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Filling the Bearpaw gap: Evidence for palaeoenvironment-driven taxon distribution in a diverse, non-marine ecosystem from the late Campanian of west-Central Alberta, Canada

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ABSTRACT

Patterns of Late Cretaceous terrestrial vertebrate diversity across North America have been interpreted primarily in terms of biogeographic provincialism driven by latitude or coastal-inland habitat gradients. A major difficulty in determining the influence of these two gradients is the existence of some large gaps in the terrestrial fossil record, notably the ‘Bearpaw gap’ caused by a transgression of the inland Bearpaw Seaway during the latter part of the Campanian. In this context, the terrestrial fauna preserved in the Campanian deposits of the Wapiti Formation (west-central Alberta, Canada) is crucial for addressing the information deficit. Deposited at the edge of the palaeo-circumpolar region, Unit 3 of the strictly terrestrial Wapiti Formation (WU3) is coeval with the ‘Bearpaw gap’, a period when the terrestrial record from better-sampled areas elsewhere in Canada and the U.S. A. gives way to marine sediments. Here we show, based largely on evidence from the recently discovered DC (Dinosaur-Chelonian) Bonebed locality, that the diverse WU3 vertebrate fauna shares similarities with lowland to marginal marine ecosystems in the Oldman and Dinosaur Park formations which were deposited in southern Alberta prior to the Bearpaw gap. In addition, a major change in faunal composition demarcates the upper boundary of WU3, related to the disappearance of the Bearpaw Sea in Canada. Data presented here help, first and foremost, to bridge an ~1.2-million-year gap in the North American record of Campanian terrestrial vertebrates. Resemblances between the WU3 vertebrate fauna and slightly older assemblages from southern Alberta underscore the importance of determining the spatiotemporal changes in environmental factors (e.g., coastal proximity). The occurrence of one seemingly endemic lizard, together with differences in relative taxon abundance, suggest additional latitude-correlated factors, implicating both latitudinal and coastal-inland habitat gradients in driving the taxonomic composition of Late Cretaceous terrestrial faunas.

1. Introduction

The Late Cretaceous terrestrial faunas of western North America provide one of the best datasets for unravelling potential relationships between fossil vertebrate communities and palaeoenvironmental factors. In southern Alberta, where this record is arguably more

comprehensive than almost anywhere else in the world (Currie and Koppelhus, 2005), the marine Bearpaw Formation—a northern expression of the epicontinental Western Interior Seaway and equivalent to ~1.5 million years of Campanian time (Hathway, 2016)—stands as a major biochronological gap between the rich terrestrial faunal assemblages of the late Campanian Dinosaur Park Formation (the upper part of

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the Belly River Group) and late Campanian–Maastrichtian Horseshoe Canyon Formation (hereafter HC Formation; the lower part of the Edmonton Group). Despite recent advances in understanding patterns of palaeoecological change through time across this interval, including the recognition of spatiotemporally discrete terrestrial vertebrate ‘biozones’ associated with different environmental and climatic conditions (Ryan and Evans, 2005; Larson et al., 2010; Mallon et al., 2012; Eberth et al., 2013; Eberth and Kamo, 2020), the hiatus in terrestrial deposition represented by the Bearpaw Formation is a major hindrance in tracing evolutionary changes and evaluating possible influences on terrestrial community structure between the Dinosaur Park and Horseshoe Canyon formations. The Bearpaw Formation accumulated diachronously over much of the Western Interior Basin (WIB) of Canada and the United States from ~76–73 Ma (Rogers et al., 2016; Eberth and Kamo, 2020; Zubalich et al., 2021) and separates the clastic wedges of the Belly River and Edmonton groups, both renowned for the information their remarkable fossil records provide on vertebrate evolution and diversity

from the Late Cretaceous (Currie and Koppelhus, 2005; Eberth and Braman, 2012; Eberth et al., 2013; Cullen and Evans, 2016; Gilbert and Bamforth, 2017). Here we refer to this terrestrial fossil record hiatus as the ‘Bearpaw gap’.

Environmental gradients (e.g., between coastal and more inland environments) have an important influence, alongside latitudinal gradients and many other abiotic factors, on the distribution and diversity of modern faunas (Whittaker, 1975; Hillebrand, 2004; Drakare et al., 2006) and therefore must be considered when interpreting species distribution in the fossil record. For example, palaeolatitudinal climatic gradients may explain observed north-south faunal variations, including endemism, whereas environmental gradients may explain the existence of disparate yet contemporaneous ecological communities in strata deposited in different settings. Both latitudinal and environmental gradients have previously been interpreted as important determinants of the composition of faunas existing near the Western Interior Seaway during the Late Cretaceous (e.g., Brinkman, 1990; Lehman, 1987, 2001;

