblages from the uppermost Judith River wedge have been described from Saskatchewan (Gilbert et al. 2018) and Montana (Case 1978b, 1979; Fiorillo 1989); therefore, faunas from these deposits are also compared to that of the Johnson Unit.

Prior work on the Johnson Unit has primarily focused on bulk sampling and screen-washing for microfossils, as opposed to surface collection (Beavan and Russell 1999; Brinkman et al. 2005). Screen-washing is often preferred in palaeoecology studies, since surface collection has a strong bias towards larger specimens (Wolff 1975). On the other hand, surface collection favours the discovery of easily identifiable larger elements (Peterson et al. 2011), which can thus allow for more specific identifications. Surface collection also generally covers a much larger study area and may allow researchers to find larger, rarer taxa. In our study, we exclusively used surface collection, with the primary intention of finding larger and more diagnostic actinopterygian elements.

Previously collected microfossil samples from the Johnson Unit largely comprise chondrichthyan teeth, and descriptive work has focused exclusively on those elements (Beavan and Russell 1999; Brinkman et al. 2005). Subsequent research on the vertebrae of freshwater actinopterygians from the DPFm, and comparison with modern taxa, has increased our ability to identify these elements (Neuman and Brinkman 2005; Brinkman 2019). In this study, we reassess the chondrichthyan and actinopterygian taxa present in the Johnson Unit and provide images of many specimens to create a guide for future work. We map the stratigraphy along the length of our study area, to assess variation in the Johnson Unit and the surrounding strata within the LCZ. We also compare our surface collected sample with the screen-washed samples of previous authors to record the differences between these methods to assess possible collection biases associated with different collection methods.

## METHODS

In August of 2024, our research team conducted fieldwork east of Dinosaur Provincial Park in the Lethbridge Coal Zone, near Iddesleigh, Alberta. The study area is on private land along the southern bank of the Red Deer River, about 6 km east of the provincial park boundary (Fig. 1). Over the course of two weeks of field work, we surface collected material from the exposed outcrop of the Johnson Unit within the study area. Surface collection focused on the fossiliferous layer near the base of the unit, across the river from where previous authors collected bulk samples for screen-washing (Beavan and Russell 1999; Brinkman et al. 2005). We defined 21 sites, each of which represents an approximately 100 m stretch along the length of the exposed outcrop. We only counted and collected fossils that were clearly identifiable. We measured a total of nine stratigraphic sections over the length of the exposed Johnson Unit, using a 1.5 m Jacob's staff and Abney level.

Some of the specimens required minor preparation prior to photography, which was done using small brushes and insect pins. Fossils with distinct surface texturing were coated with ammonium chloride prior to photography and are presented

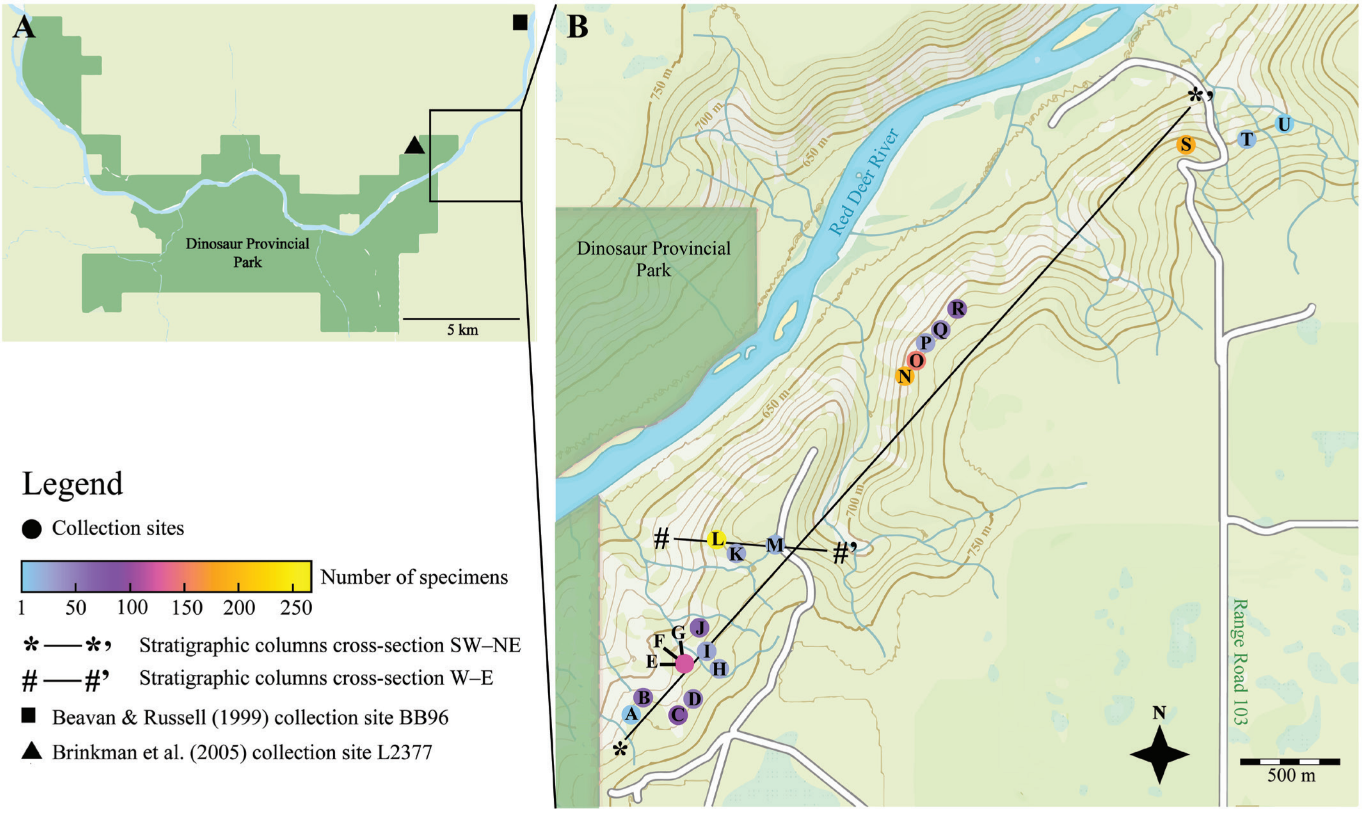


**Figure 1.** Map of study area. A, map of Dinosaur Provincial Park, dark green represents the area in the park, stars represent collection sites from Beavan and Russell (1999) and Brinkman et al. (2025); B, topographic map of study area south-east of Dinosaur Provincial Park, showing 21 collection sites (A–U) from this study and orientation of stratigraphic column cross-sections in Figures 3 and 4. Sites coloured based on the number of specimens collected.

in greyscale. When ammonium chloride was used, it is noted in the figure caption. Photographs were taken either with a Nikon DXM1200C camera on a Zeiss Discovery V.8 stereoscope using NIS-Elements F 2.20 software, or with an Olympus OM-D M10 Mark II digital mirrorless camera with a macro lens. Multiple images of each specimen were taken and focus-stacked using Adobe Photoshop. Taxon counts are based on the minimum number of elements metric following Badgley (1986), as used by previous authors working on microfossils from the coal zone (Beavan and Russell 1999). For comparisons to the samples described by previous authors, we calculated the Bray-Curtis distance on the relative abundances of each sample, using the fossil package for R (Vavrek 2011). This value ranges from 0–1 and quantifies the degree of overlap between two samples with values closer to 0 indicating more similarity between samples. The stratigraphic columns were assembled in AppleCORE version 10.5b. All specimens are catalogued in the collections of the University of Alberta Laboratory for Vertebrate Palaeontology (UALVP); these are listed in the Systematic Palaeontology section (see also Appendix 1).

Daily counts of species identified, along with estimated person-hours, were used to generate the rarefaction curve. To make comparisons with other samples from the Johnson Unit (Beavan and Russell 1999; Brinkman et al. 2005) we required consistent identifications among our sample and those from previous authors. To address this, we reidentified some specimens from their samples. In cases where specific identifications were not available for the material in all samples, we used higher categories, such as genera or families, in our comparison.

## GEOLOGY

### Lethbridge Coal Zone

The Lethbridge Coal Zone (LCZ) from the bottom to top of the study area (Fig. 1), includes the Lethbridge Coal, overlain by inclined heterolithic cross-stratification, superimposed by the marine Johnson Unit, and finally topped by non-marine sandstones/mudstones. Ramezani et al. (2022) dated a bentonite bed near the base of the LCZ at 75.017 ± 0.020 Ma, and a bed near the base of the Bearpaw Formation at 74.289 ± 0.014 Ma, bounding the Johnson Unit between these dates. The full exposure of the LCZ is visible best at Site J (Fig. 2). In the study area, the Lethbridge Coal originates at an average elevation of 721 m above sea level and overlies the fluvial sediments of the Dinosaur Park Formation (DPFm). Brinkman et al. (2005)

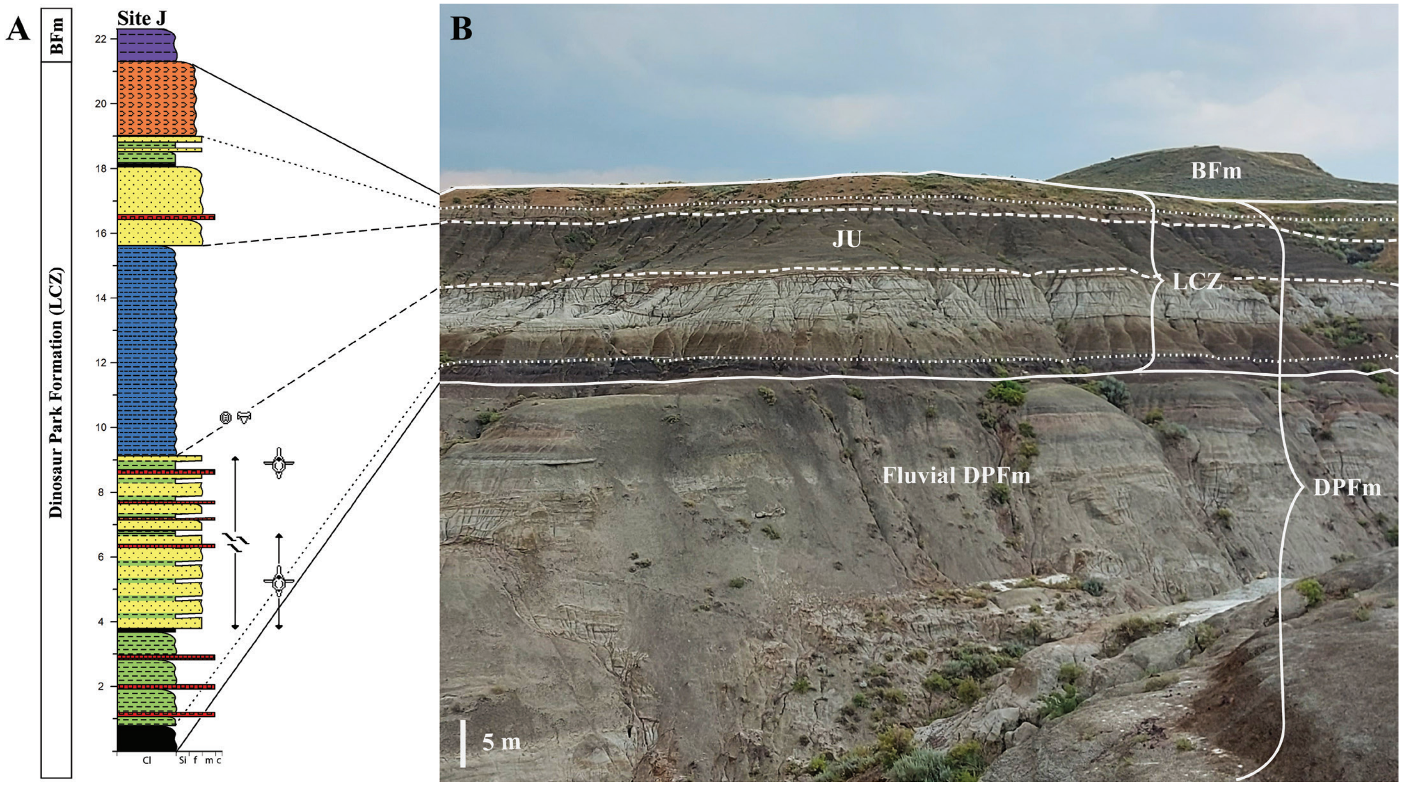


**Figure 2.** Correlation of stratigraphic column and photograph of Site J. A, stratigraphic column of Site J, numbers on the left are height in meters (m); B, photograph of Site J facing northeast, Johnson Unit bounded by fluvial DPFm sediments above and below it. Abbreviations: BFm, Bearpaw Formation; DPFm, Dinosaur Park Formation; JU, Johnson Unit; LCZ, Lethbridge Coal Zone. Grain size: Cl, clay; Si, silt; f, fine-grained sandstone; m, medium-grained sandstone; c, coarse-grained sandstone. See Figure 4 for stratigraphic column legend.

identified a thin marine unit directly above the Lethbridge Coal; this marine mudstone is variable across our measured sections and difficult to distinguish from the interbedded sandstone and mudstone above it. Marine fossils occasionally have been recovered from this level, but as they were surface collected, they may have been washed down from the fossiliferous Johnson Unit (JU) above. Because the source of the fossils from this layer is uncertain, they were not included in this study. Above this first thin marine mudstone is an extensive unit of inclined heterolithic cross-stratification (IHS) preserving interbedded sandstone and mudstone layers (Fig. 3). This unit is identified as non-marine (Brinkman et al. 2005) and preserves terrestrial organisms like dinosaurs. The IHS varies from mudstone to sandstone dominated but is typically more sandstone dominated at the base and increasingly mudstone dominated up section. Frequent ironstone layers are spaced throughout the IHS, creating flat shelves that are more resistant to erosion; these shelves occasionally accumulate terrestrial fossils from the IHS unit (Site J, Fig. 4). Marine vertebrate fossils washed down from the JU accumulate at an ironstone layer approximately one meter below the transition of IHS to the JU at several of the sites (sites O and S, Fig. 4). In some cases, mud-filled incised valleys (MFIVs) cut into the underlying IHS and are filled in with concave-up laminae, best visible at Site G (Fig. 5). The MFIVs in the study area are consistent with simple U-shaped MFIV structure (Eberth 1996), suggesting a low-energy estuarine palaeoenvironment before the complete transgression and flooding of the area by the marine Johnson Unit.

Overlying the fluvial IHS, at an average elevation of 727 m above sea level, is the base of the marine Johnson Unit. The sediment of the JU is a massive light grey mudstone, with intermittent patches of reddish iron-influenced mudstone and gypsum crystals. The fossiliferous layer sits approximately 1.5 meters above the base of the unit and is traceable across the full exposure explored in this study.

Above the marine JU, the deposition returns to non-marine sediments. This unit of terrestrial rocks includes interbedded sandstones and mudstones with occasional thin organic shale layers. A continuous 10 cm thick organic shale layer can be correlated across most of the sites (Fig. 5B) The sandstone and mudstones with interbedded organic shales transitions to a red coloured siderite-rich siltstone/sandstone. This siderite layer is on average 250 cm thick and is identified as the top of the DPFm (Eberth & Hamblin 1993). No fossils were identified in this unit in this study; however, specimens have been collected from

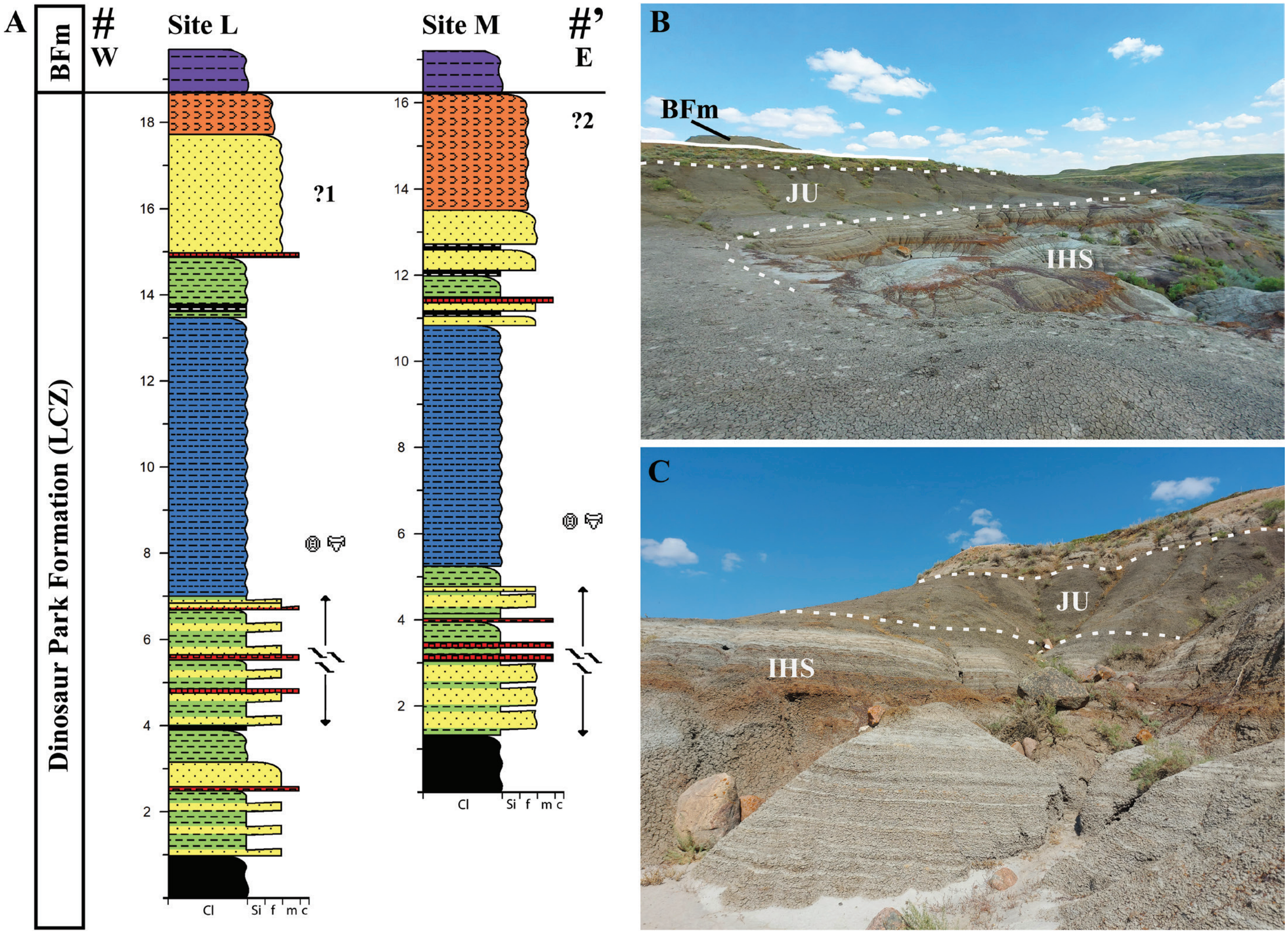


**Figure 3.** Stratigraphic cross-section roughly west to east through the study area. A, stratigraphic columns, numbers on the left of each column are height in meters (m). Facies contacts noted as ?1 are uncertain due to abundant bioturbation and vegetation. Notation ?2 indicates that the top of the DPFm is cut off by the top of the hill and the DPFm–BFm contact is difficult to determine. B, photograph of Site L facing south-east towards Site K. The Johnson Unit here is 6.47 m thick. The visible red ironstone layer is approximately 1-2 m below the beginning of the Johnson Unit. C, photograph of Site M facing north. The Johnson Unit here is 5.59 m thick. Datum, DPFm-BFm contact. Abbreviations: BFm, Bearpaw Formation; IHS, inclined heterolithic cross-stratification; JU, Johnson Unit; LCZ, Lethbridge Coal Zone. See Figure 4 for stratigraphic column legend. Grain size: Cl, clay; Si, silt; f, fine-grained sandstone; m, medium-grained sandstone; c, coarse-grained sandstone.

this layer further west along the river valley (A. Mueller personal commun. May 27, 2025). These fluvial layers above the JU are often heavily bioturbated by extant plants, making distinctions in bedding difficult (Sites O and S, Fig. 4; Site L, Fig. 3). Above this layer, are the grey shales of the Bearpaw Formation (BFm). The transition between the DPFm and the BFm is on average 739 m above sea level within the study area. The boundary shows differential erosion between the two formations, where the DPFm is more resistant to erosion than the Bearpaw shales, creating a plateau where prairie grasses and cacti grow on the siderite-rich DPFm layer. The BFm outcrop creates rounded grassy covered hills that recede from the generally semi-vertical outcrops of the DPFm. Above the Bearpaw shales are Pleistocene glacial till and overlying soils at prairie level.

## Johnson Unit

The Johnson Unit (JU) crops out on both the north and south side of the Red Deer River at the east end of Dinosaur Provincial Park. Along the south side of the river, the unit is traceable up to 2.7 kms northeast of the eastern boundary of Dinosaur Provincial Park. In this area, we explored and identified 21 collection sites (Fig. 1). Farther northeast along the river valley, exposures become limited on the south side of the river and the extent of the JU is difficult to determine in this direction. Towards the southwest, along the south side of the river, the JU becomes difficult to trace beyond the boundary of the Park due to wide coulees, and its western extent is lost to erosion. However, in the Steveville area, located at the

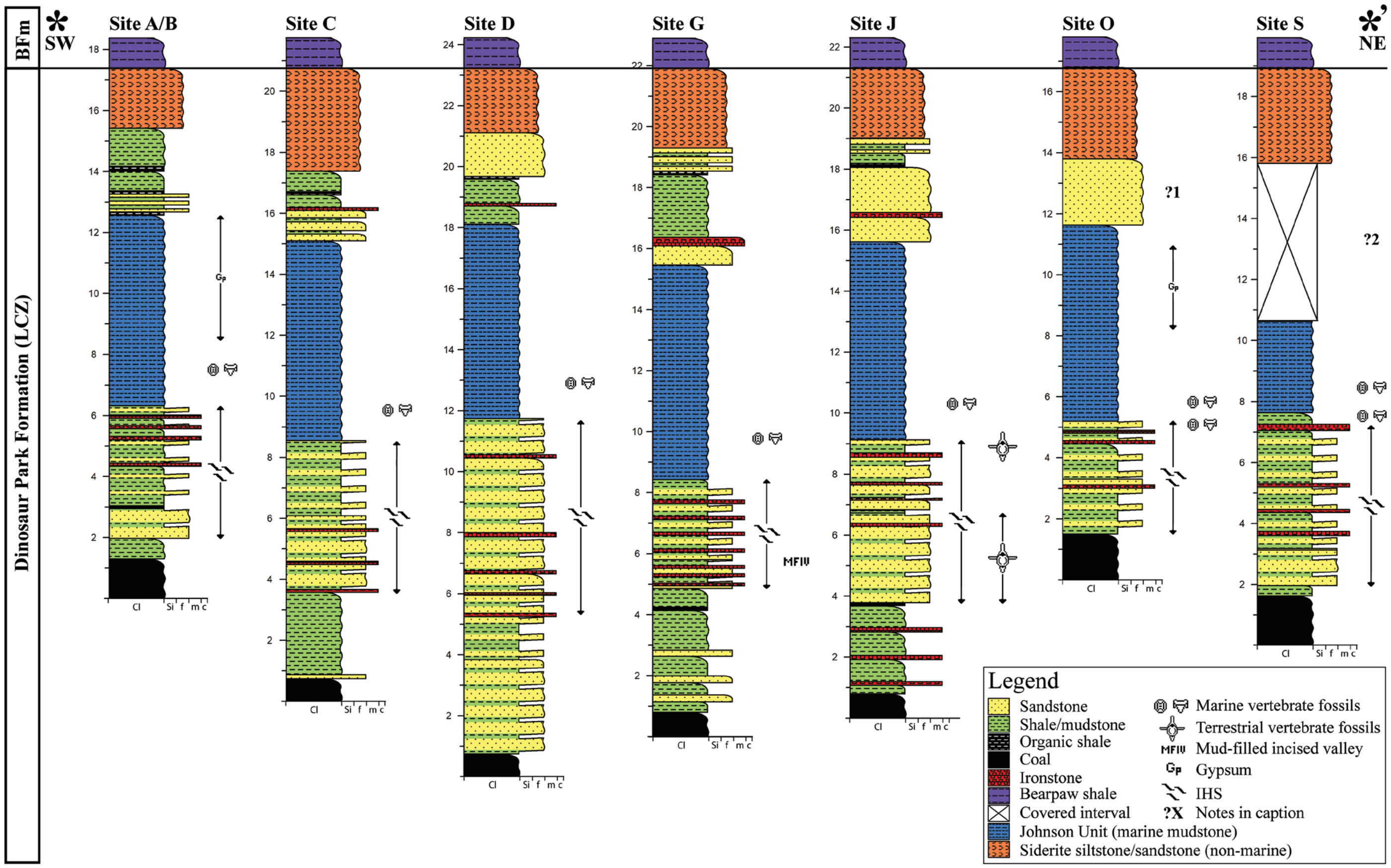


**Figure 4.** Stratigraphic cross-section south-west to north-east through the study area. Stratigraphic measurements taken with Jacob's Staff and Abney level. Numbers on the left of each column are height in meters (m). ?1, features difficult to identify due to extensive bioturbated sediments and vegetation at Johnson Unit boundary and throughout overlying fluvial sediments; ?2, Heavily bioturbated sediment and extensive vegetation cover, bedding not visible. Datum, DPFm-BFm contact. Abbreviations: BFm, Bearpaw Formation; IHS, inclined heterolithic cross-stratification; LCZ, Lethbridge Coal Zone. Grain size: Cl, clay; Si, silt; f, fine-grained sandstone; m, medium-grained sandstone; c, coarse-grained sandstone.

westernmost extent of the Park, the Lethbridge Coal Zone is exposed, and the marine shales of the Johnson Unit are absent, indicating that the Unit does not extend that far west (pers. obs. LEN, DDB).