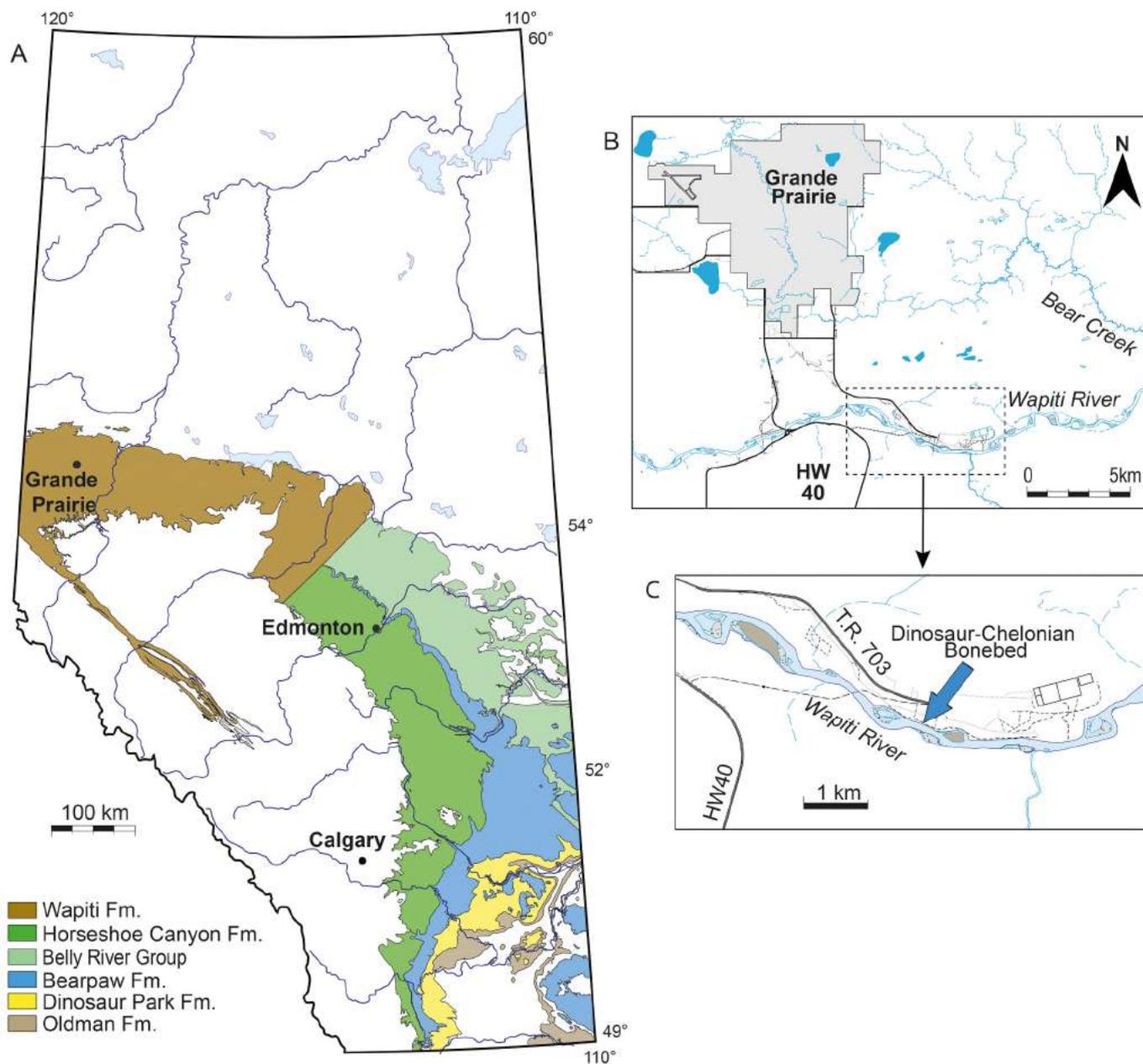


Fig. 1. A) Reference map of Alberta (western Canada) showing extent of major stratigraphic units discussed in this paper. B) Study area located in west-central Alberta, near the city of Grande Prairie. C) Location of the Dinosaur-Chelonian (DC) Bonebed.

Sampson et al., 2010; Sampson and Loewen, 2010; Burgener et al., 2021; though also see Sullivan and Lucas, 2006; Vavrek and Larsson, 2010; and Lucas et al., 2016 for critical views). However, the current literature contains few well-constrained studies of the interplay between latitudinal and depositional gradients during the Late Cretaceous and how such interactions could have shaped the vertebrate communities of the time. Furthermore, the dynamics and ecological consequences of complex, large-scale Earth system events (e.g., major transgressions and regressions), capable of reshaping the geography and environment of entire depositional basins, have been addressed only at a conceptual level (Weishampel and Horner, 1987; Horner et al., 1992; Upchurch et al., 2002; Brinkman, 2003; Bell and Snively, 2008; Butler and Barrett, 2008; Fanti and Miyashita, 2009; Mannion et al., 2012, 2014; Lucas et al., 2016; Chiarenza et al., 2019). This dearth of information is primarily due to the lack of geographic and temporal continuity among fossil-bearing localities, combined with difficulties in tracing time-representative surfaces across multiple terrestrial sedimentary units (Sullivan and Lucas, 2006; Holland and Loughney, 2021).

The terrestrial fauna preserved in the Upper Cretaceous Wapiti Formation of west-central Alberta, Canada, has emerged as a source of important palaeontological and geological information that contributes significantly to addressing these shortfalls. The formation's clastic wedge extends from the city of Edmonton, Alberta, to easternmost British Columbia, yet almost all fossil localities known to date are in the vicinity of the city of Grande Prairie, where major and minor drainage systems have provided the best exposures of this unit along the banks of waterways (Fig. 1). As such, fossils collected from the Wapiti Formation are not only geographically isolated within Alberta, but also, in the North American framework, located between the world-renowned localities of southern Alberta (e.g., Currie and Koppelhus, 2005; Eberth et al., 2013; Cullen and Evans, 2016) and the near-palaeopolar deposits of Alaska (e.g. Fiorillo, 2018). The Wapiti Formation fossil record is also distinctive in two key respects. First, it comes exclusively from terrestrial (albeit potentially near-coastal, see Zupalich et al., 2021) strata representing about 8 million years of Campanian–Maastrichtian time, critically including the interval represented elsewhere in western North America by coastal and marine deposits of the Bearpaw Formation. Second, the Wapiti Formation in the study area around Grande Prairie was deposited at a palaeolatitude close to 60°N (Matthews et al., 2016), so its fossil assemblages are unusual in representing multiple high-latitude Late Cretaceous communities that succeeded one another across the 8 Ma timespan. Over the last decade, an increasing number of papers have described the diverse vertebrate fossil record of the Wapiti Formation, documenting some of the richest Cretaceous fossil sites in North America (Currie et al., 2008; Fanti and Miyashita, 2009; Bell et al., 2014; Fanti et al., 2015; Bell and Currie, 2016; Holland et al., 2021), remarkably preserved individual specimens (Nydam et al., 2010; Bell et al., 2013a, 2014; Barbi et al., 2019), and diverse ichnofossil assemblages (Bell et al., 2013b; Fanti et al., 2013; Enriquez et al., 2020, 2021, 2022).

Here we introduce a new, highly informative multitaxic bonebed, referred to as the Dinosaur-Chelonian (DC) Bonebed, which displays a high taxonomic diversity of well-preserved, typically small (≤ 10 cm) plant and vertebrate remains. The bonebed is situated within Wapiti Formation Unit 3 (sensu Fanti and Catuneanu, 2009, 2010; hereafter WU3), a stratigraphic interval deposited in a lowland, terrestrial environment during the peak transgression of the Bearpaw Formation. We provide new chronostratigraphic and palynological data to constrain the age of the Wapiti faunal assemblage from the DC Bonebed, and discuss its significance in the context of western Canada's Campanian fossil record. Finally, we compare the WU3 vertebrate fauna with other Late Cretaceous assemblages from Alberta and explore the implications for interpreting palaeoenvironmental influences on patterns of faunal evolution in northern Laramidia.

1.1. Institutional abbreviations

TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada.

2. Geographic and geological setting

The diachronous and complex stratigraphic interval represented by the Bearpaw Formation across the northern U.S. (Montana) and western Canada (Alberta and Saskatchewan) encompasses a time period of approximately 3 Ma during the Campanian (~76–73 Ma). In Montana, the onset of transgressive conditions is documented at ~76 Ma in the contemporaneous, non-marine deposits of the Woodhawk Member of the Judith River Formation, whereas the base of the Bearpaw Formation is dated at 75.2 Ma (Rogers, 1998; Rogers et al., 2016). In Alberta, the Bearpaw Formation represents a reference marine interval that accumulated from ~74.3–73.1 Ma (Eberth and Kamo, 2020; Zupalich et al., 2021; Figs. 1A, 2). It overlies the clastic deposits of the Belly River Group and underlies the Edmonton Group, both renowned for their rich and diverse vertebrate faunas (Russell and Chamney, 1967; Dodson, 1971, 1990; Currie and Koppelhus, 2005; Larson et al., 2010; Eberth et al., 2013; Cullen and Evans, 2016). The uppermost subunit of the Belly River Group is the Dinosaur Park Formation, whose upper exposures constitute the Lethbridge Coal Zone, deposited predominantly in poorly drained, swampy environments associated with the onset of the Bearpaw transgression (Eberth, 2005). The overlying Bearpaw Formation consists of lower and upper tongues, bounding the Strathmore Member of the Horseshoe Canyon Formation (Fig. 2). In central Alberta (i.e., Drumheller–Calgary area), the coal-rich, paralic Strathmore Member has been defined solely by subcrop geophysical (well-log) signatures as the stratigraphic interval confined by the Maximum Flooding Surfaces (MFS) of the lower and upper Bearpaw tongues (Eberth and Braman, 2012; Hathway, 2016; Zupalich et al., 2021). No exposures of the Strathmore Member have been documented or sampled at the time of writing, but recent studies suggest that deposits correlative with the Strathmore Member are represented in the WU3 beds exposed in the Grande Prairie region (Fanti and Catuneanu, 2010; Zupalich et al., 2021). Given the fact that the Strathmore Member has been traced using well-logs over much of central and western Alberta (Hathway, 2016; Zupalich et al., 2021), correlative deposits within the Wapiti Formation could provide crucial information in the future about the coastal and terrestrial fauna that existed during the Bearpaw gap.

Immediately overlying the upper Bearpaw tongue, the Drumheller Member, which includes aggrading and prograding paralic and coal-rich deposits, marks the transition into the alluvial deposits of the HC Formation. The Dinosaur Park and HC formations have been subjects of detailed stratigraphic and palaeontological studies focused on defining dinosaur assemblage zones (Ryan and Evans, 2005; Mallon et al., 2012; Eberth et al., 2013). However, the intervening Bearpaw gap represents a major interruption in the latest Cretaceous terrestrial fossil record, limiting our comprehension of biogeography, evolution, and ecology during a part of the Campanian characterized by dynamic environmental and global change and, accordingly, rapid biological turnover. As this paper focuses primarily on the Alberta geological and palaeontological records, the Bearpaw gap refers herein to deposits overlying the Dinosaur Park Formation and underlying the Drumheller Member of the HC Formation (see Rogers et al., 2016 and Zupalich et al., 2021 for discussion). Exposures of paralic and marine sediments from this interval are restricted to more southerly parts of the province and do not occur in any part of the Wapiti Formation. However, integrated subsurface, outcrop and palaeontological data indicate that the fine-grained deposits of WU3 are correlative with the Bearpaw Formation of central Alberta (Fanti and Catuneanu, 2010; Zupalich et al., 2021). Sedimentological and palaeontological data also indicate that WU3 was deposited in extensive lowland environments located near (i.e., within tens of