Along the north side of the river, the JU outcrops continue further to the northeast, up to collection site BB96 (Fig. 1A) described by Beavan and Russell (1999). Aerial images suggest the unit continues further northeast of site BB96 on the north side of the river, and further on the north than the south side of the river; however, this area has yet to be explored. Towards the southwest, into Dinosaur Provincial Park along the north side of the river, there is little outcrop visible further west than collection site L2377 (Fig. 1A) described by Brinkman et al. (2005). However, further exploration of the geographical extent of the JU would give a better indication of the scale of this transgressive marine cycle.

There is little variability in thickness of the Johnson Unit across the nine stratigraphic columns that were measured in this study. The average thickness of the JU is 630.6 cm (standard deviation 47.9 cm; range 154 cm) across all measured sections. Sections taken along the SW–NE cross-section (*–*') preserve a relatively consistent thickness of the JU (Fig. 2), suggesting that the area represents an environment far enough offshore to have no significant shallowing of the water. Moving west to east along the cross-section (#–#'), Site L (647 cm), which is nearer shore, is thicker than Site M (559 cm), which is farther offshore (Fig. 3). This further supports the interpretation that the depositional environment in the study area was not directly adjacent to the shoreline and that this was a widespread transgression event.

## SYSTEMATIC PALAEONTOLOGY

Although we collected all vertebrates during fieldwork, our primary interest is the fish. Therefore, tetrapods and invertebrates are presented in an abridged format.

Class CHONDRICHTHYES Huxley, 1880

Subclass HOLOCEPHALI Bonaparte, 1832

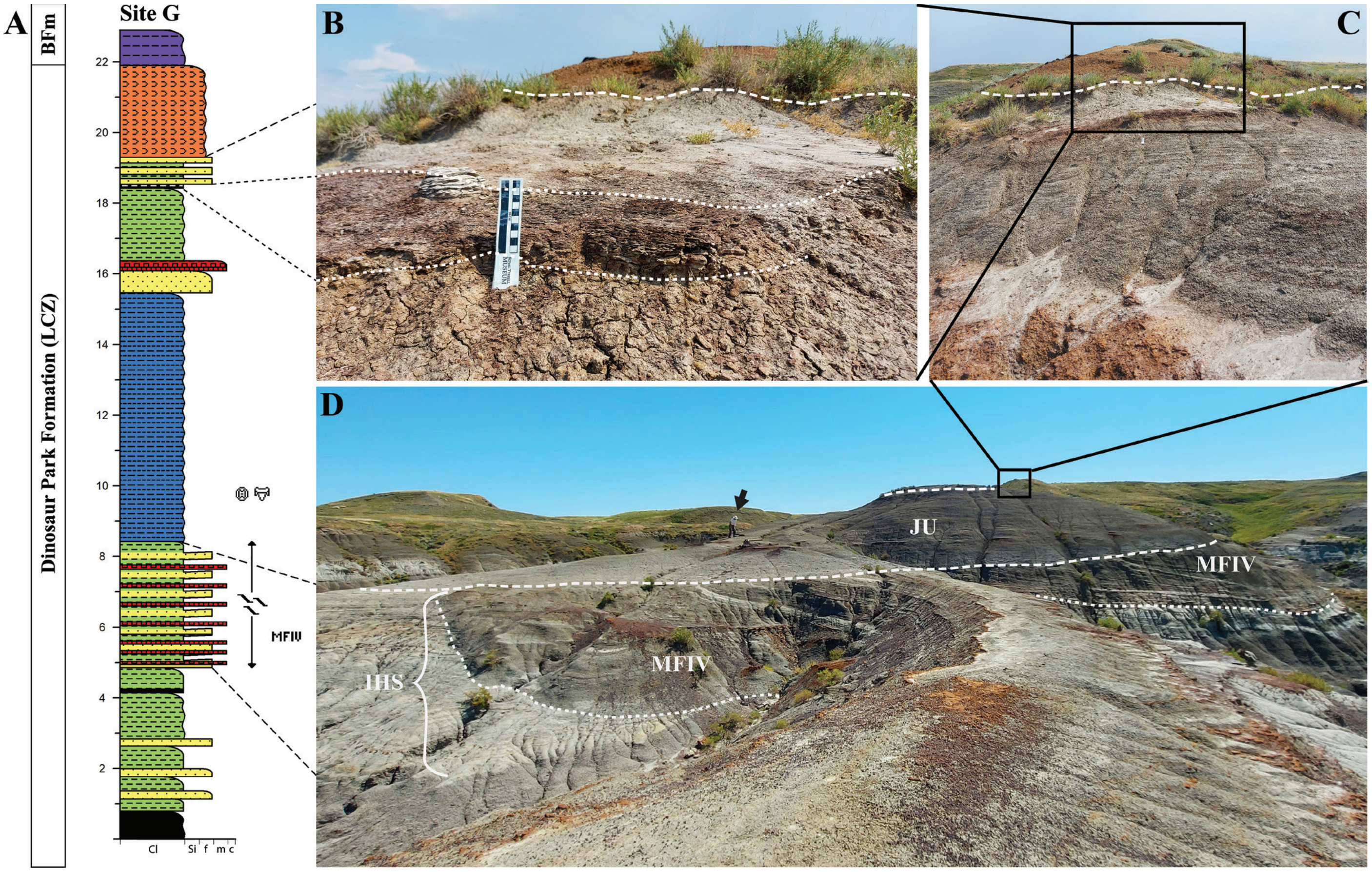


**Figure 5.** Geological features of Site G. A, stratigraphic column of Site G, numbers on the left of the column are height in meters (m); B, close up of fluvial sediments above the Johnson Unit, demonstrating the 10 cm thick organic shale and red-coloured siderite siltstone/sandstone that contacts the BFm; C, photograph of fluvial sediments above the Johnson Unit. The red ironstone at the base of the image is ironstone found just above 16 m on the stratigraphic column in A. D, photo of Site G facing south, with mud-filled incised valleys of variable thicknesses truncated by the Johnson Unit. RBH (black arrow) for scale. Abbreviations: BFm, Bearpaw Formation; IHS, inclined heterolithic cross-stratification; JU, Johnson Unit; LCZ, Lethbridge Coal Zone; MFIV, mud-filled incised valleys. Grain size: Cl, clay; Si, silt; f, fine-grained sandstone; m, medium-grained sandstone; c, coarse-grained sandstone. See Figure 4 for stratigraphic column legend.

### Order CHIMAERIFORMES Obruchev, 1953

### Family "EDAPHODONTIDAE" Owen, 1846

### Genus indeterminate

**Material:** 162 partial tooth plates. Specimen numbers UALVP64038 through UALVP64067.

**Identification:** The presence of tritors (grinding surfaces) indicates this material belongs to Chimaeriformes. "Edaphodontidae" is a problematic grouping which includes Mesozoic to early Cenozoic chimaeroid taxa known from isolated material (Popov 2020).

**Remarks:** The family Edaphodontidae is in need of further taxonomic assessment, so is used here provisionally (following the suggestion of Popov 2020). The most abundant fossil remains of chimaeriforms are their tooth plates, of which they have paired palatal, mandibular, and vomerine plates (Averianov 2001). These plates are formed from a framework of trabecular dentine interspersed with distinct sections, known as tritors, of hypermineralized coronal dentine (Johanson et al. 2020), the presence and position of which are useful to determine species (Case 1978a). In our samples, the darker trabecular dentine base and the white tritors can be identified.

Although holocephalian tooth plates are some of the most common fossils within the DPFm marine unit, the fragmentary nature of these specimens has previously hindered confident generic identification (Brinkman et al. 2005). Within the LCZ, *Elasmodus* sp. is the only previously identified holocephalian (Beavan and Russell 1999; Brinkman et al. 2005). In the contemporaneous Judith River Formation of Montana, a second taxon, *Ischyodus bifurcatus*, was identified by Case (1978a; 1979). The lack of diagnostic features in much of our material prevents assigning these partial tooth plates to a genus. Our limited diagnostic material is described below.

### Genus *Elasmodus* Egerton, 1843

### *Elasmodus* sp.

Figure 6A, B

**Material:** two tooth plates. Specimen numbers UALVP64068, UALVP64069.

**Identification:** Only two tooth plate elements were clearly identifiable to this taxon. One represents most of a right palatine tooth plate from an *Elasmodus* sp. (Fig. 6A) which is diagnosed by the presence of the lateral tritor along its cutting edge (Averianov 2001). Three other tritors are visible on the occlusal surface of the tooth plate: the anterior inner tritor, the posterior inner tritor, and the mesial tritor. As with the Judith River Formation *Elasmodus* sp. specimens described by Case (1979), the anterior and posterior inner tritors are nearly fused. The base of the tooth plate has a groove along its medial edge, which forms the basal pocket for the attachment of the jaw cartilage (Patterson 1992). The second specimen is a vomerine plate assigned to *Elasmodus* sp. (Fig. 6B). It has five closely spaced rows of columnar tritors on its occlusal surface, similar to the one figured by Case (1979: pl. 2, fig. 4). Case (1979) stated that additional tritors may have broken off his specimen, which is also likely the case with the DPFm specimen.

**Remarks:** The specimens of *Elasmodus* sp. presented here are the most complete known from the DPFm. *Elasmodus* tooth plates from the Judith River Formation were placed in *Elasmodus greenoughi* by Case (1979), a species which is otherwise only known from Western Europe (Averianov 2001). We cannot refute this identification from Case (1979) but we suggest that confident specific identification of the Judith River Group *Elasmodus* specimens requires further scrutiny and more complete mandibular tooth plate specimens. Therefore, we leave these fossils as *Elasmodus* sp., as did previous authors for material from the Campanian of Alberta (Beavan and Russell 1999; Brinkman et al. 2005; Cullen et al. 2016).

Members of *Elasmodus* have a unique dentition compared to other edaphodontids (Averianov 2001). The addition of lateral cutting edges to their otherwise durophagous dentition may be an adaptation for the scavenging of carcasses.

### Genus *Ischyodus* Egerton, 1843

### *Ischyodus bifurcatus* Case, 1978

Figure 6C

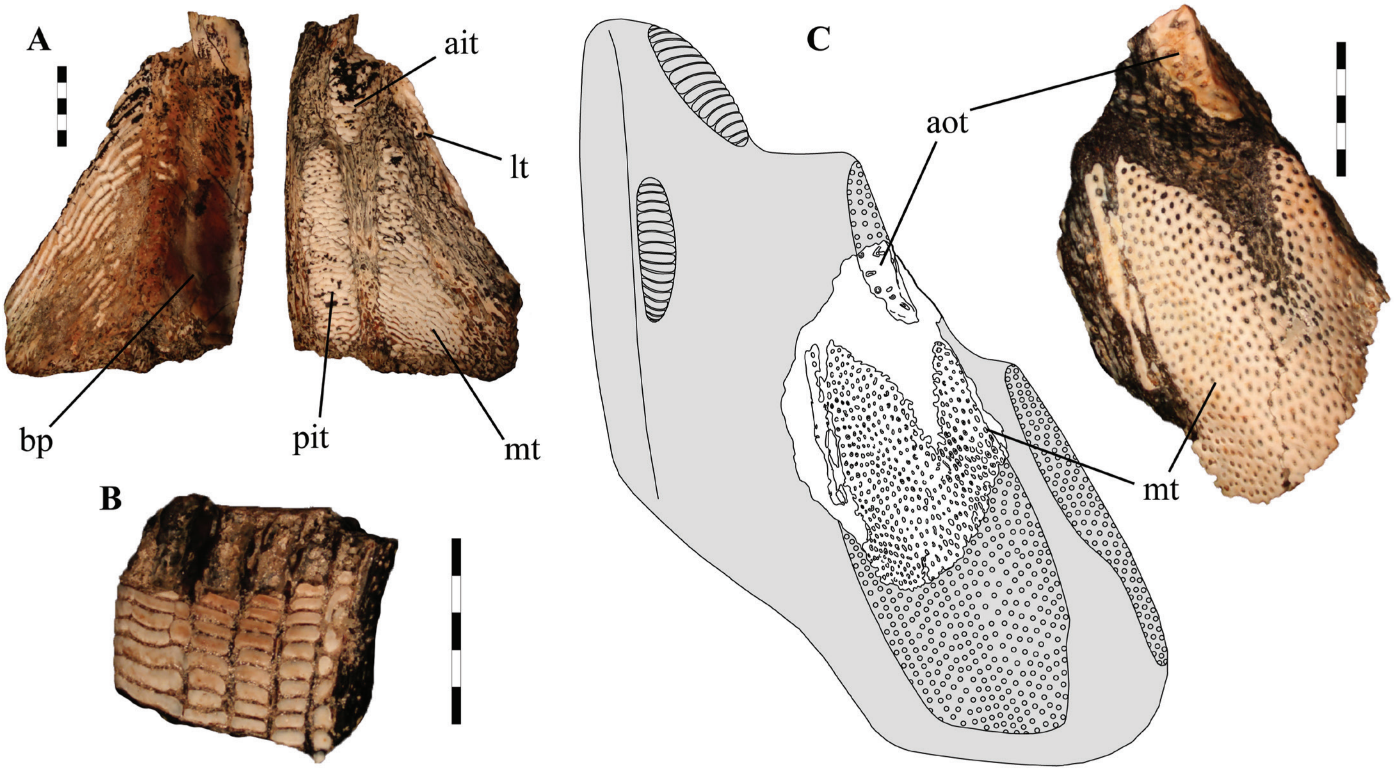


**Figure 6.** Holocephalian elements from the Johnson Unit. A, B, tooth plates from Elasmodus sp.: A, UALVP64068, left palatine plate (anterior towards top of page) in basal (left) and occlusal (right) views; B, UAVLP64069, vomerine plate in occlusal view, orientation uncertain; C, UAVLP64070, Ischyodus bifurcatus right mandibular plate in occlusal view (right; with anterior toward top of page), alongside reconstruction of hypothetical complete element, with missing portions in grey (left; figure based on those described by Johnson-Ransom et al. 2018). Abbreviations: aot, anterior outer tritor; anterior inner tritor; bp, basal pocket; mt, mesial triter; pit, posterior inner tritor; lt, lateral tritor. Scale bars = 5 mm.

**Material:** A single partial right mandibular tooth plate. Specimen number UALVP64070.

**Identification:** We identify one larger fragment as a portion of a right mandibular tooth plate as belonging to *Ischyodus bifurcatus* based on the presence of a large tritor with two branches on a flat surface with a nearby smaller tritor on a curved surface (near the true outer edge of the original element). The larger bifurcating tritor appears to be the median tritor, and the smaller one appears to be the external anterior tritor (Fig. 6C). The vascular pleromin surface of both tritors is consistent with that figured by Johnson-Ransom et al. (2018) for *Ischyodus*. The bifurcating anterior surface of the median tritor is diagnostic of *Ischyodus bifurcatus* (Case 1978a). Therefore, this specimen can be confidently attributed to both the genus and species.

**Remarks:** *Ischyodus bifurcatus* is abundant and widespread across the United States, including on the west and east coasts, and the interior (Case 1978a; Johnson-Ransom et al. 2018), so its presence in the LCZ is not unexpected. This is the first description of this taxon from Canada, although Beavan (1995) mentioned its presence in the Foremost Formation in an unpublished Master's thesis.

### Subclass ELASMOBRANCHII Bonaparte, 1838

### Cohort EUSELACHII Hay, 1902

### Family indeterminate

Figure 7A, B

**Material:** 32 centra. Specimen numbers UALVP63944 through UALVP63960.

**Identification:** These centra can confidently be identified as belonging to one or more elasmobranchs, based on the relatively smooth texture of their prismatic cartilage. This differs from the bone of actinopterygian centra which contains many pits and struts, particularly on the lateral surfaces. The miscellaneous elasmobranch centra in our sample are primarily platelike, and taller than they are long, with relatively circular and slightly amphicoelous facets. Many of the elasmobranch centra in our sample are worn and do not preserve any features that would allow them to be assigned to a lower taxonomic level.

### Family HYBODONTIDAE Owen, 1846

### Genus *Meristodonoides* Underwood and Cumbaa, 2010

### *Meristodonoides montanensis* Case, 1978

Figure 7C, D

**Material:** 172 teeth. Specimen numbers UALVP64081 through UALVP64113.

**Identification:** These are high cusped, nearly symmetrical teeth with distinct folds beginning just above the enameloid border on the lingual and labial faces and extending ¼ of the crown height. A tall central cusp gradually tapers marginally and is flanked by zero to two marginal cusplets. The roots clearly exhibit the anaulacorhizous condition, with many pores along their surface and a very flat basal surface. Complete teeth are very rare within our sample. Little heterodonty is exhibited by these teeth, but they vary slightly in cusp number, degree of curvature, and prominence of the central cusp. Most specimens are represented by central cusps, missing their tips and roots. These were, nonetheless, identifiable by their crown shape and enameloid folds.

**Remarks:** Previously attributed to *Hybodus*, the genus *Meristodonoides* was erected to encompass this species and several other North American Cretaceous hybodonts (Underwood and Cumbaa 2010). According to those authors, *Meristodonoides* teeth differ from those of *Hybodus* (defined as the close relatives of *H. reticulatus*) based on their single well-developed central cusps, low roots, and absence of a labial boss. Case (1978b) attributed the reason for the rarity of complete teeth of this species to the fragility of the highly porous roots, which seems to be the case in our sample.

### Order LAMNIFORMES Berg 1958

### Family ARCHAEOLAMNIDAE Underwood and Cumbaa, 2010

### Genus *Archaeolamna* Siverson, 1992

### *Archaeolamna kopingensis judithensis* Siverson, 1992

Figure 7E–K

**Material:** 349 teeth. Specimen numbers UALVP63818 through UALVP63863.

**Identification:** These are large teeth (up to 24 mm tall) with a very robust central cusp (compared to other sharks in our sample) typically bordered by a single pair of widely spaced marginal cusps. The enameloid is smooth, and a distinct continuous cutting edge runs along central and marginal cusps. The root is very strongly bilobed with a deep and smoothly rounded basal notch, rather than the angular basal notches of the odontaspidids. There is a prominent lingual protuberance, lacking a nutritive groove, unlike the other lamniforms in our sample.

**Remarks:** *Archaeolamna kopingensis judithensis* is the most common taxon in our sample, making up almost a quarter (24%) of our collected specimens. Cook et al. (2011) described the dentition of an articulated specimen of *Archaeolamna kopingensis* from Kansas, which allows us to roughly identify the jaw position of each specimen. Cook et al. (2011) documented a high degree of heterodonty in this taxon. Therefore, we identify the significant variation in size and shape of the teeth reported here as representative of varying position along the margins of the jaws (Fig. 7E-K).

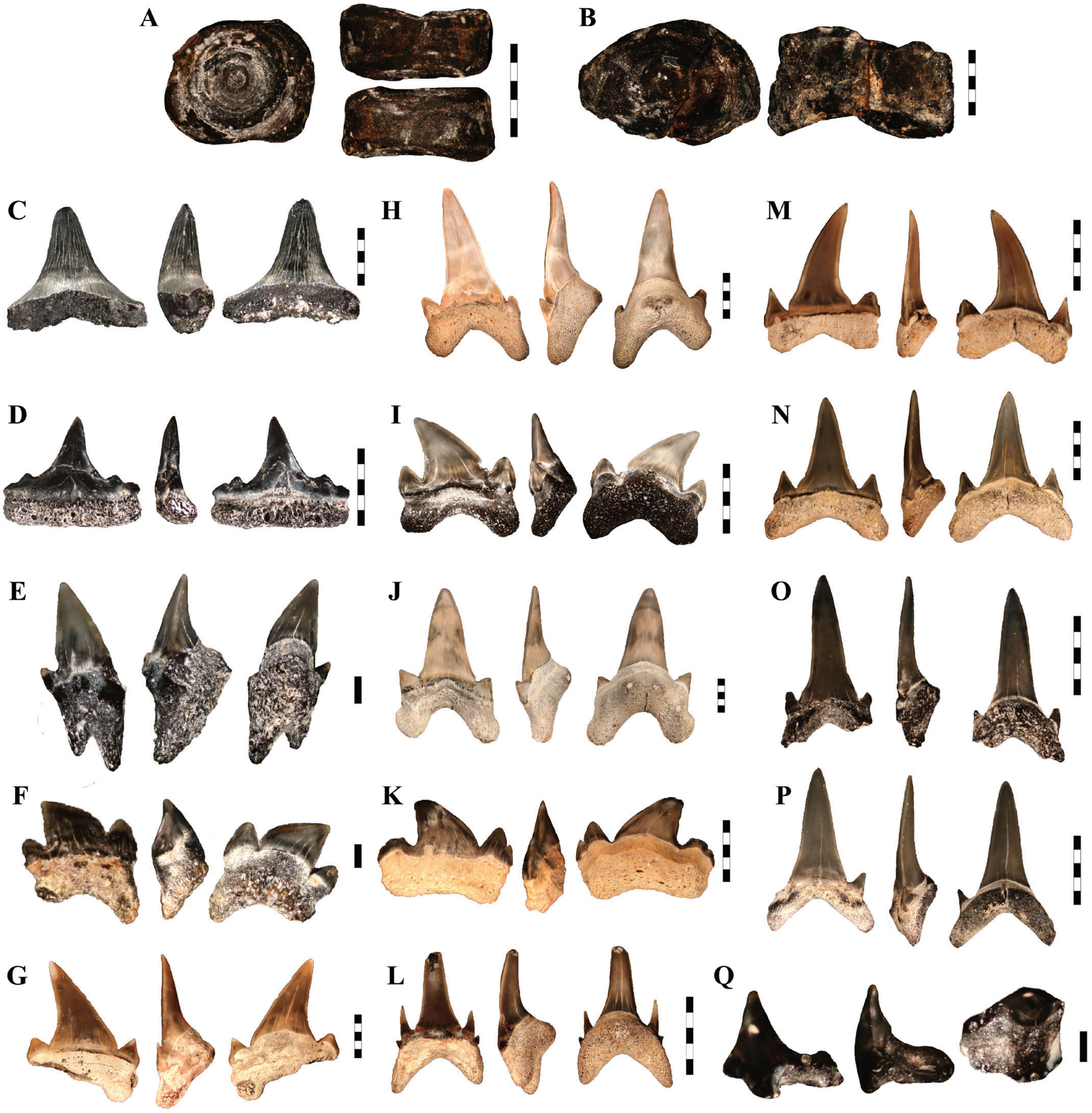


**Figure 7.** Selachian elements from the Johnson Unit. A, UALVP63946, small centrum in anterior (left), dorsal (right, top), and ventral (right, bottom) views; B, UALVP63959, large centrum in anterior (left) and dorsal (right) views; all teeth are figured from left to right in labial, profile, and lingual views; C, D, *Meristodonoides montanesis*: C, UALVP64109 anterior tooth, D, UALVP64083, lateral tooth; E–K, *Archaeolamna kopingensis judithensis*: E, UALVP63823, second lower parasymphyseal tooth, F, UALVP63834, ?upper posterior lateral tooth, G, UALVP63828, upper lateral tooth, H, UALVP63857, upper anterior tooth, I, UALVP63862, upper lateral tooth, J, UALVP63850, lower anterior tooth, K, UALVP63861, lateral tooth with accessory cusps; L, UALVP64154, *Odontaspis aculeatus* anterior tooth; M–P, *Carcharias* cf. *C. samhammeri*: M, UALVP63890, upper lateral tooth, N, UALVP63877, lower lateral tooth, O, UALVP63888, anterior tooth, P, UALVP63895, lower anterior tooth; Q, UALVP63921, *Cretorectolobus olsoni* tooth. Scale bars = 5 mm, except E, F and Q, where scale bars = 1 mm.

*Archaeolamna* differs from all other lamniforms in its dental formula, large first and second upper anterior teeth of similar height, large intermediate teeth with a strong distally curved cusp, and a reduced first lower anterior tooth (Cook et al. 2011). *Archaeolamna kopingensis judithensis* differs from other populations of *A. kopingensis* in the width and robustness of their central cusps (Cook et al. 2011), and some authors argue that the subspecies is deserving of specific rank (Underwood and Cumbaa 2010). Unlike extant lamnids, the presence of both upper and lower parasymphyseal teeth likely indicates a more basal position in lamniforms for the Archaeolamnidae (Underwood and Cumbaa 2010). The previous referral of LCZ specimens to *Archaeolamna* "*japonensis*" *judithensis* by Brinkman et al. (2005) appears to be an error. To our knowledge, that name does not appear elsewhere in the literature.

Although teeth of adult *A. kopingensis* typically possess only one pair of marginal cusps (Cook et al. 2011; Siverson 1992), three lateral teeth in our sample possess an additional pair (Fig. 7K). Accessory cusps may be present on lateral teeth in modern and fossil subadult lamniforms (Nagrodski et al. 2012; T. Cook pers. commun. Nov. 19, 2024); therefore, we tentatively interpret these teeth to have belonged to younger individuals. However, these teeth are also relatively large, which may contradict this interpretation. Further investigation into these abnormal teeth is necessary to clarify this question.