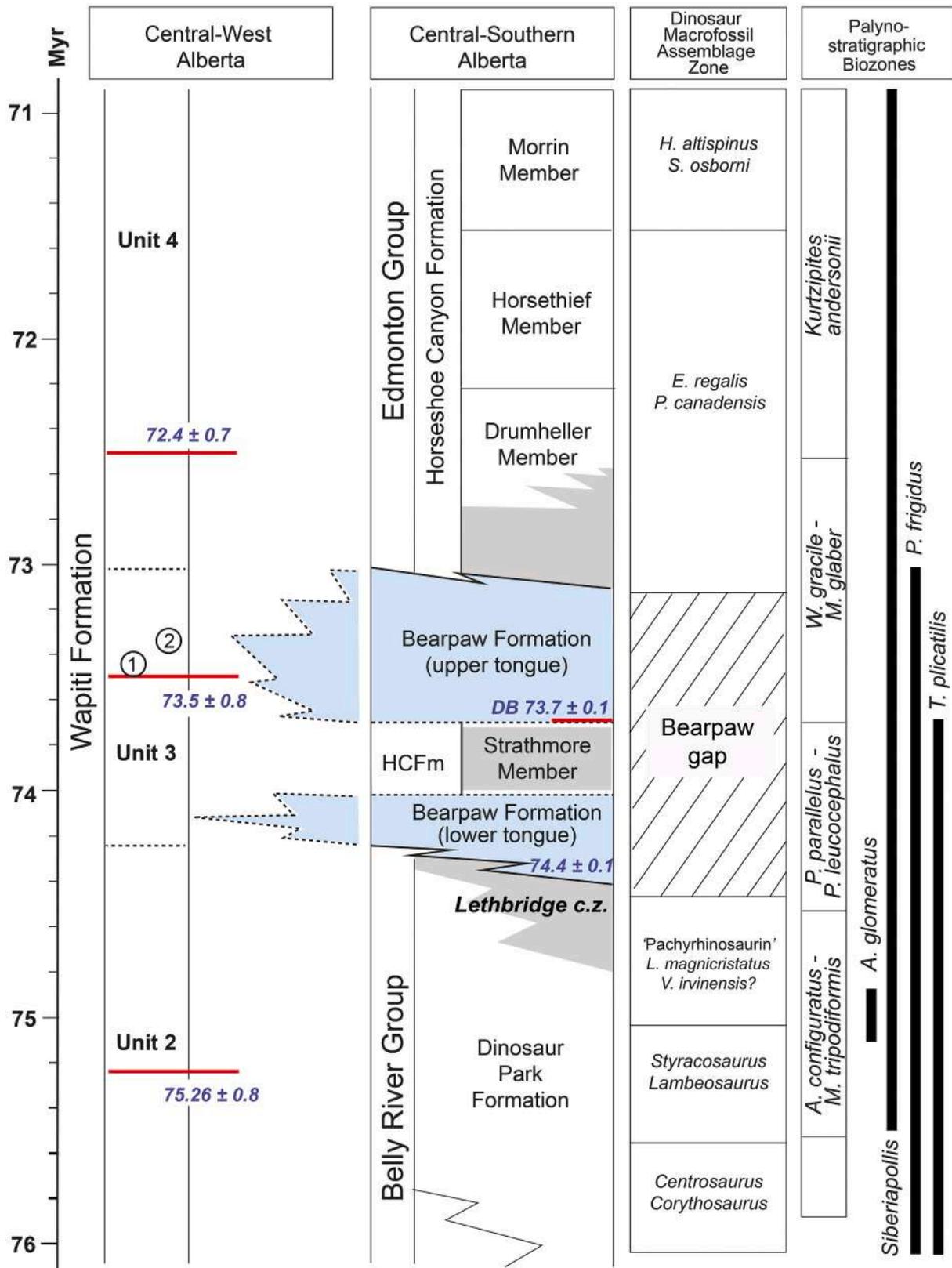


Fig. 2. Campanian lithostratigraphy and stratigraphic nomenclature for the study area. Numbers in circles represent 1, DC Bonebed, 2, Kleskun Hill. Dinosaur Macrofossil Assemblage Zones are modified from Eberth et al. (2013); Palynostratigraphic Biozones are modified from Braman, 2018. Red lines indicate dated bentonites from the Wapiti Formation (see main text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

kilometres of) the palaeo-shoreline (Fanti and Miyashita, 2009, Fanti and Catuneanu, 2010; Schroder-Adams, 2014; Koppelhus and Fanti, 2019, Chiarenza et al., 2019; Zubalich et al., 2021; this study).

3. Geology and stratigraphic correlation

Wapiti Formation Unit 3 (*sensu* Fanti and Catuneanu, 2009, 2010) includes fine-grained floodplain deposits, bentonitic palaeosols, lenticular organic-rich mudstones, coal seams, and peat horizons deposited by or associated with high-sinuosity, aggrading channels. This unit and its fossil content were extensively discussed by Fanti and Miyashita (2009), who described the WU3 fauna of the Kleskun Hill locality. Wapiti

Formation Unit 3 is characterized by low-energy environments, fine-grained sediments and high accumulation rates, resulting in a high preservation potential for vertebrate remains (Haubold, 1989; Butler et al., 2010; Fanti and Miyashita, 2009). The newly discovered DC Bonebed is located approximately 10 km southeast of Grande Prairie on the north bank of the Wapiti River (55°3'55"N, 118°41'25"W; Fig. 1). It lies within WU3 and provides insight into the sedimentology, facies analyses, and depositional architecture of WU3. Exposures along the north bank of the Wapiti River near the DC Bonebed consist of tabular mudstone and siltstone interbedded with minor channel sandstones and lenticular coal seams. The DC Bonebed occurs at the base of a single-storey, laterally isolated channel deposit exposed approximately

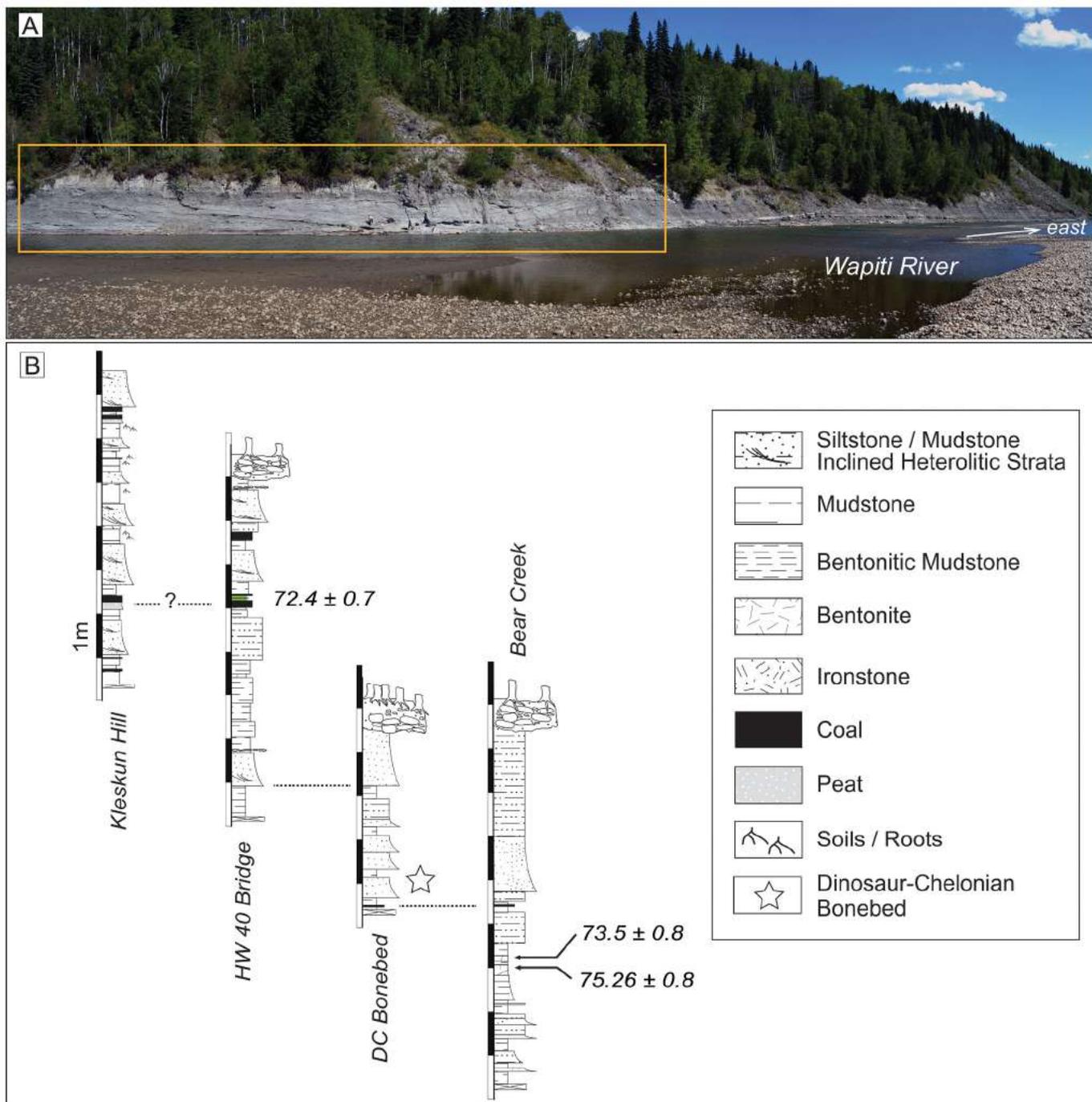


Fig. 3. A) Field photograph of the Dinosaur-Chelonian (DC) Bonebed area (yellow box); overall, the DC Bonebed occurs at the base of a laterally-isolated channel deposit. B) Measured stratigraphic sections along the Wapiti River with dated bentonitic beds indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

transverse to the palaeo-flow direction (NE–SW; Fig. 3). The deposit contains point bars that are vertically stacked, slightly asymmetric, and succession-dominated, suggesting a low rate of channel migration/avulsion. The preservation of palaeochannel geometries permits discrimination of several stages of point bar aggradation and recognition of correlative overbank and inner levee surfaces. The point bars are relatively thin, each <40 cm, and lack fine-grained components but display slightly erosive bases with common clay chips and rip-up clasts. The sandstone of the channel deposit is organic-rich and contains rare leaf impressions, conifer cones, and unidentified seeds. We infer that an aggrading fluvial system in a distal/backswamp floodplain laid down the deposits that include the DC Bonebed. Sedimentological observations and facies associations indicate that the sediments accumulated in the vicinity of a low-energy river system. For this study, additional geological sections were measured along 18 km of the Wapiti River and integrated with those presented previously for Kleskun Hill (Fanti and Miyashita, 2009), Pipestone Creek (Fanti and Currie, 2007; Currie et al., 2008), and other exposures in the Grande Prairie area (Fanti, 2009; Fanti and Catuneanu, 2009). The new composite section of WU3 in the Grande Prairie area documents the unit's major lithologies, facies distributions, and taxon occurrences. Mud-dominated facies, frequent bentonitic layers, well-developed coal seams and peat deposits are present, consistent with a water-saturated environment (see also Fanti and Miyashita, 2009; Koppelhus and Fanti, 2019).

3.1. U-Pb dating

Samples were processed from three bentonite beds, respectively located stratigraphically 11 m below (Horizon B Lower bentonite, HBL), 10 m below (Horizon B Top bentonite, HBT), and 25 m above (Highway 40 bentonite, HW40) the DC Bonebed. Zircon grains provided a weighted average age of 75.26 ± 0.8 Ma for the HBL bentonite, 73.5 ± 0.8 Ma for the HBT bentonite, and 72.4 ± 0.7 Ma for the HW40 bentonite (see Suppl. Material). These new chronostratigraphic constraints for WU3 are crucial for correlating the fossil sites discussed in this paper with the well-sampled localities of central and southern Alberta (Fig. 2). Eberth and Kamo (2020) provided a high-precision chronostratigraphy of the Bearpaw and Horseshoe Canyon Formations based on U-Pb CA-ID-TIMS ages. They dated the base of the Bearpaw Formation in southern Alberta to 74.4 ± 0.1 Ma, and a bentonite situated 5.5 m above the base of the formation to 74.308 ± 0.031 Ma. Similarly, Eberth et al. (2016) provided a $^{206}\text{Pb}/^{238}\text{U}$ date of 74.26 ± 0.03 Ma for the basalmost deposits of the Bearpaw Formation in central Alberta. Eberth and Kamo (2020) revised the age of the Dorothy Bentonite, which occurs near the base of the upper Bearpaw tongue in southern Alberta, to 73.7 ± 0.1 Ma. This bentonite was used to mark the top of the Strathmore Member of the HC Formation by Eberth and Braman (2012) and marks the transition from the *Pseudoaquilapollenites parallelus-Parviprojectus leucocephalus* palynostratigraphic biozone to the *Wodehouseia gracile-Manicorpus glaber* biozone (Braman, 2018; Eberth and Kamo, 2020 and below).

3.2. Palynology

The palynological assemblage from the DC Bonebed includes abundant fern spores and pollen from conifers and angiosperms. Eighteen species of fern spore, including microspores from heterosporous aquatic ferns, are present in the DC Bonebed sample. In some cases, they are still encased in the microsporangia (massulae) and have characteristic anchor-shaped glochidia. Fragmentary megaspores, including identifiable examples of *Ariadnesporites*, *Azolla* and *Ghoshispora*, are also present. Bisaccate conifer pollen grains are abundant but do not provide meaningful chronostratigraphic information, as they represent morphotypes with long stratigraphic ranges. Approximately 25 species of angiosperm were identified (see Supplementary Material), many of which are represented by only a few specimens. A few of these species

have relatively short stratigraphic ranges (Fig. 4). The angiosperm palynomorphs are mostly of the triprojectate type common in the Upper Cretaceous of North America, but their known temporal ranges (Braman, 2013, 2018) vary considerably. *Accuratipollis glomeratus* has the shortest range, centred at ~ 75 Ma in southern Alberta (Braman, 2018) and falling entirely within the *Aquilapollenites configuratus-Manicorpus tripodiformis* palyno-stratigraphic biozone, which extends from 75.5 to 74.5 Ma. However, this zonation is based on samples from southern Alberta, whereas very little is known about the palyno-stratigraphy of the Wapiti Formation. Other angiosperm pollen types from the DC Bonebed have longer ranges that suggest the DC Bonebed assemblage belongs to the *Pseudoaquilapollenites parallelus-Parviprojectus leucocephalus* palyno-stratigraphic biozone, which ranges from 74.5 to 73.7 Ma (Braman, 2018; Fig. 4). These results suggest that *Accuratipollis glomeratus* might have a longer range than previously proposed, extending into the *Pseudoaquilapollenites parallelus-Parviprojectus leucocephalus* biozone.