### Family ODONTASPIDIDAE Müller and Henle, 1839

### Genus *Odontaspis* Agassiz, 1838

### *Odontaspis aculeatus* Cappetta and Case, 1975

Figure 7L

**Material:** Seven teeth. Specimen numbers UALVP64154 through UALVP64157.

**Identification:** The central cusp is tall and very thin on anterior teeth; all specimens from our sample have a broken tip. Two pairs of marginal cusps flank the central cusp. The inner marginal cusps are very elongate and narrow with full-length cutting edges and curve towards the centre of the tooth in lingual view. The root is strongly bilobed, with long, thin lobes, and a deep and moderately V-shaped basal notch, both of which are features of Odontaspididae. The lingual protuberance is large and rounded in profile view; it has a distinct, long nutritive groove.

**Remarks:** Teeth of *Odontaspis aculeatus* and *Carcharias* cf. *C. samhammeri* (see below) are similar to one another, likely due to their close phylogenetic relationship as odontaspidids. The thin, long marginal cusps of *O. aculeatus* teeth differ from the more robust marginal cusps of *Carcharias* cf. *C. samhammeri*. The second pair of marginal cusps on *O. aculeatus* teeth further distinguishes these taxa (Beavan and Russell, 1999). Lastly, the *O. aculeatus* teeth in our sample possess proportionately larger lingual protuberances than the teeth of *Carcharias* cf *C. samhammeri*.

### Genus *Carcharias* Rafinesque, 1810

### *Carcharias* cf. *C. samhammeri* Cappetta and Case, 1975

Figure 7M-P

**Material:** 208 teeth. Specimen numbers UALVP63876 through UALVP63900.

**Identification:** The teeth possess a long thin central cusp flanked by two small sigmoidal marginal cusps. These marginal cusps are relatively short and stout, and anterior teeth lack an additional pair of marginal cusps. The labial faces of the teeth are smooth and lack longitudinal folds. The teeth have relatively gracile, thin crowns in profile view and strongly bilobed roots, with well-defined lingual protuberances.

**Remarks:** Previous reports on the ichthyofauna of the Lethbridge Coal Zone (Brinkman et al. 2005; Beavan and Russell 1999) included the presence of *Carcharias steineri*. Teeth from that species, which was described by Case (1987) based on specimens from Wyoming, possess characteristic longitudinal striae on their labial face. In contrast, Cook et al. (2017) tentatively attributed the Albertan Campanian *Carcharias* teeth to *Carcharias samhammeri*, first described from the Monmouth Group of New Jersey (Cappetta and Case 1975). Similar to the material examined by Cook et al. (2017), none of the *Carcharias* teeth in our sample have the longitudinal striae characteristic of *Carcharias steineri*, and instead are more similar in morphology to *C. samhammeri*.

The tooth that was figured as *Cretolamna appendiculata* by Brinkman et al. (2005) does not appear similar to any from the *C. appendiculata* tooth series that was subsequently published by Shimada (2007). After reviewing the specimens described by Brinkman et al. (2005), we identify most of the teeth in their sample as *Carcharias* cf. *C. samhammeri*, including the specimen figured by Brinkman et al. (2005; fig. 26.2D). Two teeth in their sample also appear to be worn *Archaeolamna kopingensis judithensis* teeth. This reidentification is reflected in Appendix 2.

### Order ORECTOLOBIFORMES Applegate, 1972

### Family incertae sedis

### Genus *Cretorectolobus* Case, 1978

### *Cretorectolobus olsoni* Case, 1978

Figure 7Q

**Material:** One tooth. Specimen number UALVP63921.

**Identification:** A small (3.5 mm tall) incomplete tooth with a single central cusp bordered laterally by a cutting heel bearing a single blunt marginal cusp. The left side of the tooth is broken but shows the start of a similar heel. Labially, there is a sizable apron projecting below the base of the tooth. On the lingual side, the lingual protuberance forms a characteristic wide platform which would be roughly triangular if it were complete. Towards the lingual side of the root in the basal view is a single vascular canal opening, representing the holaulocorhizous condition.

**Remarks:** Similar to previous collections from the LCZ (Beavan and Russell, 1999; Brinkman et al. 2005), orectolobiforms make up a small proportion of our sample. The triangular shape of the tooth in the basal or occlusal view differentiates it from other species. *Cretorectolobus olsoni* is one of two orectolobids reported previously from the LCZ, with the other being *Eucrossirhinus microcuspidatus* (Beavan and Russell 1999). Siverson (1995) suggested that *E. microcuspidatus* represents a juvenile condition of *C. olsoni*. A third genus, *Cederstroemia*, was described from the Judith River Group of Montana based on specimens originally classified within the type series of *Cretorectolobus olsoni* (Siverson 1995). Unlike both *Squatina* and *Cederstroemia*, the tooth reported here possesses marginal cusps. Modern carpet sharks, such as wobbegongs, are most diverse in the western Pacific and eastern Indian oceans, primarily within the southern hemisphere. However, the family was well represented in North America during the Cretaceous (Boyd and Seitz 2021).

### Superorder BATOMORPHII Cappetta, 1980

### Batormophii indet.

Figure 8A

**Material:** 14 centra. Specimen numbers UALVP63864 through UALVP63871.

**Identification:** The centra are amphicoelous and cylindrical with deeply concave facets. They are longer than they are tall or wide (unlike selachian centra), and some are also dorsoventrally depressed. The lateral surfaces lack any obvious texturing, unlike actinopterygian vertebrae.

**Remarks:** Overall, these centra are similar to those identified below to *Myledaphus bipartitus*, but they lack the spool shape that results from a central constriction.

### Order RAJIFORMES Berg, 1940

### Family SCLERORHYNCHIDAE Cappetta, 1974

### Genus *Ischyrhiza* Leidy, 1856

### *Ischyrhiza mira* Leidy, 1856

Figure 8B−E

**Material:** Seven rostral denticles, one oral tooth, one dermal denticle. Specimen numbers UALVP64072 through UALVP64080.

**Identification:** The incomplete rostral denticles consist of either the recurved crowns or the large bifurcating roots. The roots are separated by a deep basal groove (Fig. 8B), and possess longitudinal vertical grooves near their base. The rostral denticle crowns are dorsoventrally depressed, with anterior and posterior cutting edges and smooth enameloid over their length. The crowns remain wide for the proximal two-thirds of their length then narrow to form an apex (Fig. 8C).

The dermal denticle is large (7 mm in length) with a gently-sloping, recurved central peak (Fig. 8D). The base of the denticle forms an almost perfect oval. This denticle closely resembles those documented by Sternes and Shimada (2018) in both size and shape.

A single oral tooth (Fig. 8E) has a bilobed root, with a central nutrient foramen. The crown lacks enameloid ornamentation and possesses a large central uvula on its lingual face. On its labial face, the oral tooth has a large apron which projects significantly laterally and somewhat basally. The crown is labiolingually elongate and has two lateral extensions with a small cusp located near its lingual face. Atypical of *Ischyrhiza mira*, the root does not extend laterally beyond the crown in occlusal view.

**Remarks:** *Ischyrhiza mira* is a widespread and abundant sclerorhynchid known from North America (Sternes and Shimada 2018). The extinct family Sclerorhynchidae represents one of three examples of convergence towards sawfish-like morphology within elasmobranchs (Wueringer et al. 2009). The description of more complete specimens of *I. mira* from Alabama by Sternes and Shimada (2018) allows us to confidently identify the dermal denticle as belonging to this species. Unfortunately, no articulated or associated specimens of *I. mira* include oral teeth, so the oral tooth tentatively referred herein to the species follows the inferences of preceding authors (e.g., Welton and Farish 1993).

The single oral tooth we attributed to *I. mira* appears very similar to teeth identified by Brinkman et al. (2005) as *Rhinobatos incertus*. The size and shape of the apron extension, lack of lingually projecting lateral uvulae, and overall large size of the LCZ teeth do not resemble *Rhinobatos* documented from other parts of the WIS (Everhart 2007). These LCZ teeth (including the one documented here) are less laterally elongate than typical *I. mira* specimens and do not appear worn; this may be due to their position in the mouth. *Rhinobatos* teeth were not documented in the Judith River Formation Marine Unit by Case (1978b, 1979), nor in the Lethbridge Coal Zone by Beavan and Russell (1999), or Dinosaur Park Formation upper transition of Saskatchewan (Gilbert et al. 2018). Thus, we conclude that *Rhinobatos* is not yet known from the Johnson Unit. *Rhinobatos* sp. speci-

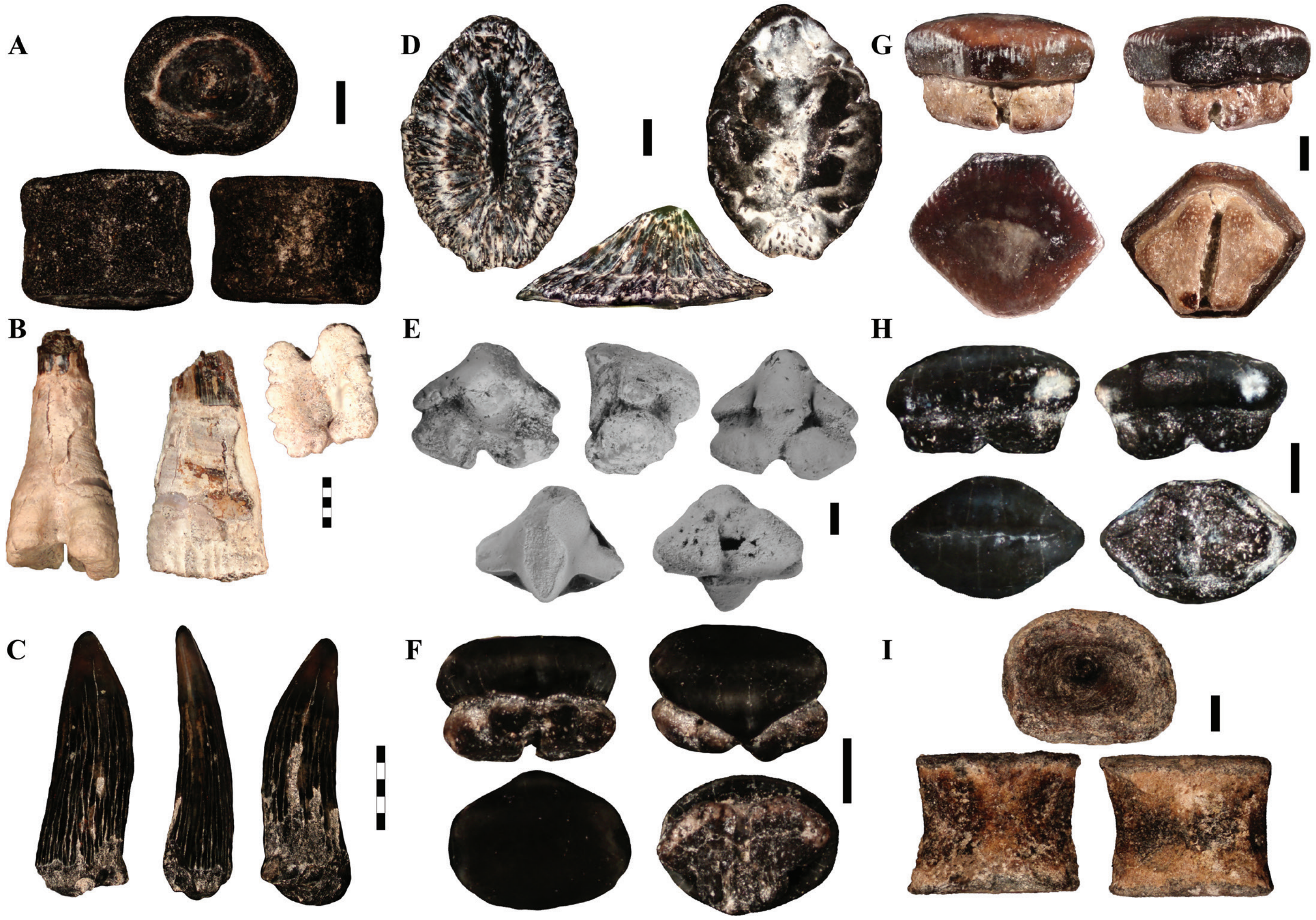


**Figure 8.** Batomorph elements from the Johnson Unit. A, UALVP63867, indeterminate batomorph centrum in anterior (top), dorsal (left, bottom) and ventral (right, bottom) views; B–E, Elements from Ischyrhiza mira: B, UALVP64072, rostral denticle base from left to right in posterior, ventral, and basal views; C, UALVP64074, rostral denticle crown from left to right in dorsal, posterior, and ventral views; D, UALVP64073, dermal denticle in apical (top, left), basal (top, right), and lateral (bottom) views; E, UALVP64079, oral tooth coated in ammonium chloride and depicted in greyscale, figured from left to right, top row in labial, profile, lingual views, and bottom row in occlusal, and basal views; F, UALVP64180, *Protoplatyrhina renae* tooth figured from left to right, top row in labial, lingual views, and borrow row in occlusal, and basal views; G–I, Elements from *Myledaphus bipartitus*: G, UALVP64138, hexagonal tooth figured from left to right, top row in labial, lingual, bottom row occlusal, and basal views; H, UALVP64134, rhomboidal tooth figured from left to right, top row in labial, lingual, bottom row in occlusal, and basal views; I, UALVP63871, centrum in anterior (top), dorsal (bottom, left), and ventral (bottom, right) views. Scale bars = 1 mm, except in B, C where scale bars = 5 mm.

mens are well known from older formations in Alberta and Saskatchewan (Cook 2013; Peng et al. 2001).

### Order RHINOPRISTIFORMES Naylor, Caira, Jensen, Rosana, Straube, and Lakner, 2012

### Family HYPSOBATIDAE Cappetta, 1992

### Genus *Protoplatyrhina* Case, 1978

### *Protoplatyrhina renae* Case, 1978

Figure 8F

**Material:** Five teeth. Specimen numbers UALVP64179 through UALVP64183.

**Identification:** The teeth have smoothly rounded oval crowns in occlusal view, lacking a transverse ridge. The lingual face has a central uvula, which protrudes to the basal edge of the root at its midpoint. The root has two lobes, which have roughly triangular basal surfaces.

**Remarks:** Although these teeth have somewhat similar form to those of *Myledaphus*, they differ in their possession of distinct uvulae on their lingual faces, and lack of a central transverse ridge on their occlusal surface. They also tend to be smaller than most *Myledaphus* teeth. Unlike other LCZ batoids, *Protoplatyrhina renae* is only known from isolated teeth; there are no partially articulated body fossils, thus its taxonomic placement is relatively uncertain (Cappetta 1987).

### Family incertae sedis

### Genus *Myledaphus* Cope, 1876

### *Myledaphus bipartitus* Cope, 1876

Figure 8G–I

**Material:** 139 teeth, 23 centra. Specimen numbers UALVP64122 through UALVP64153.

**Identification:** Batoid teeth with a high, flattened crown and a bifurcating root, lacking uvulae. The occlusal surface is divided labiolingually by a distinct central transverse ridge. Although commonly described as hexagonal, *Myledaphus* teeth vary significantly in shape based on their position in the mouth. Six different tooth morphologies were identified by Frampton (2006) from study of an almost complete specimen in the Royal Tyrrell Museum collections. Some teeth in our sample have a clearly defined sharp-angled, hexagonal occlusal surface, patterned with enameloid folds (Fig. 8G). These hexagonal teeth are the largest and positioned laterally within the jaw. Other teeth have a rhomboidal shape, with rounded corners. These tend to be smaller, with prominent transverse ridges and smoother occlusal surfaces lacking distinct enameloid folds (Fig. 8H).

Many of our small elasmobranch centra are attributed here to *M. bipartitus*, based on comparison with those reported by Wilson et al. (2013). These centra are relatively long anteroposteriorly (compared to selachian vertebrae) and have a minor constriction midway between the two articular surfaces, resulting in a slight spool shape (Fig. 8I).

**Remarks:** This species is also common in freshwater deposits within the Dinosaur Park Formation (Brinkman 1990), therefore *M. bipartitus* was likely euryhaline. The unidentified elasmobranch centrum figured by Beavan and Russell (1999) also appears to be an eroded *M. bipartitus* element.

### Class OSTEICHTHYES Huxley, 1880

### Subclass ACTINOPTERYGII Cope, 1887

### Order ACIPENSERIFORMES Berg, 1940

### Family ACIPENSERIDAE Bonaparte, 1831

### Acipenseridae gen. indet.

Figure 9A–C

**Material:** One dorsal scute, one lateral scute, 58 other dermal elements, one partial fin spine. Specimen numbers UALVP64184 through UALVP64205.

**Identification:** The specimens designated here as belonging to acipenserids are fragments of larger dermal elements, either cranial or girdle bones, or scutes, and at least one partial fin spine. The left lateral scute has a thin, hooked ridge along its length (Fig. 9A). The scute extends much further dorsal to this ridge than it does ventrally, although this is likely due to the dorsal surface being partially broken. The scute is ornamented with irregularly shaped pits, rather than raised ridges or tubercles.

The lateral wings of the dorsal scute are broken (Fig. 9B), but the median spine remains intact. This spine hooks distally over the posterior portion of the scute. The spine is ornamented with ridges, which radiate out ventrally.

The fragments of larger bones possess a moderately raised ornamentation of anastomosing ridges, separated by pits (Fig. 9C). The specimens are differentiated from those of crocodile scutes by the comparatively shallow pitting.

**Remarks:** The dorsal scute resembles those of *Anchiacipenser acanthaspis*, which was described from fluvial deposits of the Dinosaur Park Formation (Sato et al. 2018), and the lateral scute is not inconsistent with an identification as *A. acanthaspis*. However, we prefer not to assign disarticulated material to a genus or species until we have a better understanding of the diversity of sturgeons in the DPFm.

### Infraclass HOLOSTEI Müller, 1844

### Order LEPISOSTEIFORMES Hay, 1929

### Family LEPISOSTEIDAE Agassiz, 1832

### Lepisosteidae gen. indet.

Figure 9D, E

**Material:** Four ganoid scales, one dermal bone. Specimen numbers UALVP64033 through UALVP64036, and UALVP63815.

**Identification:** Several rhomboid ganoid scales with smooth edges are part of the collection. The inner surface has a central raised ridge, and the outer surface is covered in a smooth, flat layer of shiny ganoine.

We also collected a single piece of ornamented dermal skull bone, with many raised tubercles that coalesce into ridges toward one side. The bone is only a few millimeters thick. The ornamentation is not as deep as that of acipenserids, and the tubercles are smaller and more regular than our sturgeon material.

**Remarks:** Gar scales are some of the most common microfossils in the Belly River Group (Brinkman 1990), yet their taxonomic identity is difficult to determine. Historically, authors have identified gar scales from the Judith River Group as belonging to either of the extant genera *Atractosteus* and *Lepisosteus* (Brinkman 1990; Beavan and Russell 1999; Grande 2010). Grande (2010) referred

**Figure 9.** Non-teleost actinopterygian elements from the Johnson Unit. A, UALVP64186, acipenserid left lateral scute in lateral (left) and ventral views (right) with anterior to the left; B, UALVP64187, acipenserid dorsal scute in dorsal (left) and lateral (right) views with anterior to the left; C, UALVP64202, acipenserid dermal bone in external view; D, UALVP64033, lepisosteid scale in external (left) and internal (right) views, with anterior to the left; E, UALVP63815, lepisosteid skull bone in external view; F, UALVP63816, amiid centrum in anterior (top, left), posterior (top, right), and dorsal views (bottom); G, UALVP63875, *Belonostomus longirostris* premaxilla, in dorsal (left) and ventromedial (right) views. Scale bars = 1 mm, except in A, C, E, where scale bars = 5 mm.

a partial skull from the park to *Lepisosteus*; this is the most complete specimen from the formation. However, this identification does not preclude the co-occurrence of *Atractosteus*. Grande (2010) noted that the anterior flank scales of all *Lepisosteus* species possess dorsal projections, which are absent from the anterior trunk scales of some modern *Atractosteus* species; he also noted that dorsal projections are absent from the posterior scales of all gars. Our scales are rhomboidal, indicating a posterior position along the flank, and accordingly lack dorsal projections. Modern gar are primarily freshwater-dwelling, but some species, such as *Atractosteus spatula*, also live in brackish and marine environments (Daugherty et al. 2017).

### Order AMIIFORMES Hay, 1929

### Family AMIIDAE Bonaparte, 1831

### Amiidae gen. indet.

Figure 9F

**Material:** One centrum. Specimen number UALVP63816.

**Identification:** The centrum is wide mediolaterally and short anteroposteriorly, with hourglass-shaped neural arch attachment pits and oval facets. The centrum lacks fused parapophyses. The single centrum from the marine layer is missing its ventral surface. The lateral surfaces of the centrum lack clear pitting, with smooth textured bone.

**Remarks:** Previous authors reporting on the Johnson Unit did not document amiids in the marine environment (Beavan and Russell 1999; Brinkman et al. 2005). Modern bowfins are stenohaline (Hanson et al. 1976), and their closest relatives in subfamily Amiinae typically only occur in freshwater habitats (Grande and Bemis 1998). In the Late Cretaceous, other amiid taxa were found in marine environments, such as some species in the subfamily Vidalamiinae (Grande and Bemis 1998). The extremely worn condition of the amiid centrum presented here makes further taxonomic identification impossible. Due to the rarity in our sample, it is plausible that the specimen was transported from its original environment.

### Order ASPIDORHYNCHIFORMES Bleeker, 1859

### Family ASPIDORHYNCHIDAE Nicholson and Lydekker, 1889

### Genus *Belonostomus* Agassiz, 1834

### *Belonostomus longirostris* (Lambe, 1902)

Figure 9G

**Material:** Two partial premaxillae, Two dermal fragments. Specimen numbers UALVP63872 through UALVP63875.

**Identification:** These elements are identified as partial premaxillae because they have two ventrolaterally positioned tooth rows, and a groove on their dorsomedial margin, which is the margin of the nasal tract (Estes 1964). The medial tooth row bears much larger tooth sockets than those of the lateral row and the bone has ganoine ornamentation on its lateral aspect. The lateral sides of the elements are slightly rounded, with a thin ganoine layer on the surface. The elements represent only part of the total rostrum and would have articulated with the nasals dorsally. The cross section of the element has a flat ventral surface, slightly rounded lateral surfaces, and is concave dorsally with a groove for the nasal tract. Several additional fragments of dermal skull bones ornamented with ganoine from our sample are also attributed to this species, based on comparison to more complete Dinosaur Park specimens from fluvial deposits. The ganoine on these dermal bones appears shiny with small raised tubercles, and the elements have smooth rounded edges.

**Remarks:** *Belonostomus* was not reported from the Johnson Unit by previous authors (Beavan and Russell 1999; Brinkman et al. 2005) but *Belonostomus longirostris* is known from fluvial deposits in the DPFm based on incomplete jaw material indistinguishable from our specimens. Neuman and Brinkman (2005) stated that *B. longirostris* is a fully freshwater fish; however, this is potentially contradicted by the presence of several specimens from a marine environment in our sample. Nevertheless, we cannot dismiss the possibility that the specimens were displaced from a freshwater environment. Beavan and Russell (1999) figured a jaw fragment from the Johnson Unit with similarities to *Belonostomus*, which they labelled as an unidentified osteichthyan dentary. The species was reported from a marginal marine environment in Saskatchewan (Gilbert et al. 2018), and other North American occurrences of *Belonostomus* are known from such environments (Whetstone 1978; Van Vranken et al. 2019). Similarly, Brito and Suárez (2003) identified a jaw fragment from a marine environment in Chile as *B. longirostris*; however, Miyazato et al. (2025) suggested that the Chilean material probably does not belong in this species.

### Subdivision TELEOSTEI, Müller, 1845

### Order indeterminate

Figure 10A, B

**Material:** One ?palatine bone, two quadrates, 13 centra. Specimen numbers UALVP64206 through UALVP64218, and UALVP64226.

**Identification:** The possible palatine is elongate with a sigmoidal shape and the bone is dense (Fig. 10A). There are minute rounded teeth in at least two rows, although many appear to have been broken or lost. If the element is a palatine, the toothless end would have extended anter-

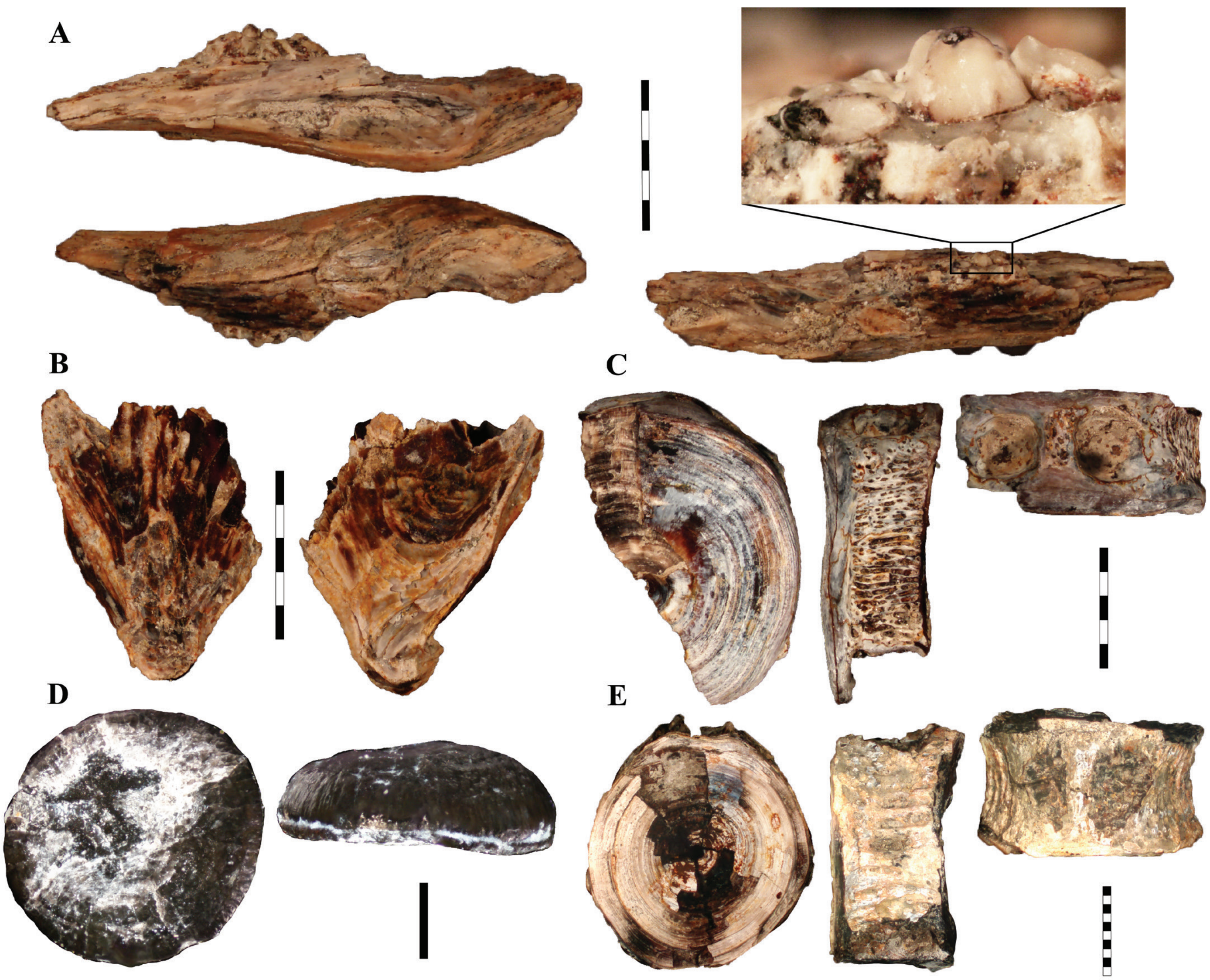


**Figure 10.** Teleost elements from the Johnson Unit. A, UALVP64226, teleost ?palatine in lateral (top), medial (bottom, left), and ventral views (bottom, right), with enlarged view of teeth; B, UALVP64214, quadrate in medial (left) and lateral (right) views; C, UALVP63967, elopiform centrum from left to right in anterior, lateral, and dorsal views; D–E, *Paralbula casei* elements: D, UALVP64160, tooth in occlusal (left) and profile (right) views; E, UALVP64166, centrum from left to right in anterior, left lateral, and dorsal views (anterior towards the top of page); Scale bars = 5 mm, except D, scale bar = 1 mm, and E, scale bar = 10 mm.

iorly to articulate with the maxilla. We tentatively attribute this bone to a teleost, due to its round and flat tooth form, which is unlike those found in non-teleosts (gars, amiids, *Belonostomus*, paddlefish, and sturgeon) from the DPFm.

The quadrates are identified by their triangular shape and rounded condyles for the articulation of the mandible (Fig. 10B); they appear most similar to those of teleosts (Patterson 1973). The quadrates of gars lack a triangular shape (Grande 2010). Unlike the quadrates of both bowfins and gars, the articular condyle in the JU quadrates is oriented right at the base of the triangle, rather than off to one side, and is distinct from the flatter fan-shaped portion of the element.

The centra are fragmentary; however, they are identified as teleost based on their convoluted, pitted bone texture and amphicoelous condition. None are complete enough to be identified more precisely.

### Family incertae sedis

### Teleost Morphotype O

Figure 11A

**Material:** One centrum. Specimen number UALVP63901.

**Identification:** A single centrum, almost circular in shape, with a convex anterior facet and a concave posterior facet is assigned to this morphotaxon. The anterior facet preserves distinct growth lines, and has a small, central depression. Although partially broken, the posterior facet is clearly smaller than the anterior facet. The neural arch

**Figure 11.** Teleost Type O centra from the Johnson Unit with comparison to those from other Late Cretaceous deposits. Centra from left to right in anterior, left lateral, posterior, dorsal, and ventral views. Centra were coated in ammonium chloride and are depicted in greyscale. A, UALVP63901, Teleost type O centrum from the Johnson Unit; B, Teleost type O centrum from the Late Campanian Kaiparowits Formation of Utah, which is roughly contemporaneous to the Johnson Unit; C, Teleost Type O centrum from the Santonian of the Milk River Formation from Southern Alberta; D, Teleost Type O centrum from the Cenomanian Dakota Formation of Utah. Scale bars = 1 mm.

pits are large, widely spaced. In lateral view, although the centrum is damaged, it seems to lack any pits in the bone surface, as well as lacking parapophyseal pits, likely indicating an anterior placement in the vertebral column (Brinkman et al. 2013).

**Remarks:** Teleost morphotype O was first recognized by Brinkman et al. (2013), based on centra which possess a distinctive rounded convex anterior facet and a concave posterior facet. It was found in several formations in the Late Cretaceous of Utah (Brinkman et al. 2013; Eaton et al. 2014) and later found in the Santonian Milk River Formation of Southern Alberta (Brinkman et al. 2017). The Utah centra are also known from the late Campanian, but from a freshwater palaeoenvironment. Their stratigraphic range extends back to the Turonian (Brinkman et al. 2013). No vertebrae of this morphotype have been previously documented in the Belly River Group (Brinkman et al. 2017), so the species represented by this morphotaxon seems to be absent from freshwater environments of the Albertan Campanian. Brinkman et al. (2017) argued that the absence of this fish from the fluvial portions of the Belly River Group implied a preference for warmer temperatures. Our specimen seems to contradict this conclusion, although the low abundance of teleost morphotype O in the Belly River Group may still be indicative of a shift southward. Although similar in overall morphology, the Albertan centrum is almost three times the size of previously described specimens. This, combined with the marine palaeoenvironment, may indicate that the Johnson Unit morphotype O centrum represents a different, but closely related, species.

### Superorder ELOPOMORPHA Greenwood, Rosen, Weitzman, and Myers, 1966

### Order ELOPIFORMES Greenwood, Rosen, Weitzman, and Myers 1966

### Elopiformes family indet.

Figure 10C

**Material:** Four partial centra. Specimen numbers UALVP63964 through UALVP63967.

**Identification:** Centra are wide, thin, and platelike with concave circular articular surfaces and distinct growth lines. In dorsal view (Fig. 10C), the centra have two widely separated, deep, circular, neural arch articulation pits. The lateral face of the centra have long thin pits, separated by fibres of bone. Based on these features, we assign the centra to Elopiformes.

**Remarks:** The most complete centrum described here is from a posterior position in the vertebral column, based on comparison to those described by Brinkman (2019). The elopiform centra from the LCZ resemble those of *Paratarpon*, which is known from full-body articulated fossils from fluvial deposits of the DPFm (Neuman and Brinkman 2005). Similar centra are known from mosasaur gut contents from the Bearpaw Formation (Konishi et al. 2011). Some modern elopiforms, including *Megalops*, are euryhaline, but *Paratarpon* has previously been reported only from freshwater deposits within the Belly River Group (Brinkman 2019). Gilbert et al. (2018) attributed several centra to *Paratarpon* from their marginal marine sample from Saskatchewan. Because of the limited material known from marine environments, we do not assign these LCZ centra beyond the order.

### Order ALBULIFORMES Nelson, 1973

### Family ALBULIDAE Bleeker, 1859

### Subfamily PHYLLODONTINAE Sauvage, 1875

### Genus *Paralbula* Blake, 1940

### *Paralbula casei* Estes, 1969

Figure 10D, E

**Material:** 20 teeth, one centrum. Specimen numbers UALVP64159 through UALVP64170.

**Identification:** Very small (3 mm) round teeth with a convex occlusal surface, and a concave base. The crown is much wider than tall. The surface of the crown has smooth ridges, which converge towards the raised centre.

A single centrum, which is taller than wide in anterior view, is in our collection. The neural arch attachment pits are spaced closer and are more oblong in shape than in the elopomorph described above. In lateral view, the centrum has fewer thick ridges which are formed from bundles of smaller fibres.

**Remarks:** Phyllodont teeth from the DPFm have previously been assigned to this species (e.g., Beavan and Russell 1999). The attribution of the albulid centra to *P. casei* follows the referral by Neuman and Brinkman (2005) of similar material based on similarity to the related extant bonefish, *Albula*. Beavan and Russell (1999) figured a centrum, labelled unidentified osteichthyan centra type 2, which may also belong to *Paralbula casei*.

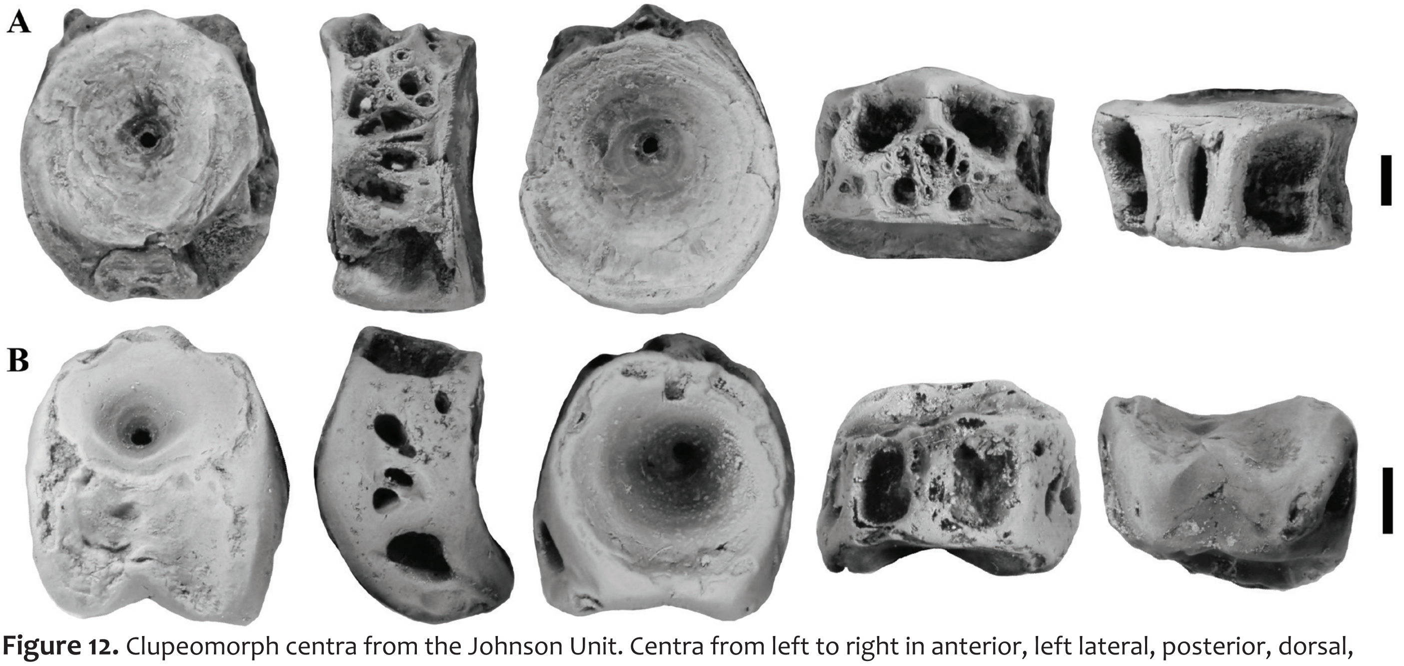


**Figure 12.** Clupeomorph centra from the Johnson Unit. Centra from left to right in anterior, left lateral, posterior, dorsal, and ventral views. Centra were coated in ammonium chloride and are depicted in greyscale. A, UALVP64218, ?clupeomorph precaudal centrum; B, UALVP64071 Horseshoeichthys anterior precaudal centrum. Scale bars = 1 mm.

### Superorder CLUPEOMORPHA Greenwood, Rosen, Weitzman, and Myers, 1966

### ?Clupeomorpha gen. indet.

Figure 12A

**Material:** One centrum. Specimen number UALVP64218.

**Identification:** An ovoid centrum which is taller than wide. The posterior facet is larger than the anterior one, and both facets are deeply concave, with a central notochordal foramen. On the dorsal surface, the deep, roughly triangular neural arch articular pits are positioned anteriorly, extending posteriorly for about half the length of the centrum. The neural arch articular pits are closely spaced, with a small bony flange separating them anteriorly. Two pits are positioned posteromedially between the neural arch pits. The lateral surface of the centrum has several small fossae separated by anteroposteriorly oriented ridges. Two large subrectangular parapophyseal pits, which extend almost halfway into the centrum in depth and cover almost the full anteroposterior length, are positioned ventrally on the lateral side. In between the parapophyseal pits on the ventral surface is a single long, thin rectangular pit.

**Remarks:** This specimen shows affinities to the centra of clupeomorphs, such as two described from freshwater deposits of the DPFm, *Horseshoeichthys* and *Diplomystus*, by possessing anteriorly positioned neural arch articular pits (Neuman and Brinkman 2005; Newbrey et al. 2010; Brinkman 2019); however, the parapophyseal pits on the ventral surface are much larger than those in either of those genera. The single long midventral pit positioned between the parapophyseal pits is more similar to that of clupeiform type G, which is known from freshwater deposits of the Belly River Group (Brinkman 2019). However, the Johnson Unit centrum is significantly more plate-like than those of clupeiform type G, and seems to represent a new morphotype.

### Order ELLIMMICHTHYIFORMES Grande, 1982

### Family SORBINICHTHYIDAE Bannikov and Bacchia, 2000

### Genus *Horseshoeichthys* Newbrey, Murray, Brinkman and Wilson, 2010

### *Horseshoeichthys* sp.

Figure 12B

**Material:** One centrum. Specimen number UALVP64071.

**Identification:** The single anterior centrum from our sample that we can assign to this genus is slightly taller than wide. The articular facets are concave, with the posterior one deeper than the anterior one. The anterior facet is approximately half the height of the posterior facet and is positioned dorsally on the element. There is a small central notochordal foramen, which is positioned dorsal to the centre of the posterior facet, and ventral to the centre of the anterior facet – this is because of the facets being vertically offset in position. In dorsal view, the centrum has two deep subrectangular pits for articulation of the neural arch, which extend nearly the entire anteroposterior length of the element. The lateral surface is smooth, solid bone pierced by several deep circular pits. In lateral view, the ventral surface of the centrum angles anterodorsally to posteroventrally. There is a shallow, median concavity on the ventral surface. No parapophyseal pits are present, indicating an anterior position in the vertebral column.

**Remarks:** The genus *Horseshoeichthys* was described subsequent to the publications by Beavan and Russell (1999) and Brinkman et al. (2005) on the Lethbridge Coal Zone. Specimens now recognized as belonging to *Horseshoeichthys* were originally grouped as morphoseries IIA–2 and IB–2 by Brinkman and Neuman (2002), and are well known from the freshwater deposits of the DPFm, along with several other Late Cretaceous formations in Alberta (Newbrey et al. 2010; Brinkman 2019). Although this is the first report of *Horseshoeichthys* from the Johnson Unit, other authors previously reported material which can now be referred to the genus. Beavan and Russell (1999) referred six centra to a morphotype, termed unidentified osteichthyan type 4, which is very similar to the *Horseshoeichthys* sp. centrum described here (although we believe it was figured upside-down). Brinkman et al. (2005) referred centra to both morphotaxa IB–2 and IIA–2 from their sample, which also belong to *Horseshoeichthys* (Brinkman 2019). Unlike the type species, *Horseshoeichthys armaserratus* Newbrey et al., 2010, paired dorsal fossae are not present between the neural arch articulations of our specimen. *Horseshoeichthys* has also been documented from a similar marginal marine palaeoenvironment in Saskatchewan (Gilbert et al. 2018). It is possible that *Horseshoeichthys* included species that were euryhaline, or even diadromous, since modern clupeomorphs include species that live in freshwater and marine environments as well as those that move between the two (Nelson et al. 2016).

### Cohort EUTELEOSTEI sensu Arratia, 1999

### Order AULOPIFORMES Rosen, 1973

### Suborder ENCHODONTOIDEI sensu Nelson, 1994

### Family DERCETIDAE Woodward, 1901

### Genus *Dercetis* Agassiz, 1834

### *Dercetis* cf. *D. magnificus* Chida, Brinkman, and Murray, 2023

Figure 13A, B

**Material:** 18 centra. Specimen numbers UALVP63930 through UALVP63942.

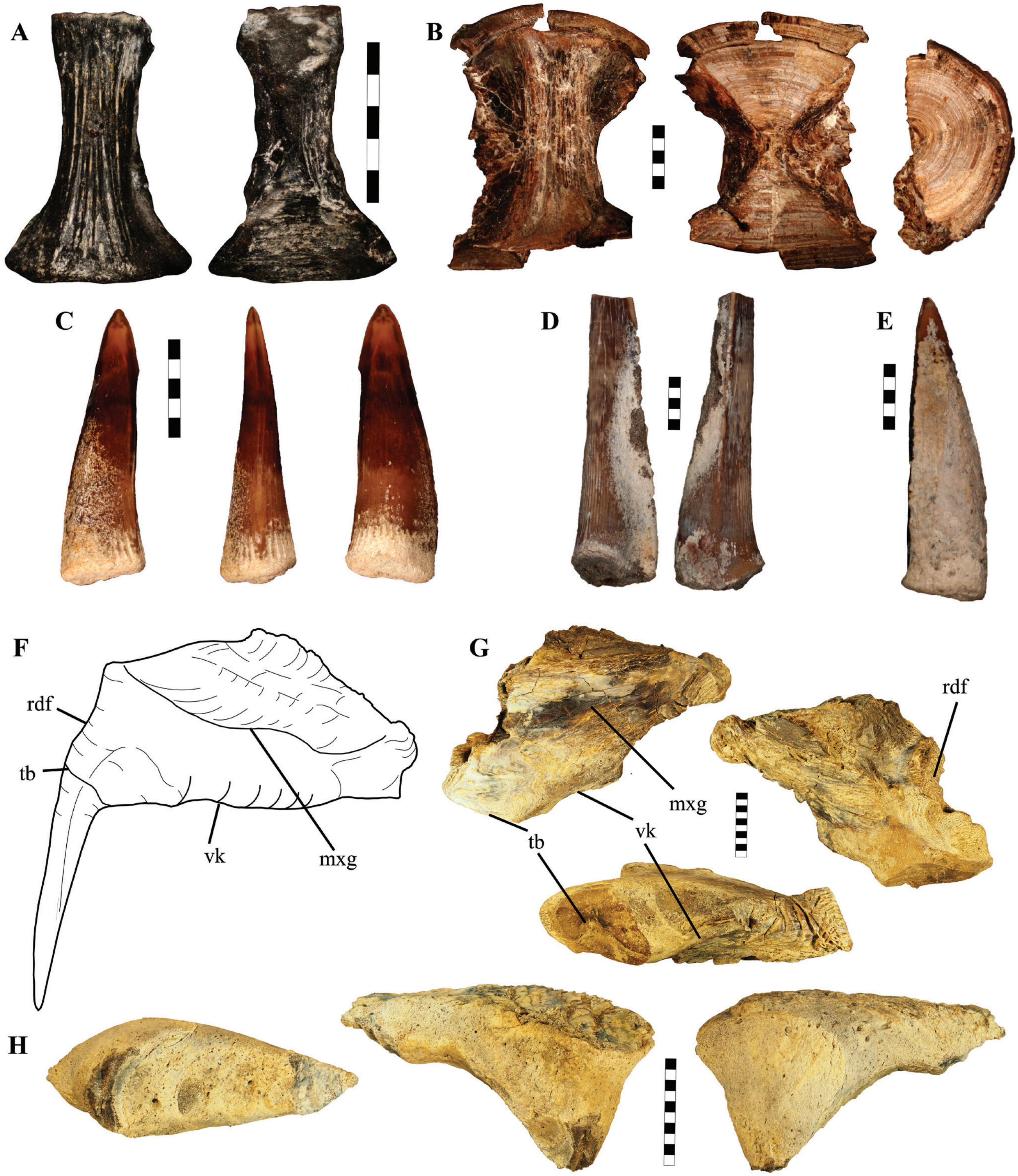


**Figure 13.** Enchodontoids from the Johnson Unit. A, B, *Dercetis magnificus* centra: A, UALVP63935, fragmentary centrum in lateral (left) and internal (right) views (anterior towards top of the page); B, UALVP63998, broken centrum in, from left to right, lateral, internal, and anterior views (anterior towards top of the page in lateral and internal views); C, UALVP63984, *Enchodus gladiolus* palatine or ectopterygoid tooth from left to right in labial, posterior, and lingual views; D, UALVP64024, *Enchodus petrosus* left palatine tooth in posteromedial (left) and lateral (right) views; E, UALVP64002, *Enchodus petrosus* dentary tooth in ?lateral view; F, drawing of a complete left dermopalatine of *Enchodus petrosus* in lateral view; G, UALVP64004, *Enchodus petrosus* left dermopalatine in lateral (left), medial (right) and ventral (bottom) views; H, UALVP64012, *Enchodus petrosus* fragmentary ectopterygoid from left to right in ventral, medial, and lateral views. Abbreviations: mxg, maxillary groove; rdf, facet for articulation of the rostrodermethmoid; tb, tooth base; vk, ventral keel. Scale bars = 5 mm in A–F, scale bar = 10 mm in G,H.

**Identification:** None of these vertebrae are complete and they tend to be broken lenthwise. These are the most abundant actinopterygian vertebrae in our sample and are relatively large and elongate with a pattern of fine striations on their lateral surfaces (Fig. 13 A, B). This vertebral morphology is congruent with those of the recently described species *Dercetis magnificus* from the Albertan Bearpaw Formation (Chida et al. 2023), and so we assign these vertebrae to *Dercetis* cf. *D. magnificus*.

**Remarks:** Beavan and Russell (1999:499) identified a similar morphotype of vertebra that they called "unidentified osteichthyan centrum, type 3", which they suggested had affinities with the enigmatic enchodontoid *Stratodus*.

### Family ENCHODONTIDAE Woodward, 1901

### Genus *Enchodus* Agassiz, 1835

### *Enchodus* indet.

**Material:** Five dermopalatines, six centra. Specimen numbers UALVP63991 through UALVP64001.

**Identification:** Dermopalatines of *Enchodus* are distinctive, and are identified by the anteroventral tooth attachment site, ventral keel with replacement scars, and anterodorsal articulation facet for the mesethmoid bone. Several of our specimens are not sufficiently complete to be confidently identified to either of the species below, but clearly belong to the genus.

The centra have round articular surfaces, and longitudinal ridges along their lengths, as well as several round pits on their lateral sides. They are relatively much taller than those attributed to *Dercetis*.

### *Enchodus gladiolus* Cope, 1872

Figure 13C

**Material:** Two dermopalatines, 31 teeth. Specimen numbers UALVP63968 through UALVP63990.

**Identification:** Dermopalatine teeth of *E. gladiolus* (Fig. 14C) possess sharp edges along the anterior length of the tooth in addition to a small postapical barb, which forms a short posterior cutting edge near the distal tip. *Enchodus gladiolus* teeth are symmetrical in cross section, and sigmoidal in profile shape (Parris et al. 2007).

**Remarks:** This is the first report of *Enchodus gladiolus* from Alberta. This species has a sympatric distribution with *E. petrosus* in many formations across North America (e.g., Becker et al. 2010), so this report is not unexpected. The dermopalatine teeth of this species occur in nearly identical proportions to those of *E. petrosus* in our sample; however, partial dermopalatine bones were much less common. This could be because of the smaller size of the dermopalatine of *E. gladiolus* resulting in a negative preservation collection bias. It is also possible that the thin, elongate shape of the dermopalatine of *E. gladiolus* makes them less easily distinguished in the field; the mesethmoid attachment and tooth attachment sites on the dermopalatine are spaced more widely in *E. gladiolus* (Goody 1976), meaning that fragments are less likely to contain both, and thus are harder to notice or identify during surface collection.

### *Enchodus petrosus* Cope, 1874

Figure 13D–H

**Material:** 13 dermopalatines, 28 teeth. Specimen numbers UALVP64002 through UALVP64032.

**Identification:** Dermopalatine teeth of *E. petrosus* possess anterior and lateral cutting edges that run the length of the tooth, a highly asymmetrical trianguloid cross section, and striations on the posteromedial face of the tooth (Goody 1976; Parris et al. 2007). The teeth are straight in profile, with no post-apical barb. In *E. petrosus*, the dermopalatine is quite deep, with a maxillary groove beginning far anterior on the element.