With regard to the depositional environment, the identified megaspores and microspores (*Aridanesporites*, *Azolla*, *Ghoshispora*) are characteristic of fresh, quiet water environments (Srivastava and Braman, 2013). Zygosporangia of presumed freshwater algae (*Botryococcus*, *Lecaniella*, *Pediastrum* and *Savitrina*) that occupy similar habitats are also relatively common in the sample. Taken together, the data suggest that shallow, marginal lacustrine settings or other quiet water environments were prevalent near the channel belt in which the DC Bonebed was deposited (Nagy, 1966; Yi, 1997; Head, 1992; Worobiec, 2014).

The palynological evidence corroborates the radiometric data presented above, reinforcing the conclusion that WU3 and its terrestrial vertebrate fauna are time-equivalent to the Bearpaw Formation of southern Alberta, particularly the Strathmore Member (HC Formation) and the upper tongue of the Bearpaw Formation.

4. Vertebrate palaeontology

Fossil vertebrate localities representing WU3 in the Grande Prairie region include the Kleskun Hill and DC Bonebed microfossil localities, the Spring Creek lambeosaurine Bonebed (Holland et al., 2021), and, potentially, the well-known Pipestone Creek *Pachyrhinosaurus* Bonebed (Fanti and Miyashita, 2009; Nydam et al., 2010; Currie et al., 2008; Bell and Currie, 2016; Cockx et al., 2020; this paper). Regarding the age of the latter, Eberth (in Currie et al., 2008) reported an age of 73.27 ± 0.25 Ma, which would place it in the upper part of WU3; however, this age should be regarded with caution, as it was based on few crystals and methodological details were not formally published (David A. Eberth pers. comm. to F.F.). The Pipestone Creek Bonebed preserves what appear to be the remains of a herd of the centrosaurine ceratopsid dinosaur *Pachyrhinosaurus lakustai* interspersed with much smaller numbers of other fossils (Currie et al., 2008). The depositional setting is consistent with the overlying, high-energy fluvial deposits of Wapiti Unit 4, which is dominated by a mixture of isolated dinosaur skeletons and massive, monospecific bonebeds (e.g., Bell et al., 2014; Fanti et al., 2015), and from which no highly productive microsites are so far known. Therefore, pending more accurate dating of this site, we refer the Pipestone Creek bonebed to the basalmost deposits of Wapiti Formation Unit 4 (see also Cockx et al., 2020).

A complete systematic review of the DC Bonebed assemblage, with justifications for our taxonomic identifications, can be found in the Supplementary Material, and only the most salient aspects of the assemblage are considered here. The WU3 microsites, namely Kleskun Hill and the new DC Bonebed locality, are highly informative. Kleskun Hill is a well-known source of diverse terrestrial and freshwater aquatic fossils, notably including fish, squamates, *Champsosaurus*, large and small theropods, hadrosaurids (both neonate and adult specimens), ceratopsids, thescelosaurids, mammals, and a possible pachycephalosaurid (Fanti and Miyashita, 2009; Nydam et al., 2010; Fox and Scott, 2010). However, the DC Bonebed provides important new complementary information regarding the diversity of the WU3 vertebrate