**Remarks:** The teleost genus *Enchodus* was identified in the LCZ by previous authors; however, the specific identification of the teeth was not given (Brinkman et al. 2005; Beavan and Russell 1999). Our sample includes many teeth from the genus, with the majority shed from the dermopalatines and pterygoids. As noted by Schein and Lewis (2007), the size and durability of *Enchodus* teeth and dermopalatines are likely to result in a preservational bias compared to elements from other actinopterygians. This likely contributes to *Enchodus* being one of the most common Late Cretaceous actinopterygians represented as microfossils from around the world (Carpenter 1996); however, high numbers of articulated fossils from the Bearpaw Formation indicate that it was also quite abundant in general.

We re-identify the tooth figured by Brinkman et al. (2005: fig. 26.3A) as belonging to *E. petrosus*. Our identification contrasts with that of Hoganson et al. (2019), who tentatively identified the tooth figured by Brinkman et al. (2005) as *Enchodus ferox*. Goody (1976) stated that teeth of *Enchodus ferox* possess serrations along their carinae but have no striations along their posteromedial margins. Examination of the holotype tooth of *E. ferox* by one of us (LEN) has confirmed the validity of the diagnostic features listed by Goody (1976). The *Enchodus* teeth in our sample all possess striations along their posteromedial margins, and none possess the serrated cutting edges along their carinae, which are characteristic of *E. ferox*. The tooth figured by Brinkman et al. (2005: fig. 26.3A) similarly lacks serrations and possesses posteromedial striations (although somewhat worn). Thus, we conclude that *Enchodus ferox* teeth are not known from the Lethbridge Coal Zone in Alberta.

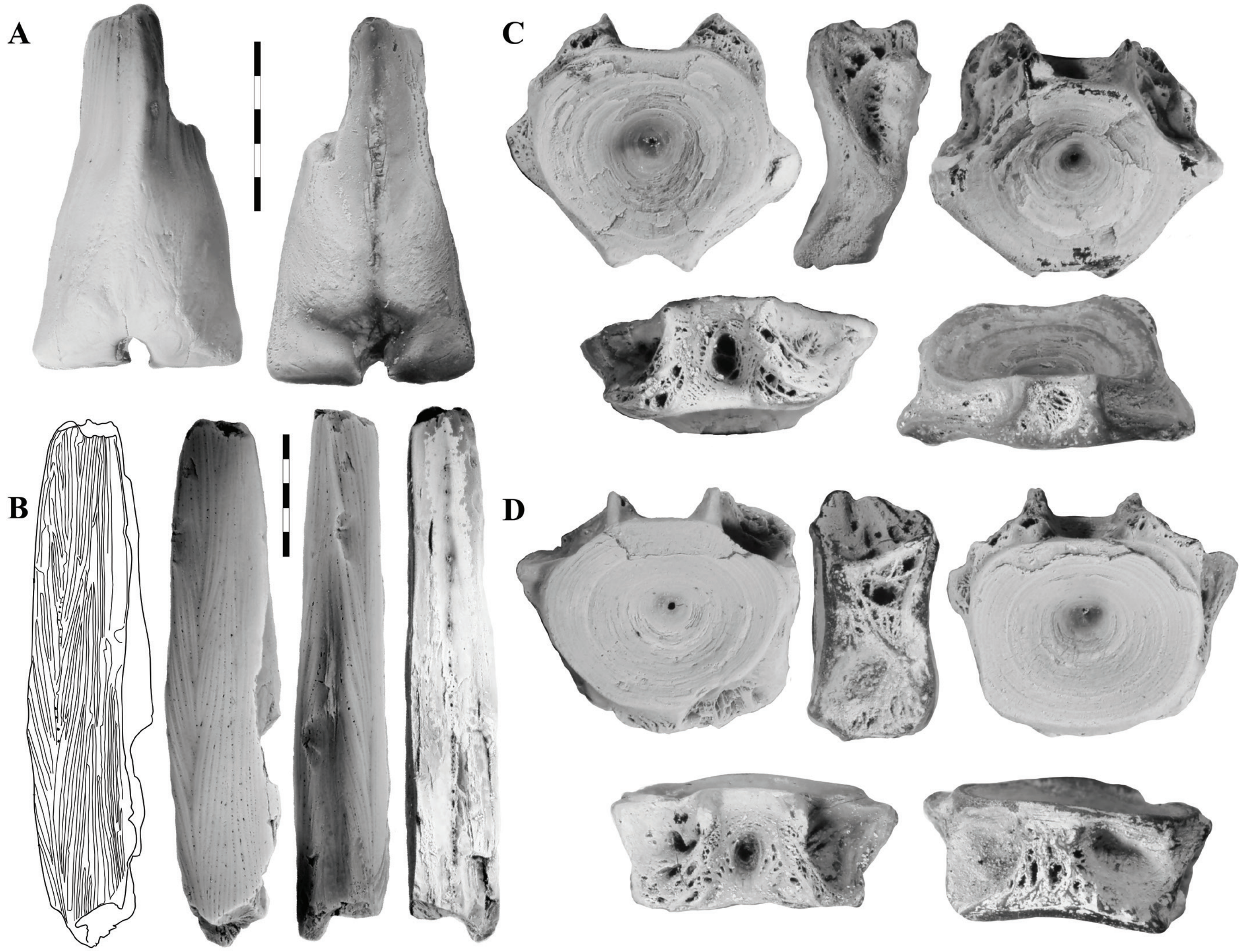


**Figure 14.** Acanthomorph specimens from the Johnson Unit, coated in ammonium chloride, depicted in greyscale. A, UALVP63806, spine base in anterior (left) and posterior (right) views; B, UALVP63810, spine shaft with ornamentation from left to right with lateral view line illustration, anterior, lateral, and posterior views; C, UALVP63808, anterior precaudal centrum figured from left to right, top row in anterior, left lateral, and posterior views, bottom row in dorsal, and ventral views. D, UALVP63813, Precaudal centrum figured from left to right, top row in anterior, left lateral, posterior, bottom row in dorsal, and ventral views. Scale bars = 5 mm.

### Sept ACANTHOMORPHA Rosen, 1973

Acanthomorpha indet.

Figure 14A–D

**Material:** Seven spines, three centra. Specimen numbers UALVP63806 through UAVLP63814.

**Identification**: The spines in our sample are true spines (i.e., single, median elements) which are diagnostic of acanthomorphs. The elements include shafts and bases; we did not find any complete spines. The largest isolated spine base has a flat, wide proximal end with a median notch, and deep V-shaped posterior groove (Fig. 14A). We cannot determine if the proximal notch on the base of the spine was open or whether there was a basal bar that is now broken. The preserved portion narrows distally and becomes laterally compressed, with surface ridges ornamenting the sides distally. Similar ridged ornamentation is visible on the lateral surfaces in two other specimens that are identified as fragmentary spine shafts lacking proximal and distal ends (Fig. 14B). The ornamentation consists of alternating anterodistally and posterodistally oriented bundles positioned diagonal to the long axis of the shaft. The shafts possess a posterior groove that is similar in shape to those of the isolated bases. The anterior surface also bears a longitudinal groove, which is shallow and ends before the distal tip of the preserved shaft. The anterior groove on these shafts is rare for acanthomorphs but would accommodate the preceding spine when the fin is flattened. We also found several smaller, worn spines. Their bases resemble those of the larger ornamented spines, with a flat proximal margin, and an open median notch.

There are two mostly complete centra and one fragmentary centrum that we attribute to acanthomorphs. The unambiguous diagnostic centrum of acanthomorphs is their tripartite first centrum (Murray and Brinkman 2023), of which we have none. Acanthomorph anterior abdominal centra possess posterolateral processes (sometimes referred to as zygapophyses, e.g., Grande 1988; Brinkman 2019), which are visible, albeit small, on one of the centra (Fig. 14C). The abdominal centra in our sample also resemble those of acanthomorphs due to the complexity of the struts on their lateral faces. These centra are compressed anteroposteriorly with ovoid facets that are wider than tall (Fig. 14C, D). The narrow anteroposterior width indicates an anterior position in the vertebral column. Dorsally, the centra have large, somewhat triangular neural arch pits, and a large, round mid-dorsal pit. In lateral view, the centra have a complex surface of many small pits, with robust triangular struts running along the surface. The large subrectangular parapophyseal pits are located ventrally. One of the two complete centra has a prominent midventral pit, and an overall anteriorly concave shape in lateral view. The other complete centrum has nearly flat faces in lateral view and lacks a mid-ventral pit.

**Remarks:** Acanthomorphs are a highly diverse group of actinopterygians, with almost 20,000 extant members (e.g., Chen et al. 2014). Freshwater acanthomorphs from the Cretaceous of Alberta include an articulated percopsiform from the Maastrichtian of the Scollard Formation (Murray et al. 2020). Isolated elements from five freshwater acanthomorph morphotypes are also known from the Belly River Group (Brinkman 2019), but none resemble the centra described here. In Albertan marine formations, the sphenocephalid acanthomorph *Xenyllion zonensis* is known from the Cenomanian Fish Scales Formation (Wilson and Murray 1996). The specimens reported here are the only other published Albertan marine acanthomorph specimens, although numerous other marine acanthomorphs are known from other areas of the WIS (Murray 2016).

There is no published widespread survey of morphological variation in extant acanthomorph spines so comparisons with modern taxa are limited to our own observations. The ornamentation on the spines from our sample resembles that of the Late Cretaceous bercyiform spines described by Becker et al. (2009). The bases of the DPFm spines appears different from those of Bercyiformes because of the lack of a basal bar; however, this lack may be an artefact of preservation. The shape of the spine bases also somewhat resembles those of extant gasterosteids, which have an open median notch (Reimchen 1983), but the DPFm spines lack ventrally projecting processes present in gasterosteid spines.

## ASSOCIATED TAXA

### Marine Reptiles

A large portion of the tetrapod material from the Johnson Unit is identified as belonging to plesiosaurs, because of the very dense and highly remodelled bone. Much of the tetrapod skeletal material is greatly fragmented so our identifications are tentative. We have excluded this material from our total number of elements in Appendix 2, reporting in that table only plesiosaur teeth and centra that we can confidently identify (Fig. 15 A–C). Plesiosaur centra in our sample are large and platycoelous with paired foramina subcentralia on their ventral surfaces, which are diagnostic of plesiosaurs (Storrs 1991; Wintrich et al. 2017). We also collected several broken large teeth with an elongate (approximately 4 cm), recurved, and conical shape that we identified as plesiosaur. The teeth lack carinae but have longitudinal surface grooves.

The plesiosaur material lacks traits diagnostic of families. Beavan and Russell (1999) attributed plesiosaur remains within the LCZ to Polycotylidae, whereas Brinkman et al. (2005) indicated that they belonged to Elasmosauridae. Sato et al. (2005) attributed much of the isolated plesiosaur material from Dinosaur Provincial Park to elasmosaurids, and indicated that several specimens identified as polycotylids from the area lack sufficient diagnostic characters for confident identification. Subsequently, the elasmosaurid *Fluvionectes sloanae* was described from the LCZ (Campbell et al. 2021), and other LCZ plesiosaur material was referred to this taxon. In the overlying Bearpaw Formation, polycotylids are common in the shallow waters of the Herschel Bonebed of Saskatchewan (Sato 2005); therefore, our non-diagnostic material cannot be assumed to represent elasmosaurids.

We found several teeth and vertebrae clearly belonging to mosasaurs in our sample. The teeth are isolated crowns, with a small pulp cavity and are labiolingually compressed with anterior and posterior carinae. They curve posteriorly, with smooth, flat, faceted labial and lingual faces (Fig. 15D). Based on their flat facets and lack of serrations or striations, they are most similar to those of *Mosasaurus* (Street et al. 2021). *Mosasaurus missouriensis* is known from the Bearpaw Formation of Alberta (Konishi et al. 2014). This identification is tentative, since none of the specimens are complete crowns, and significant convergence exists in mosasaur dental anatomy (Street et al. 2021).

The procoelous centra, most of which are quite small and worn, lack features required for precise identification. The most complete specimen is a large caudal centrum (length = 47 mm; maximum condyle width = 52 mm; maximum condyle height = 45 mm) with facets for articulation of the haemal arch, and a roughly circular articular surface (Fig.

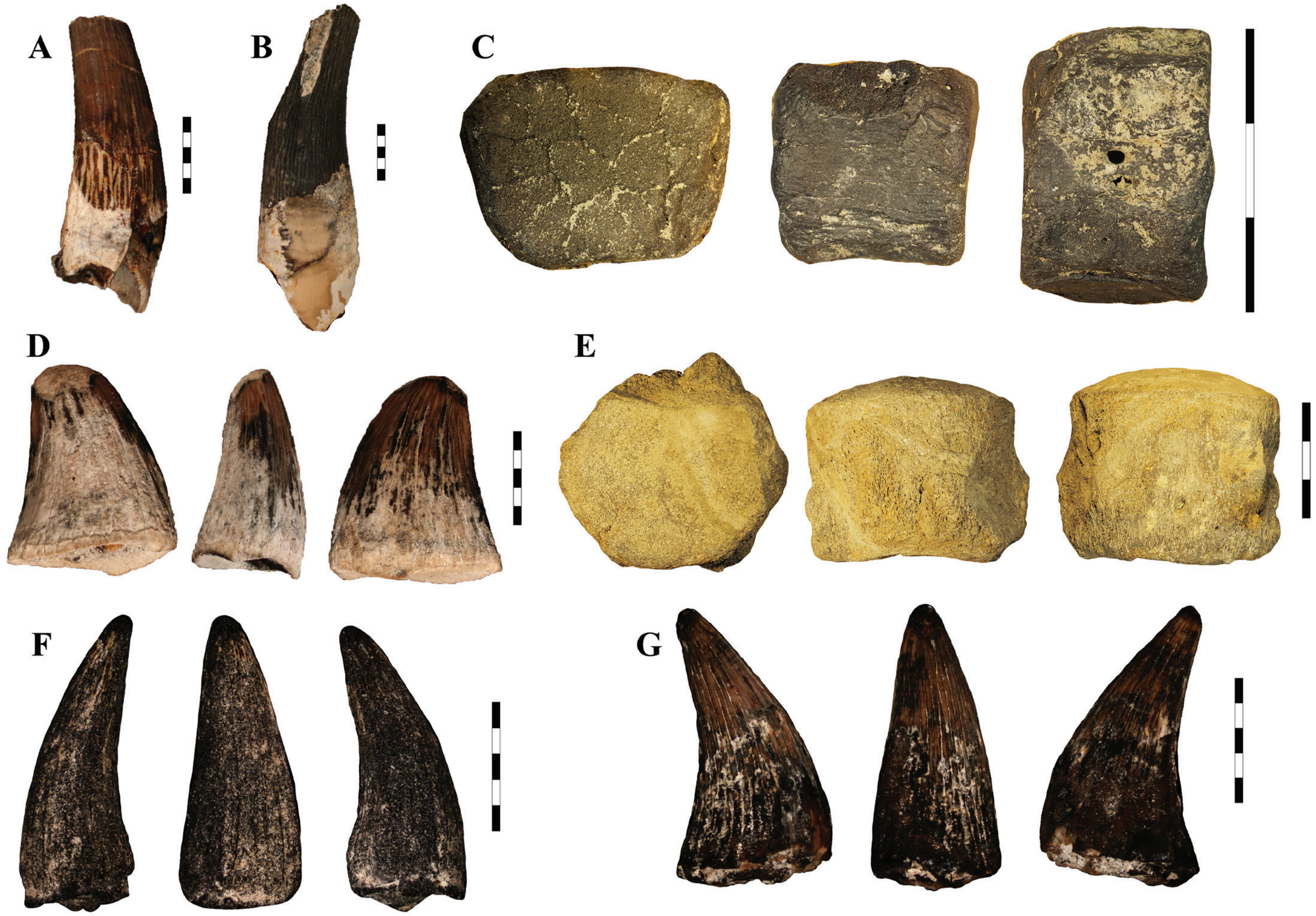


**Figure 15.** Marine reptiles from the Johnson Unit. A, UALVP63963, plesiosaur tooth, labial view; B, UALVP63962, plesiosaur tooth, ?lingual view; C, UALVP64176, plesiosaur centrum, from left to right in anterior, lateral, and ventral views; D, UALVP64117, mosasaur tooth from left to right in labial, profile, and lingual views; E, UALVP64119, mosasaur caudal centrum from left to right in anterior, dorsal, and ventral views; F, UALVP64228, ?mosasaur tooth without enamel from left to right in labial, profile, and lingual views. G, UALVP64227, ?mosasaur tooth with enamel, from left to right in labial, profile, and lingual views. Scale bars = 5 mm in A, B, D, F, G; scale bars = 3 cm in C, E.

15E). The haemal arch articular facets indicate that this centrum is not from a mosasaurine, which possess fused haemal arches (Jimenez-Huidobro et al. 2016). The size and unfused haemal arches of this centrum are consistent with the genus *Plioplatecarpus*, which is one of the most abundant mosasaurs in the overlying Bearpaw Formation (Holmes 1996). *Plioplatecarpus* has also previously been reported from the LCZ (Caldwell 2005). If this centrum is from *Plioplatecarpus*, the individual animal would have possessed an estimated snout-vent length of approximately 1.5–1.8 m, based on comparison to vertebral measurements and length estimates by Holmes (1996).

Other tetrapod material includes several smaller, highly recurved teeth with prominent longitudinal surface ridges (Fig. 15F, G). These teeth are relatively common in our sample (n=14). The teeth have two cutting edges, placed posteromedially and posterolaterally, resulting in a D–shaped cross section. The teeth are smaller, but also proportionally thicker and more recurved than is typical of isolated plesiosaur teeth from the Johnson Unit (e.g., Brinkman et al. 2005: fig. 26.3B), and from fluvial deposits in the LCZ (Campbell et al. 2021). The teeth resemble those from the LCZ identified as plioplatecarpine mosasaur (Caldwell 2005: fig. 13.3A), although the size of the prominent surface ridges may contradict this identification. We tentatively identify these teeth as ?Mosasauria.

## Other Reptiles

Turtle shell fragments in our sample are identified as belonging to two different superfamilies, Trionychoidea and Chelonoidea. The trionychoid shell fragments are typically broken sections of plastron or carapace, but we also found larger elements such as the possible hyoplastron element (Fig. 16A). Trionychoid shell elements in our sample are

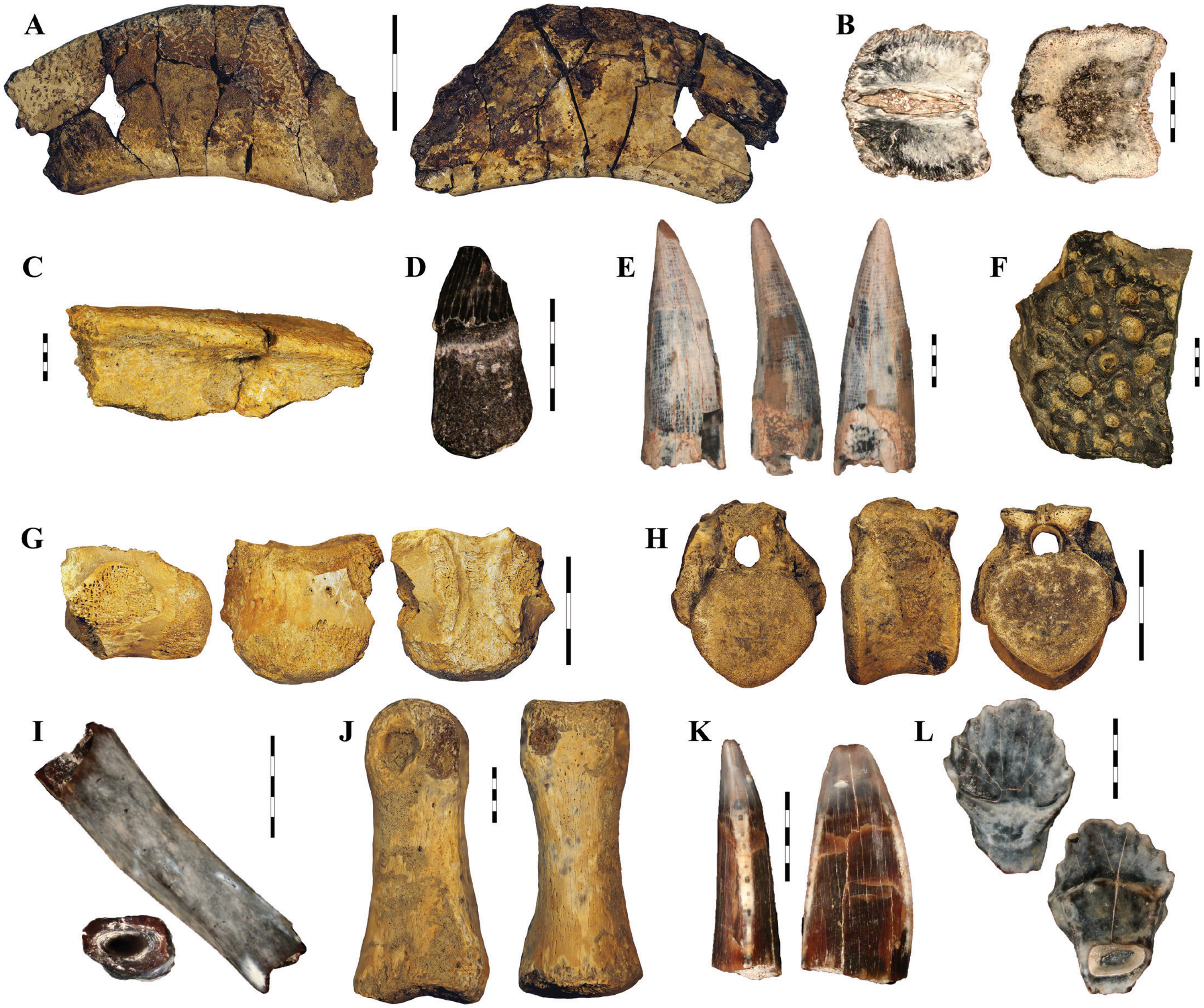


**Figure 16.** Other reptiles from the Johnson Unit. A, UALVP64222, trionychoid ?hyoplastron element in external (left) and internal (right) views; B, UALVP63913, chelonioid neural plate, in apical (left) and basal (right) views; C, UALVP63910, chelonioid peripheral plate in ventromedial view; D, UALVP63925, crocodilian molariform tooth in lateral view; E, UALVP63927, crocodilian caniniform tooth from left to right in posterior, lingual, and anterior views; F, UALVP63928, crocodilian scute, in external view; G, UALVP63922, crocodilian centrum, from left to right in lateral (anterior to the left), ventral, and dorsal views (anterior to the top of the page); H, UALVP64234, champsosaur vertebra, from left to right in anterior, lateral, and posterior views; I, UALVP63929, maniraptoran long bone fragment, in transverse (below) and lateral (above) views; J, UALVP64158, ornithomimid phalanx, in lateral (left) and dorsal (right) views; K, UALVP63943, dromaeosaur tooth, in posterior (left) and lingual (right) views; L, UALVP63817, ankylosaur tooth, in lingual (left) and labial (right) views. Scale bars for A, G, H = 3 cm; scale bars for B–F, I–L = 5 mm.

diagnosed by the series of widely separated anatomizing tubercles and ridges (Fig. 16A), or a pock-marked texture, similar to the surface of a golf ball (Brinkman 2003). Modern trionychoids venture into marine habitats (Taskavak and Akcinar 2009), and are well known from the freshwater environments of the DPFm (Brinkman 1990), thus their presence in the Johnson Unit is not unexpected.

Marine chelonioid turtles are also present in our sample. These lack the shell surface texturing of trionychoids. Chelonioids are primarily represented in our sample by peripherals, which when complete, are rod-like and triangular in cross-section, with concave median surfaces, and deeper depressions at the locations of articulation with the costals (Fig. 16C). Several chelonioids are currently known from the late Campanian of Alberta: *Nichollsemys bauri*, *Kimurachelys slobodae*, and *Lophochelys* sp. (Brinkman et al. 2015). Our material is too limited to allow a more precise identification.

The crocodylian material in our sample includes teeth (Fig. 16D, E), scutes (Fig. 16F) and a procoelous centrum (Fig. 16G), with crescentic neural arch attachment sites. The crocodile teeth in our sample are mostly molariform (Figure 16D), with the addition of a single large caniniform tooth (Fig. 16E). Beavan and Russell (1999) attributed their crocodilian material from the Johnson Unit to the genus *Leidyosuchus*, which is the best-known crocodilian from deposits in the lower portion of the DPFm. However, we refrain from this identification, since other crocodilians are known to live sympatrically with *Leidyosuchus* in the DPFm (Lindblad 2024). *Champsosaurus* vertebrae are also present in our sample (Fig. 16H). Brinkman (1990) found an increase in the abundance of *Champsosaurus* specimens with increasing marine influence in the Dinosaur Park Formation, so it seems probable that they ventured into the marine habitat of the Johnson Unit.

Remaining tetrapod material is attributed to Dinosauria, with only single specimens from several different taxa (Fig. 16I-L). The low abundance of dinosaur material, and marine setting, support the conclusion that these specimens were washed downstream postmortem.