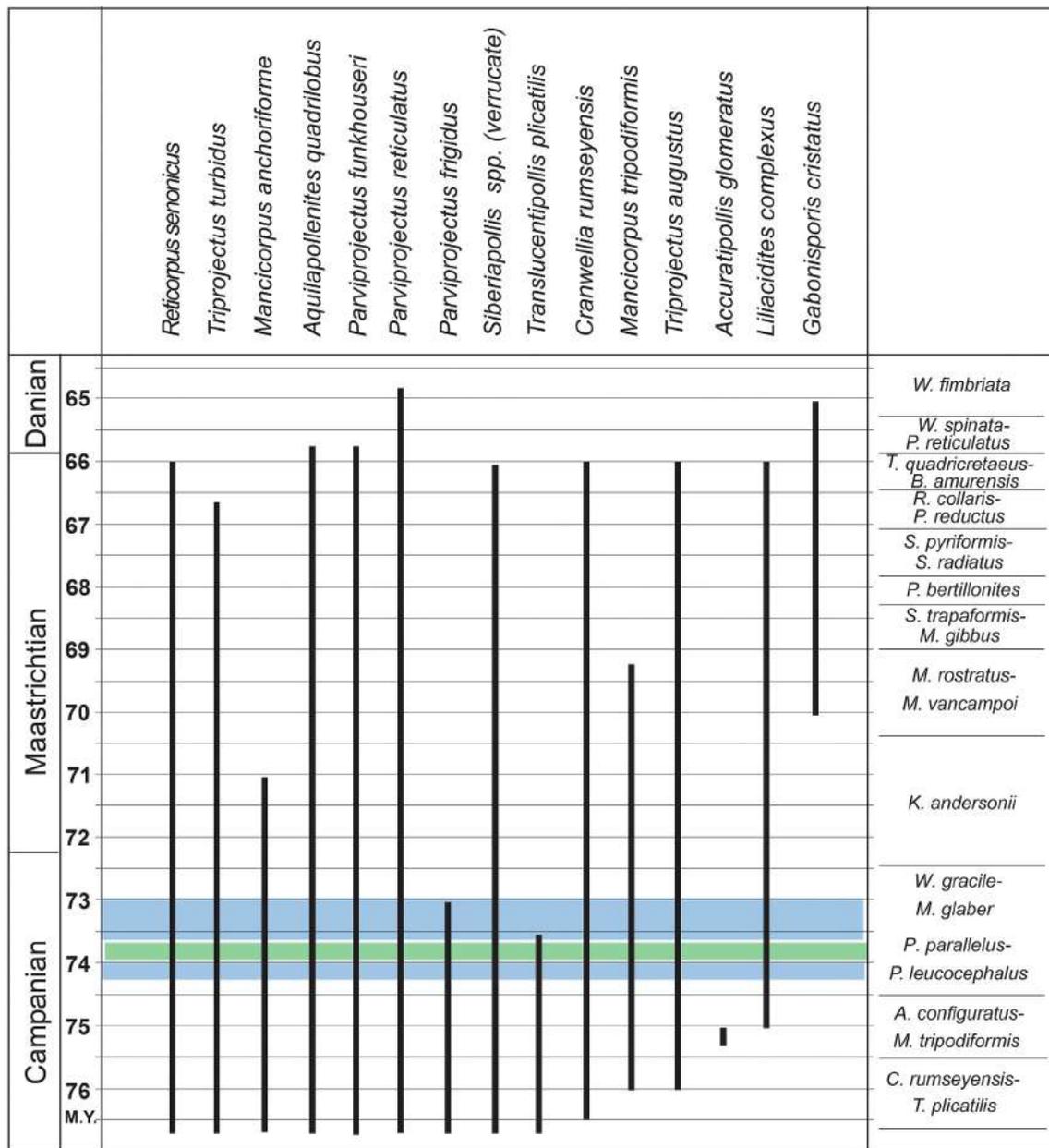


Fig. 4. Documented stratigraphic ranges (from Braman, 2018) of the various palynomorphs recovered at the DC Bonebed. Data presented in this study suggest the DC Bonebed assemblage belongs to the *Pseudoaquilapollenites parallelus* – *Parviprojectus leucocephalus* palyno-stratigraphic biozone, which ranges from 74.5 to 73.7 Ma.

assemblage.

A total of 364 identifiable (below the level of Gnathostomata) vertebrate specimens were recovered from the DC Bonebed during the 2014–2019 field seasons. Specimens described in this paper were collected from different spots within the accretionary sequence of an individual channel (Fig. 3). One specimen is a partly articulated skeleton, but the others represent small to medium-sized individual bones and teeth, primarily collected from a restricted, mud-dominated area. Specimens discussed in this paper range in size from 2.4 to 288 mm, although 92.5% of all elements measure between 25 and 60 mm in their greatest dimension, and 72% measure <50 mm; therefore, the DC Bonebed is considered a microfossil-dominated bonebed (sensu Behrensmeyer, 2007; Eberth et al., 2007; see SI2). Abiotic processes were most likely responsible for the pervasive disarticulation and size-based sorting observed at the DC Bonebed.

Fish account for some 25.8% of the specimens in the DC Bonebed sample, whereas the remainder are tetrapods, including lissamphibians

(0.5%), turtles (17.6%), *Champsosaurus* (6.6%), squamates (0.5%), eusuchian crocodyliforms (0.8%), dinosaurs (33.5%), and mammals (0.5%). The remaining specimens (14.3%) in the available sample could not be classified beyond indeterminate Archosauria, Reptilia, or Tetrapoda.

Lepisosteid (gar) remains (Fig. 5H–J) are the most abundant fish elements at the DC Bonebed, with acipenserid (sturgeon) shoulder girdle bones and osteoderms (Fig. 5M) as a distant second. Less abundant still are the distinctive hexagonal teeth (Fig. 5E, F) and centra (Fig. 5C, D) of the rhinobatoid (guitarfish) *Myledaphus bipartitus*. A number of additional osteichthyan skeletal elements not referable to Lepisosteidae or Acipenseridae are also present, notably including a premaxilla of the aspidorhynchid *Belonostomus* (Fig. 5N–O), three amiid centra (Fig. 5A, B), a single scale of the ‘Holostean A’ morphotype known from southern Alberta (Fig. 5K–L), and a dentary referable to the osteoglossomorph *Coriops* (Fig. 5G).