### Invertebrates

Previous studies on the Johnson Unit did not report any invertebrate remains (Brinkman et al. 2005; Beavan and Russell 1999). We identified several invertebrates and their traces in our study, including remains of molluscs, crustaceans, and infilled worm burrows. Partial *Placenticeras* ammonites are common in the overlying Bearpaw Formation (Tsujita and Westerman 1998). To our knowledge, the disc-shaped fragment from our sample (Fig. 17A) is the first report of *Placenticeras* from the Dinosaur Park Formation. We also found gastroliths of crayfish and lobsters (Fig. 17B). In other formations, these have previously been misidentified as actinopterygian dental elements (Brinkman et al. 2013; Panzeri et al. 2024). They can be differentiated from the teeth of albulid actinopterygians by their multi-banded interior (Brinkman et al. 2013). The remains of the clawed lobster *Palaeonephrops browni* are well known from the Bearpaw Formation (Tsujita 2003). A crustacean tail from our sample (Fig. 17C) resembles that of *Palaeonephrops*, although its poor preservation means this diagnosis is tentative. The specimens did not appear to be reworked, since they occurred within the fossiliferous layer of the Johnson Unit. These taxa appear generally similar to those known from the Bearpaw Formation, indicating that some of the open marine invertebrates of the Bearpaw also occupied the nearshore environment of the LCZ.

## JOHNSON UNIT SAMPLES

We collected and identified a total of 1431 vertebrate microfossils (Appendix 1) representing 40 taxa. Many of the specimens can only be identified to higher level taxa or morphotypes, rather than to generic or specific levels. The rarefaction curve from our ten field days (Fig. 18) depicts the relationship between person-sampling-hours and taxa recovered, and shows a decreasing slope at the end of our field work. This supports the sufficiency of our sampling.

The Bray-Curtis distance (ranging from 0–1, with values closer to 0 indicating a more similar composition) between the relative abundances of taxa in our combined sample, and those of Beavan and Russell (1999), and Brinkman et al. (2005), was 0.6958 and 0.7754, respectively. On the other hand, the two screen-washing samples had a Bray-

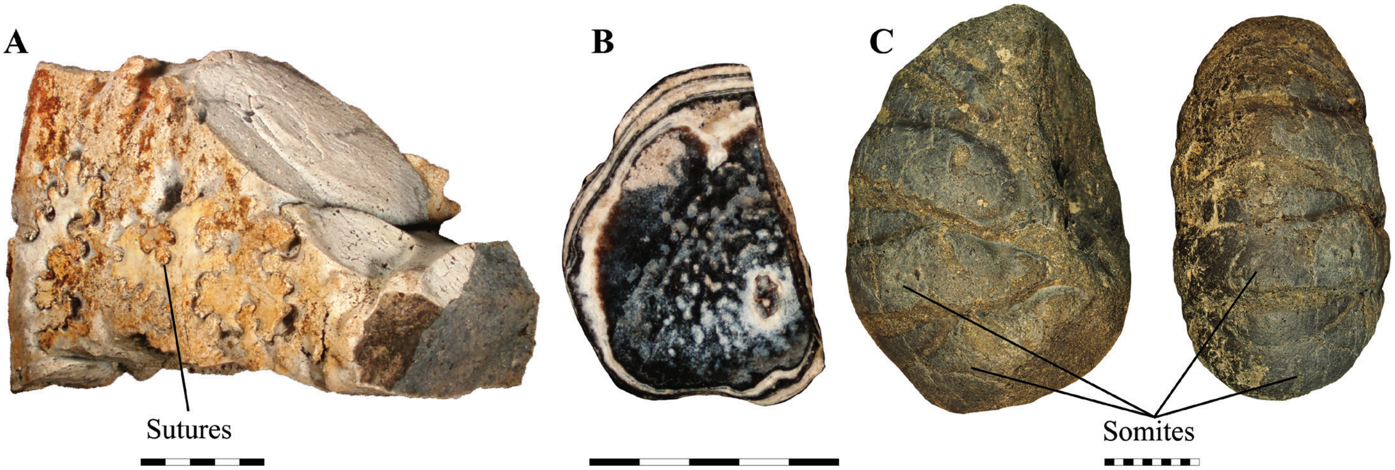


**Figure 17.** Invertebrate fossils from the Johnson Unit. A, UALVP64354 *Placenticeras* ammonite fragment, in lateral view; B, UALVP64355, crawfish stone in cross sectional view; C, UALVP64356, clawed lobster tail, potentially *Palaeonephrops* sp., from left to right in lateral and dorsal views. Scale bars = 5 mm, except C, where scale bar =10 mm.

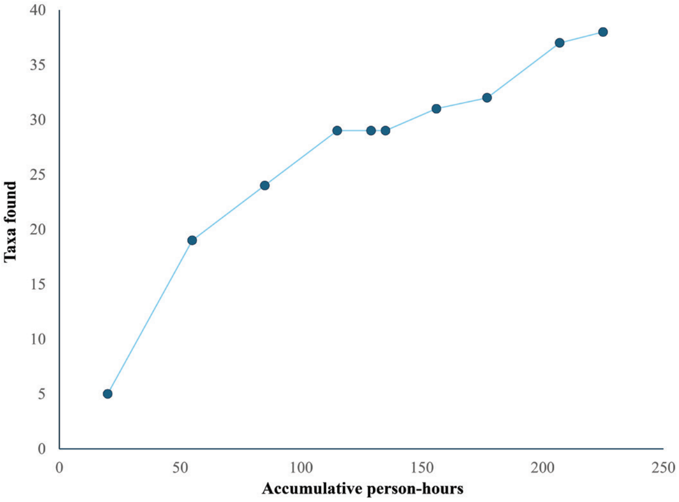


**Figure 18.** Rarefaction curve, depicting the relationship between sampling effort (person-hours; total=225), and new species collected. Species counts represent the minimum number of species. Each data point represents the running total of all species collected at the end of each of the ten field days.

Curtis distance of 0.2129 between one another, indicating that they were far more similar to each other than either is to our surface collected sample.

# DISCUSSION

## Comparison to previous Johnson Unit samples

Relative abundance and presence/absence data within our sample are markedly different from previously reported screen-washed samples from the Johnson Unit (Fig. 19). Several of the taxa with the smallest specimens (*Myledaphus bipartitus*, *Protoplatyrhina renae*, and *Paralbula casei*) are comparatively rare in our collection. On the other hand, these were the three most common taxa in the sample studied by Brinkman et al. (2005), and three of the top four most common in that of Beavan and Russell (1999). Several small chondrichthyan teeth previously reported from the LCZ (Brinkman et al. 2005) are entirely absent from our sample; these are *Squatina* sp., *Ptychotrygon blainensis*, and *Eucrossirhinus microcuspidatus*. Our most abundant three taxa, *Archaeolamna kopingensis judithensis*, *Meristodonoides montanensis*, and *Carcharias* cf. *C. samhammeri*, are overrepresented in our sample compared to the screen-washed samples. Our sample includes two species of holocephalians, which are recognized for the first time in the LCZ. One of them, *Ischyodus bifurcatus*, has not been previously described from Canada. We have also identified the presence of eight actinopterygian taxa previously unreported from the Johnson Unit: *Belonostomus longirsotris*, Amiidae gen. indet., Elopiformes gen. indet., *Horseshoeichthys* sp., *Enchodus gladiolus*, *Dercetis* cf. *D. magnificus*, Acanthomorpha indet., and Teleost Morphotype O. This is the first record of Teleost Morphotype O in the Belly River Group, and the first record of *Enchodus gladiolus* in Alberta. We have also identified a large sample of *Enchodus* dermopalatines, none of which were complete, but nonetheless were identifiable based on their articulation facets and general shape.

## Marine faunal changes in similar environments

Our microfossil sample collected from the marine deposits of the Johnson Unit can be compared to other marine faunas to increase our understanding of faunal changes. In particular, we compare the fauna with three other regional assemblages. The first is that of the Bearpaw Formation, which immediately overlies the LCZ, and thus reflects changes in the fauna over time. The second is that of the Diefenbaker microsite in Saskatchewan which is thought to be nearly contemporaneous with the LCZ, and of a somewhat similar environment (Gilbert et al. 2018). The third is the marine influenced sections of the Foremost Formation, which were deposited at the base of the Belly River Wedge, as the WIS was undergoing regression (Cullen et al. 2016).

The Bearpaw Formation is a deeper water palaeoenvironment than the Johnson Unit (Tsujita and Westermann 1998). Taphonomic factors during deposition of the Bearpaw Formation differed significantly from that of the Johnson Unit, favouring the preservation of large articulated tetrapod skeletons (Newbrey and Konishi 2015) in the former, rather than disarticulated microfossils in the latter. Since their material properties are similar, assemblages of shark teeth are potentially comparable, regardless of taphonomic differences between the formations (Brinkman 2008). Therefore, we here compare the shallower water fauna of the Johnson Unit with that of the Bearpaw Fm.

Chondrichthyans are primarily known from teeth found in association with large tetrapod skeletons recovered from the Bearpaw Formation (e.g., Konishi et al. 2011, 2014), although isolated *Cretolamna* teeth have also been reported (Gardiner 1966). Cook et al. (2017) described a euselachian microfossil assemblage from the Bearpaw Formation that contained seven species of euselachians: *Meristodonoides montanensis*, *Paraorthacodus andersoni*, *Squalus worlandensis*, *Cretoxyrhina mantelli*, *Carcharias* cf. *C. samhammeri*, *Odontaspis aculeatus*, and *Archaeotriakis ornatus*. This assemblage shares three pelagic shark species with the Johnson Unit (*M. montanensis*, *O. aculeatus*, and *C.* cf. *C. samhammeri*), but differs significantly in overall composition. The Bearpaw sample entirely lacks batoids, which are a major component of all assemblages reported from the Johnson Unit (Beavan and Russell 1999; Brinkman et al. 2005; this study). Cook et al. (2017) attributed this lack to the dysoxic

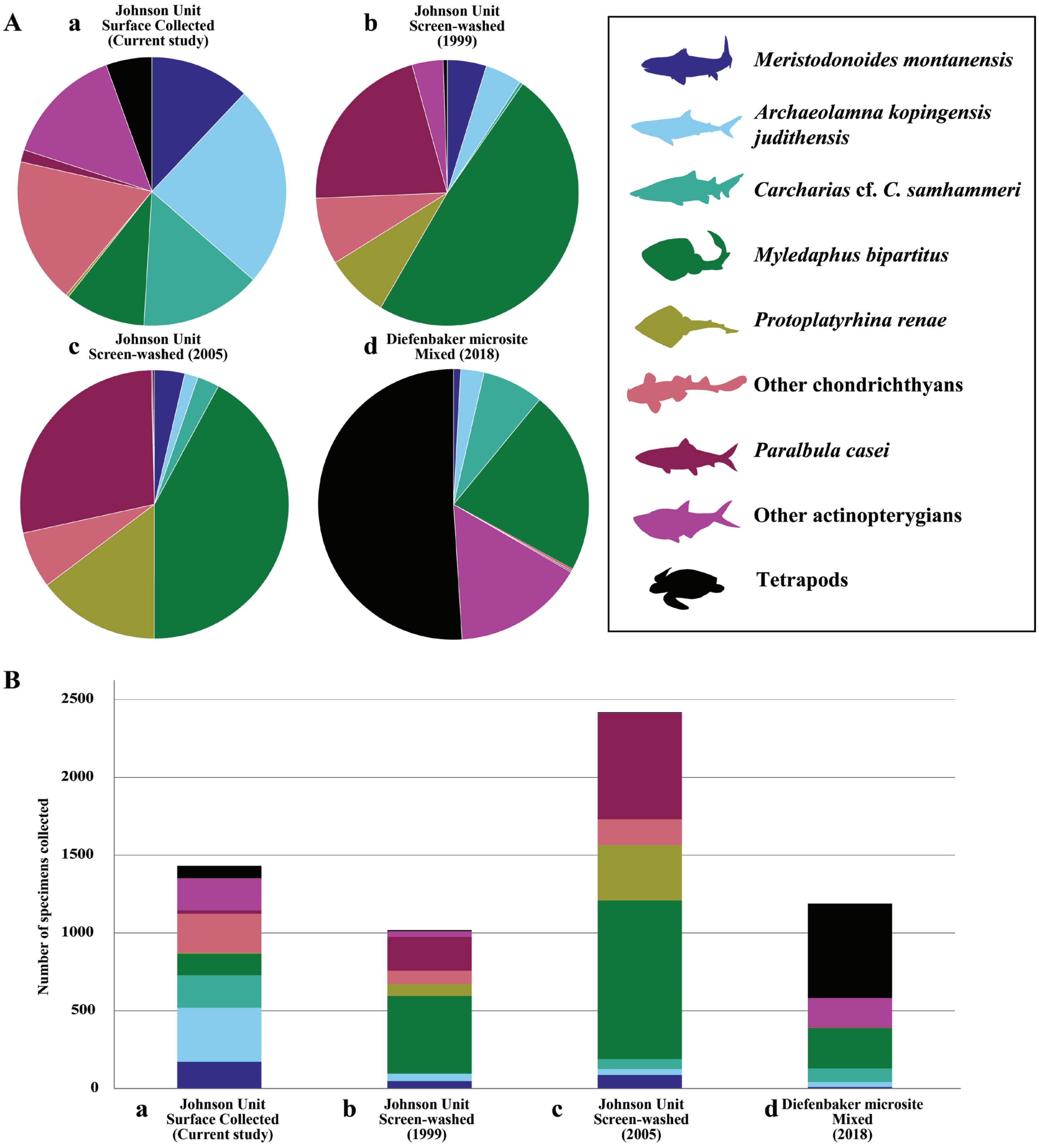


**Figure 19.** Comparison of four microfossil samples: a, the sample described in the current study; b, the sample described by Beavan and Russell (1999); c, the sample described by Brinkman et al. (2005); and d, the Saskatchewan sample described by Gilbert et al. (2018). A, Pie charts depicting proportional abundances; B, stacked bar chart depicting absolute abundances.

benthos of the Bearpaw Formation. An additional component missing from the Bearpaw assemblage is *Archaeolamna kopingensis judithensis*, which is the most abundant taxon in our sample. In contrast, two different large lamniforms, *Squalicorax* sp. and *Cretoxyrhina mantelli*, are known from the Bearpaw Formation instead (Konishi et al. 2011, 2014; Cook et al. 2017). It is possible that *A. kopingensis judithensis* was more prevalent in near-shore environments as represented by the Johnson Unit (this is supported by its prevalence in the Foremost Formation – see below), while other large lamniforms occupied open water environments represented by the Bearpaw Formation. Further sampling of chondrichthyans in deposits of the Bearpaw Formation is required to support this hypothesis.

Plesiosaurs and mosasaurs are present in both the Johnson Unit and the Bearpaw Formation, although their abundance patterns differ. Mosasaur remains are well represented in the Bearpaw Formation from ammolite mines south of Lethbridge (e.g., Konishi et al. 2011, 2014), with a lower abundance of plesiosaurs in the same mines. On the other hand, in the Johnson Unit, broken, disarticulated plesiosaur remains are quite abundant, with far fewer mosasaur elements. This may indicate an environmental preference of plesiosaurs for the shallow coastal waters of the Johnson Unit.

The Saskatchewan microfossil site described by Gilbert et al. (2018) was interpreted as a late Campanian marginal marine environment, similar (although likely not exactly contemporaneous) to that of the Johnson Unit. Although many of the same taxa appear in both localities, their proportional abundances differ significantly. Tetrapods make up more than 50% of the Saskatchewan microfossil collection, and are stated by Gilbert et al. (2018) to be very diverse. This contrasts with a tetrapod contribution of only 5% in our sample, and even smaller proportions of tetrapods in the screen-washed samples reported by Brinkman et al. (2005) and Beavan and Russell (1999). The Saskatchewan sample also contains higher proportions of freshwater vertebrates, such as amiids, amphibians, and freshwater turtles. Unlike our sample, which was collected from a thin fossiliferous layer within the Johnson Unit, the Saskatchewan sites are time-averaged from two facies with different depositional environments (Gilbert et al. 2018). The geology and fauna of the Saskatchewan sites (Gilbert et al. 2018) support a palaeoenvironment with a stronger freshwater influence than that of the Johnson Unit, which would have resulted in a mix of marine and non-marine vertebrates.

At the base of the Belly River Group, the Foremost Formation (FFm) preserves similar coastal palaeoenvironments to the Johnson Unit. Microfossils from the Foremost Formation were described by Beavan (1995), with a focus on the elasmobranchs, and additional samples were described by Peng et al. (2001), Brinkman et al. (2004), Frampton (2006), and Cullen et al. (2016). The taxa within these studies overlap with many of the taxa identified in the Johnson Unit, except for rarer taxa in the FFm. Beavan (1995) reported many similar chondrichthyan taxa to those found in our study, including *Meristodonoides montanensis*, Archaeolamna *kopingensis judithensis*, *Odontaspis aculeatus*, *Carcharias* cf. *C. samhammeri*, *Protoplatyrhina renae*, *Myledaphus bipartitus*, *Ischyrhiza mira*, *Elasmodus* sp., and *Ischyodus bifurcatus*, but also included a large number of additional chondrichthyan taxa, such as *Centrophoroides worlandensis*, *Squatina* cf. *S. hassei*, *Carcharias* (*Synodontaspis*) *hardingi*, *Synodontaspis holmdelensis*, *Squalicorax kaupi*, *Paraorthacodus turneri*, and *Synecodus* sp. According to Cullen et al. (2016), the FFm teeth attributed by Beavan (1995) to *Myledaphus bipartitus* instead belong to the subsequently described genus *Pseudomyledaphus*, which indicates faunal turnover between the FFm and the DPFm Johnson Unit. The most common batoid in Beavan's (1995) sample was *Protoplatyrhina renae*, which far outnumbered *Myledaphus*-type teeth, which were comparatively quite rare. Conversely, in other FFm sites, *Myledaphus*-type teeth were more common (Frampton 2006; Cullen et al. 2016). As with our study, *Archaeolamna kopingensis judithensis* was the most common shark taxon in Beavan's sample (1995). Peng et al. (2001) and Frampton's (2006) FFm samples added several additional taxa which are not known to be present in the Johnson Unit, including *Cretolamna* sp., *Rhinobatos* sp., *Chiloscyllium missouriense*, *Squatirhina roessingi*. In contrast, *Cretorectolobus olsoni* was identified by Peng et al. (2001) and Frampton (2006), and is present in our sample. With future sampling, it is possible that some of the FFm taxa not currently known from the Johnson Unit may be recovered there. Some differences, such as the presence of *Pseudomyledaphus*, likely represent distinct taxonomic differences over the ~5 million years of time between deposition of the FFm and the DPFm Johnson Unit (Brinkman et al. 2004).

## Collection methods and microfossil studies

Any sampling of fossils for the purposes of ecological reconstruction suffers from both preservation bias and collection bias (Nanglu and Cullen 2023). Preservation bias is always present in fossil data, regardless of collection methodology, although many have argued that the effects of it can be mitigated by comparing environments with similar preservation (e.g., Blob and Fiorillo 1996) and using subsets of specimens with similar preservation factors (Brinkman 2008). For the comparison of our sample to those described by Brinkman et al. (2005) and Beavan and Russell (1999), these criteria were met, since we sampled similar specimens from the same horizon as those previous authors. Since preservation bias and environmental differences can't be used to explain differences between our sample and those previous ones, we attribute these large differences primarily to collection bias. Like preservation bias, collection bias will always be present in some form, since a census of all preserved fossils from a unit is unattainable, and true random sampling is not possible within methodological constraints of specimen collection (see below). Unlike preservation bias, the magnitude and direction of collection bias are significantly affected by methodological decisions of the researcher (Mckenna 1962; Peterson et al. 2011).

Vertebrate microfossil sampling via surface collection has been critiqued by various authors (Mckenna 1962; Wolff 1975; Kidwell and Flessa 1995), for the increased abundance of large specimens that is believed to result from this methodology, thus misrepresenting their in-situ relative abundances. Mckenna (1962) and Wolff (1975) hypothesized that two independent sets of factors favour the collection of larger specimens by surface collection. First, larger specimens are more likely to be noticed by researchers and are therefore overrepresented in surface-collected samples simply because they are collected more often. Second, weathering and erosion, which effect specimens on the surface more than those that are buried, are dependent on the size and material properties of the specimens (Mckenna 1962; Wolff 1975; Peterson et al. 2011). Erosional processes are more likely to wash away or cover smaller specimens, while large specimens are more often left behind and partially visible on the surface (Wolff 1975).

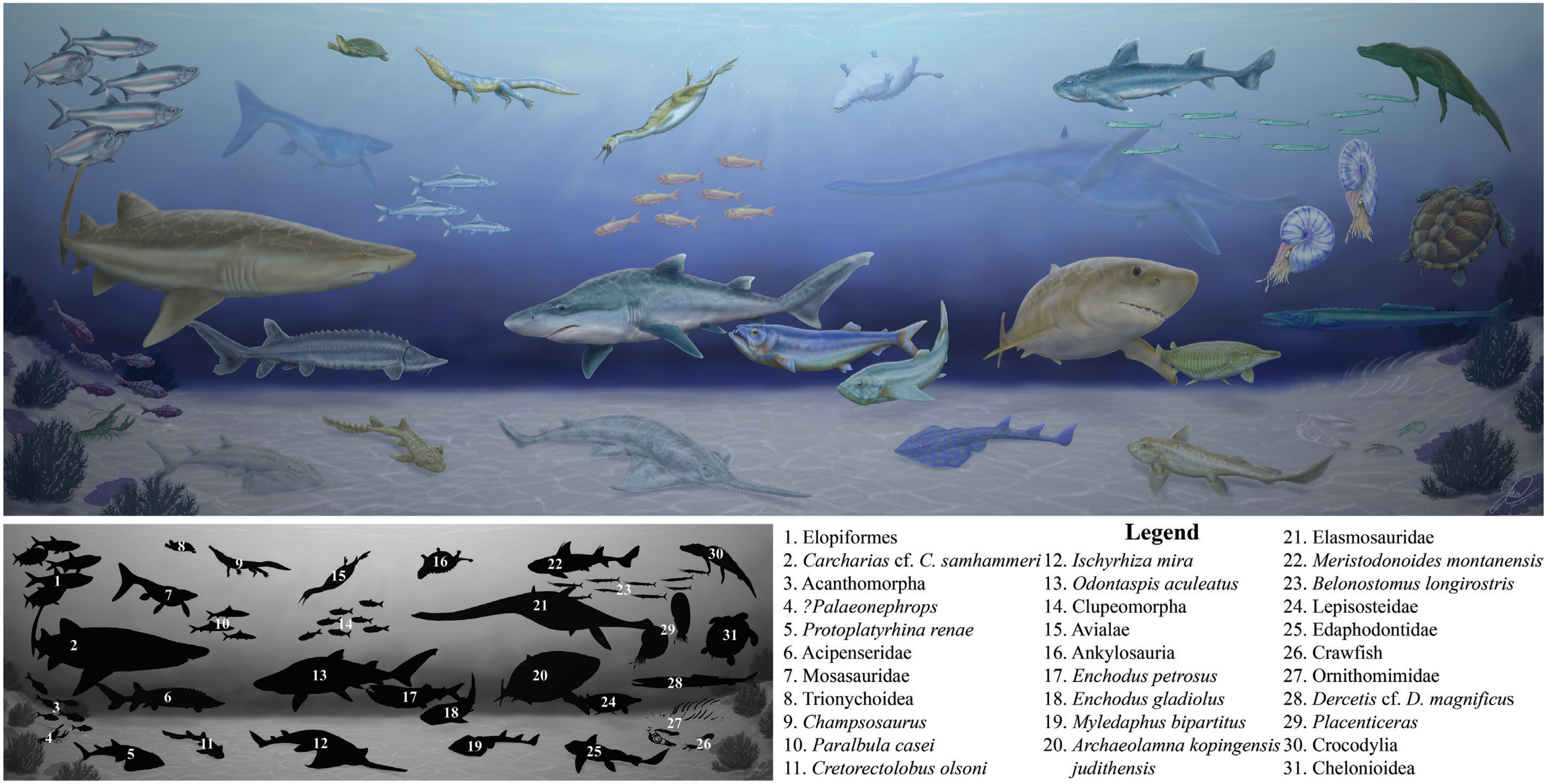
In recent years, several studies have tested the claims about biases of surface collection made by previous authors, by comparing compositions of surface collected and screen-washed samples from the same units (Peterson 2011; Forcino and Stafford 2020; Gasca et al. 2023). The results of these studies confirm that the different methods result in very different sample compositions, which is also the case with our comparison. Specifically, Peterson et al. (2011) found that surface samples from the Hell Creek Formation were made up of higher concentrations of weathered, abraded, larger, and more durable fossils than those from in-situ bulk sampling. Collection bias toward large specimens in surface-collected samples could potentially be mitigated by comparing proportional abundances between similarly sized surface-collected specimens (e.g., comparing abundances of turtles within a formation based on similarly sized shell specimens, as by Brinkman 2003). Surface collection also results in a less certain stratigraphic position (Forcino and Stafford 2020), as surface specimens are more likely to have been displaced from overlying rocks. In our study, we are confident about the stratigraphic position of our specimens, because only a thin layer of the Johnson Unit is densely fossiliferous, and other overlying rocks (the uppermost fluvial LCZ, and the Bearpaw Formation) have a comparatively very low density of vertebrate fossils.

In theory, bulk sampling and screen-washing more closely approximate a simple random sampling technique, similar to the quadrat used by botanists for sampling extant plants (McKenna 1962; Jamniczky et al. 2008). Thus, a screen-washed sample is likely to be more representative of the proportional abundances of the preserved specimens in situ (Mckenna 1962; Peterson et al. 2011). Screen-washing is also less subject to the variation in surface-collected samples resulting from the skill and experience levels of prospectors involved (Peterson et al. 2011). There are practical limitations, such as the destruction of some fossils during washing (Cifelli 1996), choice of screen mesh size (Baszio 2008), as well as selection bias from the choice of sampling location (users typically sample in a particularly densely fossiliferous section of outcrop; Cifelli 1996) which may also induce collection biases into screen-washing.

Our surface collecting resulted in the recovery of similar species richness to that reported by previous authors from the Johnson Unit (Beavan and Russell 1999; Brinkman et al. 2005), but with different composition. As predicted, surface collecting proportionally undercounted taxa represented by small specimens, and favoured the recovery of large specimens. These large specimens are required to identify some taxa, particularly many large-bodied taxa (Oreska et al. 2013), and have contributed to the first identifications of many new taxa from the Johnson Unit. The ability to identify specimens precisely is necessary when determining stratigraphic and geographic ranges of extinct organisms, meaning that surface collection is well-suited for biogeographic and biostratigraphic research questions. Our results indicate that vertebrate microfossil samples from surface collection should not be treated as being equivalent to screen-washed samples in palaeoecology studies, as methodological differences have large impacts on the composition of the resulting samples. Because of this, proportional abundance datasets from different methods should not be combined, but rather kept separate (as noted by Stringer et al. 2020), since combined datasets cannot be effectively compared with other samples. Each sampling method has advantages and disadvantages (Oreska et al. 2013), and vertebrate microfossil surface collection provides valuable contributions. Our results support the conclusions of previous authors (e.g., Peterson et al. 2011; Oreska et al. 2013; Forcino and Stafford 2020) that a two-pronged approach of both surface collection and bulk sampling is ideal.

## CONCLUSION

The marine unit, which we name here as the Johnson Unit, was deposited within a diverse marginal marine habitat, under a temporary transgression of the Western Interior Seaway over the coastal floodplains in Southern Alberta. The diverse fauna described within this study has



**Legend**

1. Elopiformes
2. *Carcharias* cf. *C. samhammeri*
3. Acanthomorpha
4. ?*Palaeonephrops*
5. *Protoplatyrhina renae*
6. Acipenseridae
7. Mosasauridae
8. Trionychoidea
9. *Champsosaurus*
10. *Paralbula casei*
11. *Cretorectolobus olsoni*
12. *Ischyrhiza mira*
13. *Odontaspis aculeatus*
14. Clupeomorpha
15. Avialae
16. Ankylosauria
17. *Enchodus petrosus*
18. *Enchodus gladiolus*
19. *Myledaphus bipartitus*
20. *Archaeolamna kopingensis judithensis*
21. Elasmosauridae
22. *Meristodonoides montanensis*
23. *Belonostomus longirostris*
24. Lepisosteidae
25. Edaphodontidae
26. Crawfish
27. Ornithomimidae
28. *Dercetis* cf. *D. magnificus*
29. *Placenticeras*
30. Crocodylia
31. Chelonioidea

**Figure 20.** Artistic reconstruction of the Johnson Unit marine fauna. Artist: Joshua Doyon.

been reconstructed in Figure 20. This sample of vertebrate microfossils expands our knowledge of the marine actinopterygians and chondrichthyans that were present in the late Campanian of Alberta. Several taxa are reported formally for the first time in Canada (*Ischyodus bifurcatus*), Alberta (*Enchodus gladiolus*), or within the Dinosaur Park Formation (Teleost morphotype O, *Dercetis* cf. *D. magnificus*) whilst others likely represent new taxa, such as the acanthomorph specimens. Using surface collecting resulted in distinctly different proportional abundances than screen-washed samples. This resulted in an overrepresentation of large diagnostic specimens. Future sampling of fishes, particularly actinopterygians, in Albertan marine formations such as the Bearpaw Formation, will be necessary to increase our understanding of the faunal changes that occurred in these ecosystems.

## ACKNOWLEDGEMENTS

We thank the Stennes family and Gene Johnson and his family, for allowing us to prospect on their land. We also thank Todd Cook, Michael Caldwell, Patrick Druckenmiller, Henry Sharpe, and Mark Powers for consultation on some of the microfossil identifications. We thank Todd Cook, an anonymous reviewer, and the handling editor Jordan Mallon for their helpful comments during the review process. We also thank Romain Palmgren, Meghan Dueck, and Khoi Nguyen for their advice with various computer software used in the project. Thank you to Murray Gingras for the use of his software for stratigraphic columns. We could not have completed the stratigraphic column measurements without assistance from the staff from the Royal Tyrrell Museum of Palaeontology, particularly Joe Sanchez, who helped us borrow a Jacob's staff. We also thank Eva Koppelhus and Phil Currie for their advice with field work in the area, and for lending us some of their field equipment. Stratigraphic columns, fossil collection, and sorting were completed with help from Madison Prairie. This work was funded by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant 327448 (AMM). LEN was supported by an NSERC Canadian Graduate scholarship.

## LITERATURE CITED

Agassiz, L. 1832. Die Untersuchungen über fossilen Süfswasser — Fische der tertiären Formationen. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1832:129–138.

Agassiz, L. 1833–1844. Recherches sur les Poissons Fossiles. Neuchâtel: Petîtpierre. 1420 pp.

Agassiz, L. 1834. Abgerissene bemerkungen über fossil fische. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, 1834:379–390.

Applegate, S.P. 1972. A revision of the higher taxa of orectolobids. Journal of the Marine Biological Association of India 14:743–751.

Arratia, G. 1999. The monophyly of stem group teleosts. Consensus and disagreements; pp. 265–334 in G. Arratia and H.-P. Schultze (eds.). Mesozoic Fishes 2. Verlag Dr. Friedrich Pfeil, München, Germany.

Averianov, A.O. 2001. Systematics of the Cretaceous–Paleogene chimaeroid fish of the genus *Elasmodus* (Chondrichthyes, Holocephali). Palaeontological Journal 35:289–300.

Badgley, C. 1986. Counting individuals in mammalian fossil assemblages from fluvial environments. Palaios 1:328–338.

Bannikov, A.F., and F. Bacchia. 2000. A remarkable clupeomorph fish (Pisces, Teleostei) from a new Upper Cretaceous marine locality in Lebanon. Senckenbergiana Lethaea 80:3–11.

Baszio, S. 2008. Information from microvertebrate localities: potentials and limits; pp. 3–8 in J.T. Sankey and S. Baszio (eds.). Vertebrate Microfossil Assemblages. Indiana University Press, Bloomington and Indianapolis, Indiana.

Beavan, N.R. 1995. A marine fossil assemblage from the Foremost Formation (Cretaceous, Campanian), Southern Alberta, and an evaluation of North American Cretaceous elasmobranch biostratigraphy. MSc thesis. University of Calgary, Calgary, Alberta. 162 pp.

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

Becker, M.A., J.A. Chamberlain, J.G. Lundberg, W.J. L'amoreaux, R.B. Chamberlain, and T.M. Holden. 2009. Beryciform-like fish fossils (Teleostei: Acanthomorpha: Euacanthopterygii) from the Late Cretaceous — Early Tertiary of New Jersey. Proceedings of the Academy of Natural Sciences of Philadelphia 158:159–181. DOI 10.1635/053.158.0108

Becker, M.A., C.S. Mallery, and J.A. Chamberlain. 2010. Osteichthyans from an Arkadelphia Formation–Midway Group lag deposit (late Maastrichtian–Paleocene), Hot Spring County, Arkansas, U.S.A. Journal of Vertebrate Paleontology 30:1019–1036. DOI 10.1080/02724634.2010.483603

Berg, L.S. 1940. Classification of fishes both recent and fossil. Traveaux de l'Institut Zoologique de l'Académie des Sciences de l'U.R.S.S. 5:1-517.

Berg, L.S. 1958. System der Rezenten und Fossilen Fischartigen und Fisch. Hochschulbücher für Biologie, Berlin, Germany. 310 pp.[not seen]

Blake, S.F. 1940. *Paralbula*, a new fossil fish based on dental plates from the Eocene and Miocene of Maryland. Journal of the Washington Academy of Sciences 30:205–209.

Bleeker, P.E. 1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. Acta Societatis Regiae Scientiarum Indo-Neêrlandicae 6:1–276.

Blob, R.W., and A.R. Fiorillo. 1996. The significance of vertebrate microfossil size and shape distributions for faunal abundance reconstructions: a Late Cretaceous example. Paleobiology 22:422–435. DOI 10.1017/S0094837300016377

Bonaparte, C.L. 1831. Saggio di una distribuzione metodica degli animali vertebrati. Giornale Arcadico di Scienze, Lettere, ed Arti 49:1–77

Bonaparte, C.L. 1832–1841. Iconografia della fauna italica: per le quattro classi degli animali vertebrati. Tomo III. Tip. Salviucci, Roma.

Bonaparte, C.L. 1838. Synopsis vertebratorum systematis. Nuovi Annali delle Scienze Naturali 2:105–133.

Boyd, B.M., and J.C. Seitz. 2021. Global shifts in species richness have shaped carpet shark evolution. BMC Ecology and Evolution 21:192. DOI 10.1186/s12862-021-01922-6

Brinkman, D.B. 1987. Paleoecology of aquatic communities of the Judith River Formation of Dinosaur Provincial Park: evidence from stratigraphic distributions; pp. 30-35 in P.J. Currie and E.H. Koster (eds.). Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Drumheller.

Brinkman, D.B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. Palaeogeography, Palaeoclimatology, Palaeoecology 78:37–54.

Brinkman, D.B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. Canadian Journal of Earth Sciences 40:557–571. DOI 10.1139/e02-080

Brinkman D.B. 2008. The structure of Late Cretaceous (late Campanian) nonmarine aquatic communities: a guild analysis of two vertebrate microfossil localities in Dinosaur Provincial Park, Alberta, Canada; pp. 33-60 in J.T. Sankey and S. Baszio (eds). Vertebrate Microfossil Assemblages. Indiana University Press, Bloomington and Indianapolis, Indiana.

Brinkman, D.B. 2019. Teleost abdominal centra from the Belly River Group of Alberta, Canada. Paludicola 12:109–152.

Brinkman, D.B., and A.G. Neuman. 2002. Teleost centra from uppermost Judith River Group (Dinosaur Park Formation, Campanian) of Alberta, Canada. Journal of Paleontology 76:138–155.

Brinkman, D.B., D.R. Braman, A.G. Neuman, P.E. Ralrick, and T. Sato. 2005. A vertebrate assemblage from the marine shales of the Lethbridge Coal Zone; pp. 486–500 in P.J. Currie, and E.B. Koppelhus (eds.). Dinosaur Provincial Park, a spectacular ancient ecosystem revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Brinkman, D.B., M. Densmore, M. Rabi, M.J. Ryan, and D.C. Evans. 2015. Marine turtles from the Late Cretaceous of Alberta, Canada. Canadian Journal of Earth Sciences 52:581–589. DOI 10.1139/cjes-2014-0189

Brinkman, D.B., A.G. Neuman, and J.D. Divay. 2017. Nonmarine fish of the late Santonian Milk River Formation of Alberta, Canada – evidence from vertebrate microfossil localities. Vertebrate Anatomy Morphology Palaeontology 3:7–46. DOI 10.18435/B5PP41

Brinkman, D.B., M.G. Newbrey, A.G. Neuman, and J.G. Eaton. 2013. Freshwater Osteichthyes from the Cenomanian to late Campanian of Grand Staircase — Escalante National Monument, Utah; pp. 195–236 in A.L. Titus and M.A. Loewen (eds.). At the top of the Grand Staircase: The Late Cretaceous of southern Utah. Indiana University Press, Bloomington and Indianapolis, Indiana: .

Brinkman, D.B., A.P. Russell, D.A. Eberth, and J. Peng. 2004. Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology 213:295–313.

Brito, P.M., and M.E. Suárez. 2003. Late Cretaceous *Belonostomus* (Pisces, Actinopterygii, Aspidorhynchidae) from Algarrobo, Chile, with comments on aspidorhynchid paleodistribution in South America. Revista Geológica de Chile 30:117–127.

Caldwell, M.W. 2005. The Squamates; pp. 235–248 in P.J. Currie, and E.B. Koppelhus (eds.). Dinosaur Provincial Park, a Spectacular Ancient Ecosystem Revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Campbell, J.A., M.T. Mitchell, M.J. Ryan, and J.S. Anderson. 2021. A new elasmosaurid (Sauropterygia: Plesiosauria) from the non-marine to paralic Dinosaur Park Formation of southern Alberta, Canada. PeerJ 9: e10720. DOI 10.7717/peerj.10720

Cappetta, H. 1974. Sclerorhynchidae nov. fam., un exemple de parallélisme chez les sélaciens. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, séries D 278:225–226.

Cappetta, H. 1980. Les sélaciens du Crétacé supérieur du Liban. II. Batoides. Palaeontographica, Abteilung A 168(5-6):149–229. [not seen]

Cappetta, H. 1987. Handbook of Paleoichthyology: Chondrichthyes II Mesozoic and Cenozoic Elasmobranchii. München, Germany: Friedrich Pfeil. 512 pp.

Cappetta, H. 1992. Nouveaux Rhinobatoidei (Neoselachii, Rajiformes) à denture spécialisée du Maastrichtien du Maroc. Remarques sur l'évolution dentaire des Rajiformes et des Myliobatiformes. Neues Jahrbuch für Geologie und Paläontologie 187:31–52.

Cappetta, H., and G.R. Case. 1975. Contribution à l'étude des sélaciens du groupe Monmouth (Campanien–Maastrichtien) du New Jersey. Palaeontographica Abteilung A 151:1–46.

Carpenter, K. 1996. Sharon Springs Member, Pierre Shale (Lower Campanian) depositional environment and origin of its vertebrate fauna, with a review of North American Cretaceous plesiosaurs. PhD thesis, University of Colorado, Boulder, CO. 251 pp.

Case, G.R. 1978a. *Ischyodus bifurcatus*, a new species of chimaeroid fish from the Upper Cretaceous of New Jersey. Geobios 11:21–29.

Case, G.R. 1978b. A new selachian fauna from the Judith River Formation (Campanian) of Montana. Palaeontographica Abteilung A 160:176–205.

Case, G.R. 1979. Additional fish records from the Judith River Formation (Campanian) of Montana. Geobios 12:223–233.

Case, G.R. 1987. A new selachian fauna from the Late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). Palaeontographica Abteilung A 197:1–37.

Chen, W.-J., F. Santini, G. Carnevale, J.-N. Chen, S.-H. Liu, S. Lavoué, and R.L. Mayden. 2014. New insights on early evolution of spiny-rayed fishes (Teleostei: Acanthomorpha). Frontiers in Marine Science 1:1–17.

Chida, M., D.B. Brinkman, and A.M. Murray. 2023. A large, new dercetid fish (Teleostei: Aulopiformes) from the Campanian Bearpaw Formation of Alberta, Canada. Cretaceous Research 150:105579. DOI 10.1016/j.cretres.2023.105579

Cifelli, R.L. 1996. Techniques for recovery and preparation of microvertebrate fossils. Oklahoma Geological Survey Special Publication 96:1–36.

Cook, T. D., E. Brown, P.E. Ralrick, and T. Konishi. 2017. A late Campanian euselachian assemblage from the Bearpaw Formation of Alberta, Canada: some notable range extensions. Canadian Journal of Earth Sciences 54:973–980. DOI 10.1139/cjes-2016-0233

Cook, T.D., M.G. Newbrey, A.M. Murray, M.V.H. Wilson, K. Shimada, G.T. Takeuchi, and J.D. Stewart. 2011. A partial skeleton of the Late Cretaceous lamniform shark, *Archaeolamna kopingensis*, from the Pierre Shale of western Kansas, U.S.A. Journal of Vertebrate Paleontology 31:8–21.

Cook, T.D., M.V.H. Wilson, A.M. Murray, A.G. Plint, M.G. Newbrey, and M.J. Everhart. 2013. A high latitude euselachian assemblage from the early Turonian of Alberta, Canada. Journal of Systematic Palaeontology 11:555–587.

Cope, E.D. 1872. On the families of fishes of the Cretaceous formation of Kansas. Proceedings of the American Philosophical Society 12:327–357.

Cope, E.D. 1874. Review of the Vertebrata of the Cretaceous period found west of the Mississippi River. Bulletin of the United States Geographical Survey of the Territories 2:5–77.

Cope, E.D. 1876. Descriptions of some vertebrate remains from the Fort Union Beds of Montana. Proceedings of the Academy of Natural Sciences of Philadelphia 28:248–261.

Cope, E.D. 1887. Zittel's Manual of Palaeontology. The American Naturalist 21:1014–1019.

Cullen, T.M., F. Fanti, C. Capobianco, M.J. Ryan, and D.C. Evans. 2016. A vertebrate microsite from a marine-terrestrial transition in the Foremost Formation (Campanian) of Alberta, Canada, and the use of faunal assemblage data as a paleoenvironmental indicator. Palaeogeography, Palaeoclimatology, Palaeoecology 444:101–114.

Daugherty, D.J., K.L. Pangle, W. Karel, F. Baker, C.R. Robertson, D.L. Buckmeier, N.G. Smith, and N. Boyd. 2017. Population structure of alligator gar in a Gulf Coast river: Insights from otolith microchemistry and genetic analyses. North American Journal of Fisheries Management 37:337–348.

Eaton, J.G., J.D. Gardner, J.I. Kirkland, D.B. Brinkman, and R.L. Nydam. 2014. Vertebrates of the Iron Springs Formation, Upper Cretaceous, southwestern Utah; pp: 523–555 In J.S. MacLean, R.F. Biek, and J.E. Huntoon (eds.). Geology of Utah's far South. Utah Geological Association, Salt Lake City, UT.

Eberth, D.A. 1996. Origin and significance of mud-filled incised valleys (Upper Cretaceous) in southern Alberta, Canada. Sedimentology 43:459–477.

Eberth, D.A. 2005. The Geology; pp. 54–82 in P.J. Currie and E.B. Koppelhus (eds.). Dinosaur Provincial Park, a Spectacular Ancient Ecosystem Revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Eberth, D.A. 2024. Stratigraphic architecture of the Belly River Group (Campanian, Cretaceous) in the plains of southern Alberta: revisions and updates to an existing model and implications for correlating dinosaur-rich strata. PloS One 19: e0292318.

Eberth, D.A., and A.P. Hamblin. 1993. Tectonic, stratigraphic, and sedimentologic significance of a regional discontinuity in the upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. Canadian Journal of Earth Sciences 30:174–200.

Egerton, M.P. 1843. On some new species of fossil chimaeroid fishes, with remarks on their general affinities. Proceedings of the Geological Society of London 4:53–158.

Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation Eastern Wyoming. University of California Publications in Geological Sciences 49:1–171.

Estes, R. 1969. Studies on fossil phyllodont fishes: interrelationships and evolution in the Phyllodontidae (Albuloidei). Copeia 1969:317–331.

Everhart, M.J. 2007. New stratigraphic records (Albian-Campanian) of *Rhinobatos* sp. (Chondrichthyes; Rajiformes) from the Cretaceous of Kansas. Transactions of the Kansas Academy of Science 110:225–235. DOI 10.1660/0022-8443(2007)110[225:NSRAOR]2.0.CO;2

Fiorillo, A. 1989. The vertebrate fauna from the Judith River Formation (Late Cretaceous) of Wheatland and Golden Valley Counties, Montana. The Mosasaur 4:127–142.

Forcino, F.L., and E.S. Stafford. 2020. The influence of collection method on paleoecological datasets: In-place versus surface-collected fossil samples in the Pennsylvanian Finis Shale, Texas, USA. PLoS One 15(2):e0228944. DOI 10.1371/journal.pone.0228944

Frampton, E.K. 2006. Taphonomy and palaeoecology of mixed invertebrate-vertebrate fossil assemblage in the Foremost Formation (Cretaceous, Campanian), Milk River Valley, Alberta. MSc thesis, University of Calgary, Calgary, Alberta. 294 pp. https://prism.ucalgary.ca. DOI 10.11575/PRISM/1148

Gardiner, B.G. 1966. Catalogue of Canadian Fossil Fishes. University of Toronto Press, Toronto, Canada. 154 pp.

Gasca, J.M., J. Parrilla-Bel, M. Moreno-Azanza, P. Navarro-Lorbés, and J.I. Canudo. 2023. Testing the usefulness of the surface collecting method in a vertebrate microfossil site from the Barremian of Spain (Los Menires, Mirambel Formation). Diversity 15(135):1–18. DOI 10.3390/d15020135

Gilbert, M.M., E.L. Bamforth, L.A. Buatois, and R.W. Renaut. 2018. Paleoecology and sedimentology of a vertebrate microfossil assemblage from the easternmost Dinosaur Park Formation (Late Cretaceous, Upper Campanian) Saskatchewan, Canada: reconstructing diversity in a coastal ecosystem. Palaeogeography, Palaeoclimatology, Palaeoecology 495:227–244.

Goody, P.C. 1976. *Enchodus* (Teleostei: Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of the North American enchodontid species. Palaeontographica Abteilung A 152:91–112.

Grande, L. 1982. A revision of the fossil genus †*Diplomystus*, with comments on the interrelationships of clupeomorph fishes. American Museum Novitates 2728:1–34.

Grande, L. 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. Copeia 2010(supplement 2A):1–871. https://www.jstor.org/stable/20787269

Grande, L., and W.E. Bemis. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Journal of Vertebrate Palaeontology 18 (supp1ement Memoir 4):1–696. http://www.jstor.org/stable/3889331

Greenwood, P. H., D.E. Rosen, S.H. Weitzman, and G.S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131:341–456.

Hanson, R.C., D. Duff, J. Brehe, and W.R. Fleming. 1976. The effect of various salinities, hypophysectomy, and hormone treatments on the survival and sodium and potassium content of juvenile bowfin, *Amia calva*. Physiological Zoology 49:376–385. DOI 10.1086/physzool.49.3.30155695

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bulletin of the U.S. Geological Survey 179:1–868.

Hay, O.P. 1929. Second Bibliography and Catalogue of the Fossil Vertebrata of North America (Vol. 1). Washington D.C.: Carnegie Institution of Washington. 916 pp.

Hoganson, J.W., J.M. Erickson, and F.D. Holland. 2019. Chondrichthyan and osteichthyan paleofaunas from the Cretaceous (late Maastrichtian) Fox Hills Formation of North Dakota, USA: paleoecology, paleogeography, and extinction. Bulletins of American Paleontology 398:1–94.

Holmes, R.B. 1996. *Plioplatecarpus primaevus* (Mosasauridae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of the North American Western Interior Seaway. Journal of Vertebrate Paleontology 16:673–687.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, or more precisely the Mammalia. Proceedings of the Zoological Society of London 43:649–662.

Jamniczky, H.A., D.B. Brinkman, and A.P. Russell. 2008. How much is enough? A repeatable, efficient, and controlled sampling protocol for assessing taxonomic diversity and abundance in vertebrate microfossil assemblages; pp. 9–16 in J.T. Sankey and S. Baszio (eds.). Vertebrate Microfossil Assemblages. Indiana University Press Bloomington and Indianapolis, Indiana.

Jimenez-Huidobro, P., and M.W. Caldwell. 2016. Reassessment and reassignment of the early Maastrichtian mosasaur *Hainosaurus bernardi* Dollo, 1885, to *Tylosaurus* Marsh, 1872. Journal of Vertebrate Paleontology 36:e1096275. DOI 10.1080/02724634.2016.1096275

Johanson, Z., E. Manzanares, C. Underwood, B. Clark, V. Fernandez, and M. Smith. 2020. Evolution of the dentition in holocephalans (Chondrichthyes) through tissue disparity. Integrative and Comparative Biology 60(3):630–643. https://doi.org/10.1093/icb/icaa093

Johnson-Ransom, E.D., E.V. Popov, T.A. Deméré, and K. Shimada. 2018. The Late Cretaceous chimaeroid fish, *Ischyodus bifurcatus* Case (Chondrichthyes: Holocephali), from California, USA, and its paleobiogeographical significance. Paleontological Research 22:364–372. DOI 10.2517/2018PR004

Kauffman, E.G., and W.G.E. Caldwell. 1993. The Western Interior Basin in space and time; pp. 1–30 in W.G.E. Caldwell and E.G. Kauffman (eds.). Evolution of the Western Interior Basin. Geological Association of Canada Special Paper 39.

Kidwell, M.K., and K.W. Flessa. 1995. The quality of the fossil record: populations, species and communities. Annual Review of Ecology and Systematics 26:269–299.

Konishi, T., D.B. Brinkman, J.A. Massare, and M.W. Caldwell. 2011. New exceptional specimens of *Prognathodon overtoni* (Squamata, Mosasauridae) from the upper Campanian of Alberta, Canada, and the systematics and ecology of the genus. Journal of Vertebrate Paleontology 31:1026–1046. DOI 10.1080/02724634.2011.601714

Konishi, T., M.G. Newbrey, and M.W. Caldwell. 2014. A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, western Canada, and the first stomach contents for the genus. Journal of Vertebrate Paleontology 34:802–819. DOI 10.1080/02724634.2014.838573

Koster, E.H., P.J. Currie, D.A. Eberth, D.B. Brinkman, P. Johnston, and D. Braman. 1987. Sedimentology and palaeontology of the Upper Cretaceous Judith River/Bearpaw Formation at Dinosaur Provincial Park, Alberta. Field Trip Guidebook. Saskatoon: Geological Association of Canada. 130 pp.

Lambe, L.M. 1902. New genera and species from the Belly River series (mid-Cretaceous). Contributions to Canadian Palaeontology 3:23–81.

Leidy, J. 1856. Notices of remains of extinct vertebrated animals of New Jersey, collected by Prof. Cook of the State Geological Survey under the direction of Dr. W. Kitchell. Proceedings of the Academy of Natural Sciences of Philadelphia 8:216–257.

Lindblad, K. 2024. Diversity and structure of Late Cretaceous–Paleogene crocodyliform communities in southern

Saskatchewan, Canada. MSc thesis, University of Saskatchewan, Saskatoon, SK. 136 pp.

Mckenna, M.C. 1962. Collecting small fossils by wasing and screening. Curator 5:221–235. DOI 10.1111/j.2151-6952.1962.tb01586.x

Miyazato, M., L.E. Nelson, J.A. Doyon, D.B. Brinkman, and A.M. Murray. 2025. Cranial anatomy of a Late Cretaceous aspidorhynchid fish (Neopterygii: Aspidorhynchiformes) from Alberta, Canada. Anatomical Record (in press).

Müller, J. 1844. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. Druckerei der Königlichen Akademie der Wissenschaften Berlin: 91–141.

Müller, J., and J. Henle. 1839. Systematische beschreibung der Plagiostomen. Veit und comp, Berlin, Germany. 200 pp.

Murray, A.M., and D.B. Brinkman. 2023. Morphological variation in the first vertebra among acanthomorph fishes – a guide for identifying fossil centra from microvertebrate sites. Vertebrate Anatomy Morphology Palaeontology 11:42–90. DOI 10.18435/vamp29392

Murray, A.M. 2016. Mid-Cretaceous acanthomorph fishes with the description of a new species from the Turonian of Lac des Bois, Northwest Territories, Canada. Vertebrate Anatomy Morphology Palaeontology 1:101–115. DOI: 10.18435/B5CC78

Murray, A.M., D.B. Brinkman, M.G. Newbrey, and A.G. Neuman. 2020. Earliest North American articulated freshwater acanthomorph fish (Teleostei: Percopsiformes) from Upper Cretaceous deposits of Alberta, Canada. Geological Magazine 157:1087–1096. DOI 10.1017/S0016756819001328

Nagrodski, M., K. Shimada, and B.A. Schumacher,. 2012. Marine vertebrates from the Hartland Shale (Upper Cretaceous: upper Cenomanian) in southeastern Colorado, USA. Cretaceous Research 37:76–88. DOI10.1016/j.cretres.2012.03.007

Nanglu, K., and T.M. Cullen. 2023. Across space and time: A review of sampling, preservational, analytical, and anthropogenic biases in fossil data across macroecological scales. Earth-Science Reviews 244:104537. DOI 10.1016/j.earscirev.2023.104537

Naylor, G.J.P., J.N. Caira, K. Jensen, K.A.M. Rosana, N. Straube, and C. Lakner. 2012. Elasmobranch phylogeny: a mitochondrial estimate based on 595 species; pp. 31–56 in J. Carrier, J.A. Mesick, and M.R. Heithaus (eds.). The Biology of Sharks and their Relatives. CRC Press, Boca Raton, FL.

Nelson, G.J. 1973. Relationships of clupeomorphs, with remarks on the structure of the lower jaw in fishes; pp. 333–349 in P.H. Greenwood, R.S. Miles, and C. Patterson (eds.). Interrelationships of Fishes. Academic Press, New York, NY.

Nelson, J.S. 1994. Fishes of the World (3rd Edition). John Wiley and Sons, Hoboken, NY. 600 pp.

Nelson, J.S., T.C. Grande, and M.V.H. Wilson. 2016. Fishes of the World (5th Edition). John Wiley and Sons, Hoboken, NY. 707 pp.

Neuman, A.G., and D.B. Brinkman. 2005. Fishes of the fluvial beds; pp. 167–185 in P.J. Currie and E.B. Koppelhus (eds.). Dinosaur Provincial Park, A Spectacular Ancient Ecosystem Revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Newbrey, M.G., and T. Konishi. 2015. A new lizardfish (Teleostei, Aulopiformes) from the Late Cretaceous Bearpaw Formation of Alberta, Canada, with a revised diagnosis of *Apateodus* (Aulopiformes, Ichthyotringoidei). Journal of Vertebrate Paleontology 35:e918042.

Newbrey, M.G., A.M. Murray, D.B. Brinkman, and M.V.H. Wilson. 2010. A new articulated freshwater fish (Clupeomorpha, Ellimmichthyiformes) from the Horseshoe Canyon Formation, Maastrichtian, of Alberta, Canada. Canadian Journal of Earth Sciences, 47:1183–1196. DOI 10.1139/E10-041

Nicholson, H., and R. Lydekker. 1889. A Manual of Palaeontology for the use of Students with a General Introduction on the Principles of Palaeontology (vol. 2). William Blackwood and Sons, Edinburgh, UK; 890–1624.

Obruchev, D.V. 1953. Studies on edestids and the works of A.P. Karpinski. USSR Academy of Science, Palaeontological Institute Publication 45:1–86 [not seen]

Oreska, M.P., and M.T. Carrano. 2019. Paleocommunity mixing increases with marine transgression in Dinosaur Park Formation (Upper Cretaceous) vertebrate microfossil assemblages. Paleobiology 45:136–153.

Oreska, M.P.J., M.T. Carrano, and K.M. Dzikiewicz. 2013. Vertebrate paleontology of the Cloverly Formation (Lower Cretaceous), I: faunal composition, biogeographic relationships, and sampling. Journal of Vertebrate Palaeontology 33:264–292.

Owen, R. 1846. Lectures on the comparative anatomy and physiology of the vertebrate animals: delivered at the Royal College of Surgeons of England (Part 1, Fishes). Longman, Brown, Green, and Longmans, London, England.

Panzeri, K.M., S. Bogan, M.S. Raigemborn, M.A. Pagani, N. Chimento, F.L. Agnolín, and A.G. Martinelli. 2024. Purported crushing teeth of actinopterygian fishes from the Late Cretaceous of Patagonia reinterpreted as crustacean bio-gastroliths. Journal of South American Earth Sciences 149:1–10. DOI 10.1016/j.jsames.2024.105179

Parris, D.C., B.S. Grandstaff, and W.B. Gallagher. 2007. Fossil fish from the Pierre Shale Group (Late Cretaceous): clarifying the biostratigraphic record; pp. 99-109 in J.E. Martin and D.C. Parris (eds.). The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas. Geological Society of America. DOI 10.1130/2007.2427(07)

Patterson, C. 1973. Interrelationships of holosteans; pp. 233-306 in P.H. Greenwood, R.S. Miles, and C. Patterson (eds.). Interrelationships of fishes. Academic Press, London, UK.

Patterson, C. 1992. Interpretation of the toothplates of chimaeroid fishes. Zoological Journal of the Linnean Society 106:33–61. DOI 10.1111/j.1096-3642.1992.tb01239.x

Peng, J., D.B. Brinkman, and A.P. Russell 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River group (Campanian) of Southeastern Alberta: an illustrated guide. Provincial Museum of Alberta, Edmonton, AB. DOI 10.5962/bhl.title.115853

Peterson, J.E., R.P. Scherer, and K.M. Huffman. 2011. Methods of microvertebrate sampling and their influences on taphonomic interpretations. Palaios 26:81–88.

Popov, E.V. 2020. Systematic reassessment of *Edaphodon eyrensis* Long, 1985 (Holocephali, Chimaeroidei) from the Early Cretaceous of South Australia. Journal of Vertebrate Paleontology 40:e1884564. DOI 10.1080/02724634.2020.1884564

Rafinesque, S. 1810. Indice d'ittiologia siciliana ossia catalogo metodico dei nomi Latini, Italiani, e Siciliani dei Pisci, che si rinvengono in Sicilia diposti secondo un metodo naturale eseguito da un appendice che contiene la descrizione di alcuni nuovi pesci siciliani. Giovanni del Nobolo, Messina, Italy.

Ramezani, J., T.L. Beveridge, R.R. Rogers, D.A. Eberth, and E.M. Roberts. 2022. Calibrating the zenith of dinosaur diversity in the Campanian of the Western Interior Basin by CA-ID-TIMS U-Pd geochronology. Scientific Reports 12:e16026. DOI 10.1038/s41598-022-19896-w

Reimchen, T.E. 1983. Structural relationships between spines and lateral plates in threespine stickleback (*Gasterosteus aculeatus*). Evolution 37:931–946.

Rosen, D.E. 1973. Interrelationships of higher euteleostean fishes; pp. 397–513 in P.H. Greenwood, R.S. Miles, and C. Patterson (eds.). Interrelationships of Fishes. Academic Press, New York, NY.

Ryan, M.J., D.A. Eberth, D.B. Brinkman, P.J. Currie, D.H. Tanke, and B.J. Chinnery-Allgeier. 2010. A new *Pachyrhinosaurus*-like ceratopsid from the upper Dinosaur Park Formation (late Campanian) of southern Alberta, Canada; pp. 141–155 in M.J. Ryan, B.J. Chinnery–Allgeier, and D.A. Eberth (eds.). New Perspectives on Horned Dinosaurs. Indiana University Press, Bloomington and Indianapolis, Indiana.

Sato, H., A.M. Murray, O. Vernygora, and P.J. Currie, 2018. A rare, articulated sturgeon (Chondrostei: Acipenseriformes) from the Upper Cretaceous of Dinosaur Provincial Park, Alberta, Canada. Journal of Vertebrate Paleontology 38:1–15. DOI 10.1080/02724634.2018.1488137

Sato, T. 2005. A new polycotylid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous Bearpaw Formation in Saskatchewan, Canada. Journal of Paleontology 79:969–980. DOI 10.1666/0022-3360(2005)079[0969:ANPPRS]2.0.CO;2

Sato, T., D.A. Eberth, E.L. Nicholls, and M. Manabe. 2005. Plesiosaurian remains from non-marine to paralic sediments; pp. 248–276 in P.J. Currie, and E.B. Koppelhus (eds.). Dinosaur Provincial Park, a Spectacular Ancient Ecosystem Revealed. Indiana University Press, Bloomington and Indianapolis, Indiana.

Sauvage, H.E. 1975. Note sur le genre *Nummopalatus* et sur les espèces de ce genre trouvées dans les terrains tertiaires de la France. Bulletin de la Société Géologique de France (série 3) 3:613–643.

Schein, J.P., and R.D. Lewis. 2007. Actinopterygian fishes from Upper Cretaceous rocks in Alabama, with emphasis on the teleostean genus *Enchodus*. Paludicola 6:41–86.

Shimada, K. 2007. Skeletal and dental anatomy of lamniform shark, *Cretalamna appendiculata*, from upper Cretaceous Niobrara Chalk of Kansas. Journal of Vertebrate Paleontology 27:584–602.

Siverson, M. 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. Palaeontology 35:519–554.

Siverson, M. 1995. Revision of *Cretorectolobus* (Neoselachii) and description of *Cederstroemia* n. gen., a Cretaceous carpet shark (Orectolobiformes) with a cutting dentition. Journal of Paleontology 69:974–979.

Smith, A.G., D.G. Smith, and B.M. Funnel. 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge, UK.

Sternes, P.C., and K. Shimada. 2018. Paleobiology of the Late Cretaceous sclerorhynchid sawfish, *Ischyrhiza mira* (Elasmobranchii: Rajiformes), from North America based on new anatomical data. Historical Biology 30:1–18. DOI 10.1080/08912963.2018.1452205

Storrs, G.W. 1991. Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. Bulletin of the Peabody Museum of Natural History 44:1–151.

Street, H.P., A.R.H. LeBlanc, and M.W. Caldwell. 2021. A histological investigation of dental crown characters used in mosasaur phylogenetic analyses. Vertebrate Anatomy Morphology Palaeontology 9:83–94. DOI 10.18435/vamp29372

Stringer, G.L., W. Schwarzhans, G. Phillips, and R. Lambert. 2020. Highly diversified Late Cretaceous fish assemblage revealed by otoliths (Ripley Formation and Owl Creek Formation, Northeast Mississippi, USA). Rivista Italiana di Paleontologia e Stratigrafia 126:111–155.

Taskavak, E., and S.C. Akcinar. 2009. Marine records of the Nile soft-shelled turtle, *Trionyx triunguis* from Turkey. Marine Biodiversity Records 2:e9. DOI 10.1017/S1755267208000092

Tsujita, C.J. 2003. Smothered scampi: taphonomy of lobsters in the Upper Cretaceous Bearpaw Formation, Southern Alberta. Journal of Taphonomy 1:187–206.

Tsujita, C.J., and E.G. Westermann. 1998. Ammonoid habitats and habits in the Western Interior Seaway: a case study from the Upper Cretaceous Bearpaw Formation of southern Alberta, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 144:135–160. DOI 10.1016/S0031-0182(98)00090-X

Underwood, C.J., and S.L. Cumbaa. 2010. Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. Palaeontology 53:903–944. DOI 10.1111/j.1475-

4983.2010.00969.x

Van Vranken, N.E., C. Fielitz, and J.A. Ebersole. 2019. New occurrences of *Belonostomus* (Teleostomorpha: Aspidorhynchidae) from the Late Cretaceous of the North American Gulf Coastal Plain, USA. Palaeontologia Electronica 22.3.58 (11pp.). palaeo-electronica.org/content/2019/2725-new-belonostomus-record

Vavrek, M.J. 2011. Fossil: palaeoecological and palaeogeographical analysis tools. Palaeontologia Electronica 14(1), 1T. R package version 0.4.0.

Welton, B.J., and R.F. Farish. 1993. The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas. Before Time, Lewisvill, TX. 204 pp.

Whetstone, K. 1978. *Belonostomus* sp. (Teleostei, Aspidorhynchidae) from the Upper Cretaceous Tombigbee Sand of Alabama. The University of Kansas Paleontological contributions 89:17–19.

Wilson, A.E., M.G. Newbrey, D.B. Brinkman, T.D. Cook and A.G. Neuman. 2013. Age and growth in *Myledaphus bipartitus*, a Late Cretaceous freshwater guitarfish from Alberta, Canada. Canadian Journal of Earth Sciences 50:930–944. DOI 10.1139/cjes-2013-0001

Wilson, M.V.H., and A.M. Murray. 1996. Early Cenomanian acanthomorph teleost in the Cretaceous Fish Scale Zone, Albian/Cenomanian boundary, Alberta, Canada; pp. 369–382 in G. Arratia and G. Viohl (eds.). Mesozoic fishes: Systematics and paleoecology. Verlag Dr. Friedrich Pfiel, München, Germany.

Wintrich, T., M. Scaal, and P.M. Sander. 2017. Foramina in plesiosaur cervical centra indicate a specialized vascular system. Fossil Record 20:279–290. DOI 10.5194/fr-20-279-2017

Wolff, R.G. 1975. Sampling and sample size in ecological analyses of fossil mammals. Paleobiology 1:195–204.

Woodward, A. 1901. Catalogue of the Fossil Fishes in the British Museum (Natural History). Vol.4. Order of the Trustees of the British Museum, London, UK.

Wueringer, B.E., L. Squire, and S.P. Collin. 2009. The biology of extinct and extant sawfish (Batoidea: Sclerorhynchidae and Pristidae). Reviews in Fish Biology and Fisheries 19:445–464. DOI 10.1007/s11160-009-9112-7

**Appendix 1.** Material collected from surface collection in the Johnson Unit, separated by taxon and element type. Specimen numbers are listed for each taxon (in many cases, multiple specimens are catalogued under one number).

| Taxon | Element | Abundance | Specimen number(s) |
|---|---|---|---|
| Edaphodontidae gen. indet. | tooth plates | 162 | UALVP64038–UALVP64067 |
| *Elasmodus* sp. | tooth plates | 2 | UALVP64068, UALVP64069 |
| *Ischyodus bifurcatus* | tooth plate | 1 | UALVP64070 |
| Elasmobranchii indet. | centra | 32 | UALVP63944–UALVP63960 |
| *Meristodonoides montanensis* | teeth | 172 | UALVP64081–UALVP64113 |
| *Archaeolamna kopingensis judithensis* | teeth | 349 | UALVP63818–UALVP63863 |
| *Odontaspis aculeatus* | teeth | 7 | UALVP64154–UALVP64157 |
| *Carcharias* cf. *C. samhammeri* | teeth | 208 | UALVP63876–UALVP63900 |
| *Cretorectolobus olsoni* | teeth | 1 | UALVP63921 |
| Batomorphii indet. | centra | 14 | UALVP63864–UALVP63871 |
| *Ischyrhiza mira* | rostral denticle | 7 | UALVP64072, UALVP64074- UALVP64078, UALVP64080 |
| *Ischyrhiza mira* | dermal denticle | 1 | UALVP64073 |
| *Ischyrhiza mira* | oral teeth | 1 | UALVP64079 |
| *Protoplatyrhina renae* | teeth | 5 | UALVP64179–UALVP64183 |
| *Myledaphus bipartitus* | teeth | 139 | UALVP64122, UALVP64124–UALVP64127, UALVP64129, UALVP64131, UALVP64133-UALVP64140, UALVP64142, UALVP64143, UALVP64145, UALVP64146, UALVP64148-UALVP64152 |
| *Myledaphus bipartitus* | centra | 23 | UALVP64123, UALVP64128, UALVP64130, UALVP64132, UALVP64141, UALVP64144, UALVP64147, UALVP64153 |
| Acipenseridae gen. indet. | Dermal elements | 61 | UALVP64184–UALVP64205 |
| Lepisosteidae gen. indet. | ganoid scale | 4 | UALVP64033–UALVP64036 |
| Lepisosteidae gen. indet. | dermal bone | 1 | UALVP63815 |
| Amiidae gen. indet. | centra | 1 | UALVP63816 |
| *Belonostomus longirostris* | jaw element | 2 | UALVP63873, UALVP63875 |

**Appendix 1 continued.**

| Taxon | Element | Abundance | Specimen number(s) |
|---|---|---|---|
| *Belonostomus longirostris* | Dermal fragment | 2 | UALVP63872, UALVP63874 |
| Teleost indet. | jaw | 1 | UALVP64226 |
| Teleostei indet. | quadrates | 2 | UALVP64210, UALVP64214 |
| Teleostei indet. | centra | 13 | UALVP64206–UALVP64209, UALVP64211–UALVP64213, UALVP64215–UALVP64217 |
| Teleost morphotype O | centra | 1 | UALVP63901 |
| Elopiformes indet. | centra | 4 | UALVP63964–UALVP63967 |
| *Paralbula casei* | teeth | 20 | UALVP64159–UALVP64165, UALVP64167–UALVP64170 |
| *Paralbula casei* | centra | 1 | UALVP64166 |
| Clupeomorpha indet. | centra | 1 | UALVP64218 |
| *Horseshoeichthys* sp. | centra | 1 | UALVP64071 |
| *Enchodus* indet. | dermopalatines | 5 | UALVP63991, UALVP63992, UALVP63994, UALVP63999, UALVP64001 |
| *Enchodus* indet. | centra | 6 | UALVP63993, UALVP63995–UALVP63998, UALVP64000 |
| *Enchodus gladiolus* | teeth | 31 | UALVP63968–UALVP63985, UALVP63987, UALVP63988, UALVP63990 |
| *Enchodus gladiolus* | dermopalatines | 2 | UALVP63986, UALVP63989 |
| *Enchodus petrosus* | teeth | 28 | UALVP64002, UALVP64003, UALVP64006, UALVP64013–UALVP64022, UALVP64024–UALVP64027, UALVP64030, UALVP64031 |
| *Enchodus petrosus* | dermopalatines | 13 | UALVP64004, UALVP64005, UALVP64007–UALVP64012, UALVP64023, UALVP64028, UALVP64029, UALVP64032 |
| *Dercetis* cf. *D. magnificus* | centra | 18 | UALVP63930–UALVP63942 |
| Acanthomorph indet. | centra | 3 | UALVP63808, UALVP63813 |
| Acanthomorph indet. | fin spine | 7 | UALVP63806, UALVP63807, UALVP63809–UALVP63812, UALVP63814 |
| Chelonioidea gen. indet. | shell element | 14 | UALVP63909–UALVP63920 |
| Trionychoidea gen. indet. | shell element | 6 | UALVP64219–UALVP64224 |
| Plesiosauria gen. indet. | centra | 11 | UALVP64171–UALVP64178 |
| Plesiosauria gen. indet. | teeth | 5 | UALVP63961–UALVP63963 |
| ?Mosasauria gen. indet. | teeth | 14 | UALVP64227–UALVP64233 |
| Mosasauridae gen. indet. | centra | 6 | UALVP64115, UALVP64116, UALVP64119, UALVP64120, UALVP64121 |
| Mosasauridae gen. indet. | teeth | 3 | UALVP64114, UALVP64117, UALVP64118 |
| *Champsosaurus* sp. | centra | 7 | UALVP63902–UALVP63908 |
| Crocodylia gen. indet. | teeth | 3 | UALVP63924, UALVP63925, UALVP63927 |
| Crocodylia gen. indet. | scute | 3 | UALVP63923, UALVP63926, UALVP63928 |
| Crocodylia gen. indet. | centra | 1 | UALVP63922 |
| Ornithopoda gen. indet. | teeth | 1 | UALVP64037 |
| Ankylosauria gen. indet. | teeth | 1 | UALVP63817 |
| Tyrannosauria gen. indet. | teeth | 1 | UALVP64225 |
| Maniraptora gen. indet. | bone shaft | 1 | UALVP63929 |
| Ornithomimidae gen. indet. | phalanx | 1 | UALVP64158 |
| Dromaeosauridae gen. indet. | teeth | 1 | UALVP63943 |
|  | **Total elements:** | **1431** |  |

**Appendix 2.** Comparison of number of elements of taxa collected from the Johnson Unit from three collecting expeditions: the current study, and those reported by Beavan and Russell (1999) and Brinkman et al. (2005). The data in the current study is based on surface collections, whereas the other two expeditions used screen-washing of bulk samples. In this table, taxa are grouped into the smallest common taxonomic unit which was used in all three studies (for example, *Enchodus* remains were not identified to species by previous workers). Taxa which we identified to a lower level in our sample are discussed above in the text. We also modified some of the identifications made by the previous authors — these reidentifications are discussed earlier in the remarks of the Systematic Palaeontology section.

| Taxon | Current study | Beavan and Russel (1999) | Brinkman et al. (2005) |
|---|---|---|---|
| Edaphodontidae gen. indet. | 165 | 5 | 40 |
| Dermal denticle type 1 | 0 | 5 | 0 |
| Dermal denticle type 2 | 0 | 1 | 0 |
| Elasmobranchii | 69 | 54 | 0 |
| *Meristodonoides montanensis* | 172 | 49 | 88 |
| *Squatina* sp. | 0 | 0 | 27 |
| *Archaeolamna kopingensis judithensis* | 349 | 46 | 39 |
| *Odontaspis aculeatus* | 7 | 1 | 37 |
| *Carcharias* cf. *C. samhammeri* | 208 | 4 | 64 |
| *Archaeotriakis* sp. | 0 | 0 | 3 |
| *Cretorectolobus olsoni* | 1 | 2 | 38 |
| *Eucrossirhinus microcuspidatus* | 0 | 1 | 0 |
| *Ischyrhiza mira* | 9 | 12 | 19 |
| *Ptychotrygon blainensis* | 0 | 2 | 1 |
| *Protoplatyrhina renae* | 5 | 79 | 356 |
| *Myledaphus bipartitus* | 139 | 496 | 1019 |
| Polyodontidae indet. | 0 | 1 | 1 |
| Acipenseridae gen. indet. | 61 | 13 | 0 |
| *Belonostomus longirostris* | 4 | 4 | 0 |
| Lepisosteidae gen. indet. | 5 | 8 | 0 |
| Amiidae gen. indet. | 1 | 0 | 0 |
| Teleost indet. | 16 | 0 | 0 |
| Teleost morphotype O | 1 | 0 | 0 |
| Elopiforms indet. | 4 | 0 | 0 |
| *Paralbula casei* | 21 | 217 | 679 |
| Clupeomorpha gen. indet. | 1 | 0 | 0 |
| *Horseshoeichthys* sp. | 1 | 6 | 3 |
| *Enchodus* | 85 | 4 | 0 |
| *Dercetis* cf. *D. magnificus* | 18 | 3 | 0 |
| Acanthomorph indet. | 10 | 0 | 0 |
| Chelonioidea gen. indet. | 14 | 0 | 0 |
| Trionychoidea gen. indet. | 6 | 0 | 0 |
| Plesiosauria gen. indet. | 16 | 2 | 1 |
| ?Mosasauria | 14 | 0 | 0 |
| Mosasauridae gen. indet. | 9 | 1 | 0 |
| Champsosaurus sp. | 7 | 0 | 1 |
| Crocodylia gen. indet. | 7 | 1 | 1 |
| Ceratopsidae gen. indet. | 0 | 1 | 0 |
| Ornithopoda gen. indet. | 1 | 0 | 0 |
| Ankylosauria gen. indet. | 1 | 0 | 0 |
| Tyrannosauria gen. indet. | 1 | 0 | 0 |
| Maniraptora gen. indet. | 1 | 0 | 0 |
| Ornithomimidae gen. indet. | 1 | 0 | 0 |
| Dromaeosauridae gen. indet. | 1 | 0 | 0 |

**Appendix 2 continued.**

| Taxon | Current study | Beavan and Russel (1999) | Brinkman et al. (2005) |
|---|---|---|---|
| ?Bird | 0 | 0 | 1 |
| Metatheria | 0 | 0 | 1 |
| Totals | 1431 | 1018 | 2419 |