Among tetrapods, the only amphibian elements from the DC

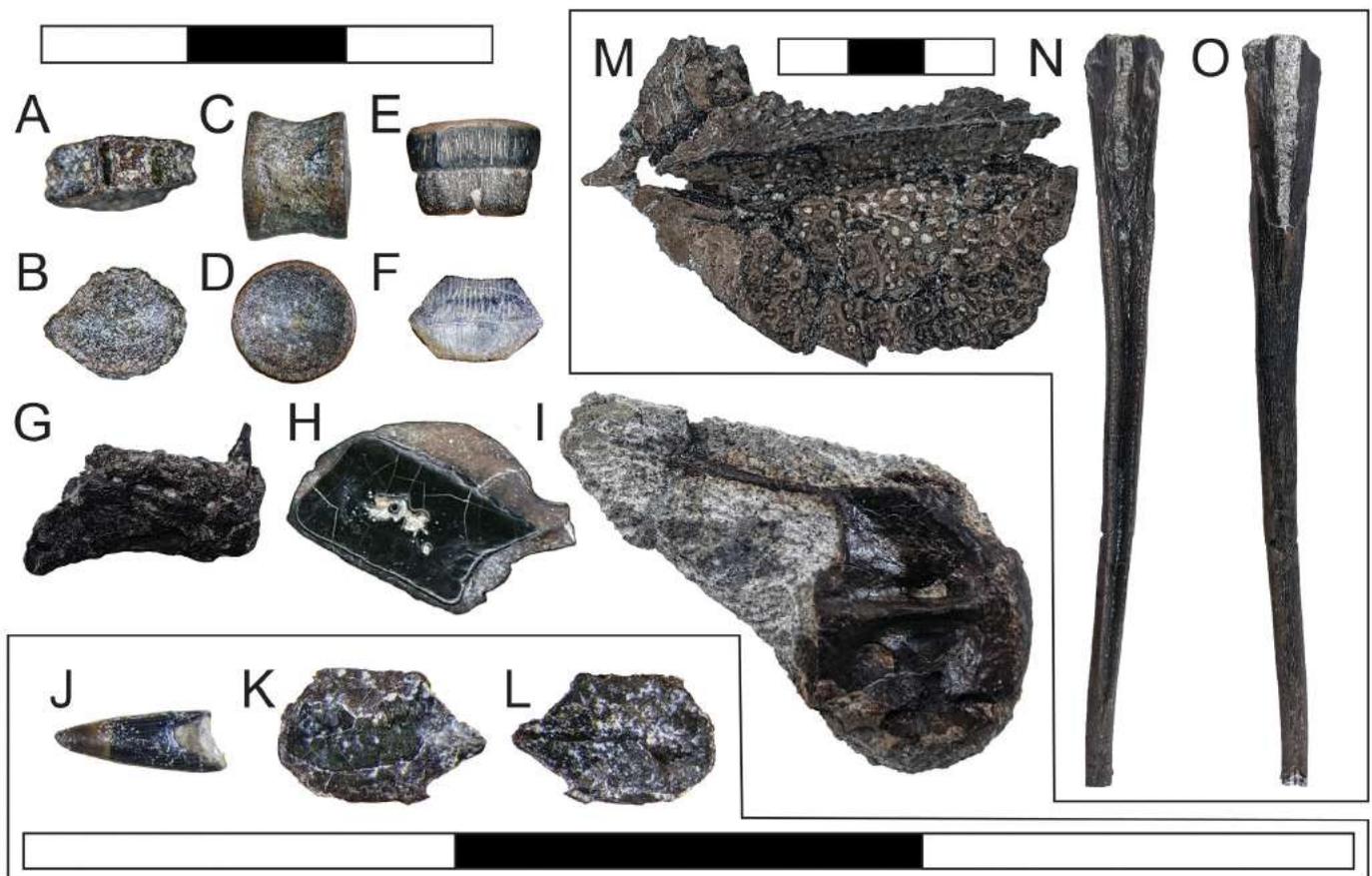


Fig. 5. Chondrichthyan and osteichthyan specimens from the DC Bonebed. UALVP 60786 Amphicoelous amiid centrum in A) dorsal and B) anterior views, with paired, elongate depressions for neural arch articulation visible in dorsal view. Deeply amphicoelous *Myledaphus bipartitus* centrum (UALVP 60802) in C) dorsal and D) anterior views. *Myledaphus bipartitus* shed crown (UALVP 59115) in E) lateral and F) occlusal views, with characteristic marginal vertical grooves seen in lateral view, and enamel folds (rather than tubercles seen in *M. pustulosus*) seen in occlusal view. G) Right *Coriops* dentary fragment (UALVP 60773) in lateral view, exhibiting deep ramus, lateral foramina, and one remaining conical tooth. H) Lepisosteid scale (UALVP 23122) exhibiting typical polygonal shape, enamelled surface, and weakly developed articular peg morphology. I) Anteriorly convex lepisosteid caudal vertebra (UALVP 70744) in right lateral view. Distinctive horizontal ridge, as in extant gar, is present on lateral surface. J) Conical, longitudinally striated lepisosteid tooth (UALVP 23117), with enameloid cap at apex. ‘Holostean A’ scale (UALVP 60812) in K) external and L) internal views, showing typical peg-and-depression morphology. M) Acipenserid dorsal scute (UALVP 59844) in dorsal view (anterior to the left) showing characteristic pitted ornamentation. Nearly complete *Belonostomus* fused premaxillae (UALVP 60781) in N) dorsal and O) ventral views, exhibiting two rows of closely packed teeth, and delicate ganoine ornamentation on the dorsal surface. Note that each boxed panel has own scale bar. Scale bars 3 cm.

Bonebed are two vertebrae (Fig. 6H) referable to the scapherpetontid salamander *Hedronchus* (*Scapherpeton*; see Dubois and Frétey, 2019). Turtles are remarkably abundant and diverse at the DC Bonebed, with three major clades represented in the sample (Fig. 6A–E). Nearly half of the turtle elements that can be identified below the level of Testudines pertain to Trionychidae, and many of these specimens are shell fragments referable to *Aspideretoides foveatus* on the basis of their ornamentation. A partial trionychid skull from the bonebed is reminiscent of the large trionychid *Axestemys* from the Upper Cretaceous and Paleocene of western North America (Vitek, 2012; Joyce et al., 2019). Baenid turtle elements are also relatively abundant, and most—including a nearly complete skull—appear referable to *Plesiobaena antiqua*, a species known from the Campanian of Montana and southern Alberta (Brinkman, 2003; Lyson and Joyce, 2009). Chelydridae are represented by several partial shell elements.

Squamates are represented by two large elements, namely a monstersaurian right frontal and an astragalocalcaneum of indeterminate affinities (Fig. 6G). Specimens of the choristodere *Champsosaurus* are relatively common at the site and include isolated cranial and post-cranial elements (Fig. 6F) that are indeterminate at the specific level. Crocodyliforms are extremely rare in the Wapiti Formation, although a single osteoderm has been previously reported from the Pipestone Creek Bonebed (Currie et al., 2008). The DC Bonebed sample includes three

small eusuchian teeth (Fig. 6I).

Ornithischian specimens predominate overwhelmingly in the DC Bonebed over theropod ones. Some 12 thescelosaurid elements, representing at least two individuals, are known from the DC Bonebed (Fig. 7D). Unexpectedly, a partial skeleton of an immature lambeosaurine hadrosaurid (UALVP 57103) was collected from a sandstone (pointbar) deposit almost immediately adjacent, in the upstream direction, to the mud-dominated area that represents the DC Bonebed proper. The taxonomy of this specimen and its implications will be detailed elsewhere. Indeterminate hadrosaurid material accounts for nearly half of all elements from the bonebed that can be identified below the level of Dinosauria (Fig. 7F, G). The bonebed yielded a single ankylosaurid tooth (Fig. 7A). Non-avian theropods are represented by four tyrannosaurid teeth (Fig. 7C), several dromaeosaurid bones (Fig. 7E), an ornithomimid metacarpal and pubis (Fig. 7H), a troodontid pedal phalanx (Fig. 7B), and three small caenagnathid elements, including an ilium (Fig. 7I), a pubis, and a pair of fused dentaries that we refer to Caenagnathidae cf. *Chirosstenotes*. The only avian specimen is the tarsometatarsus of an undoubtedly aquatic hesperornithiform.

The only mammalian specimens from the DC Bonebed are a stagodontid marsupial premolar referable to *Eodelphis* cf. *E. browni*, and a partial, indeterminate therian left mandible with the tooth crowns broken away.

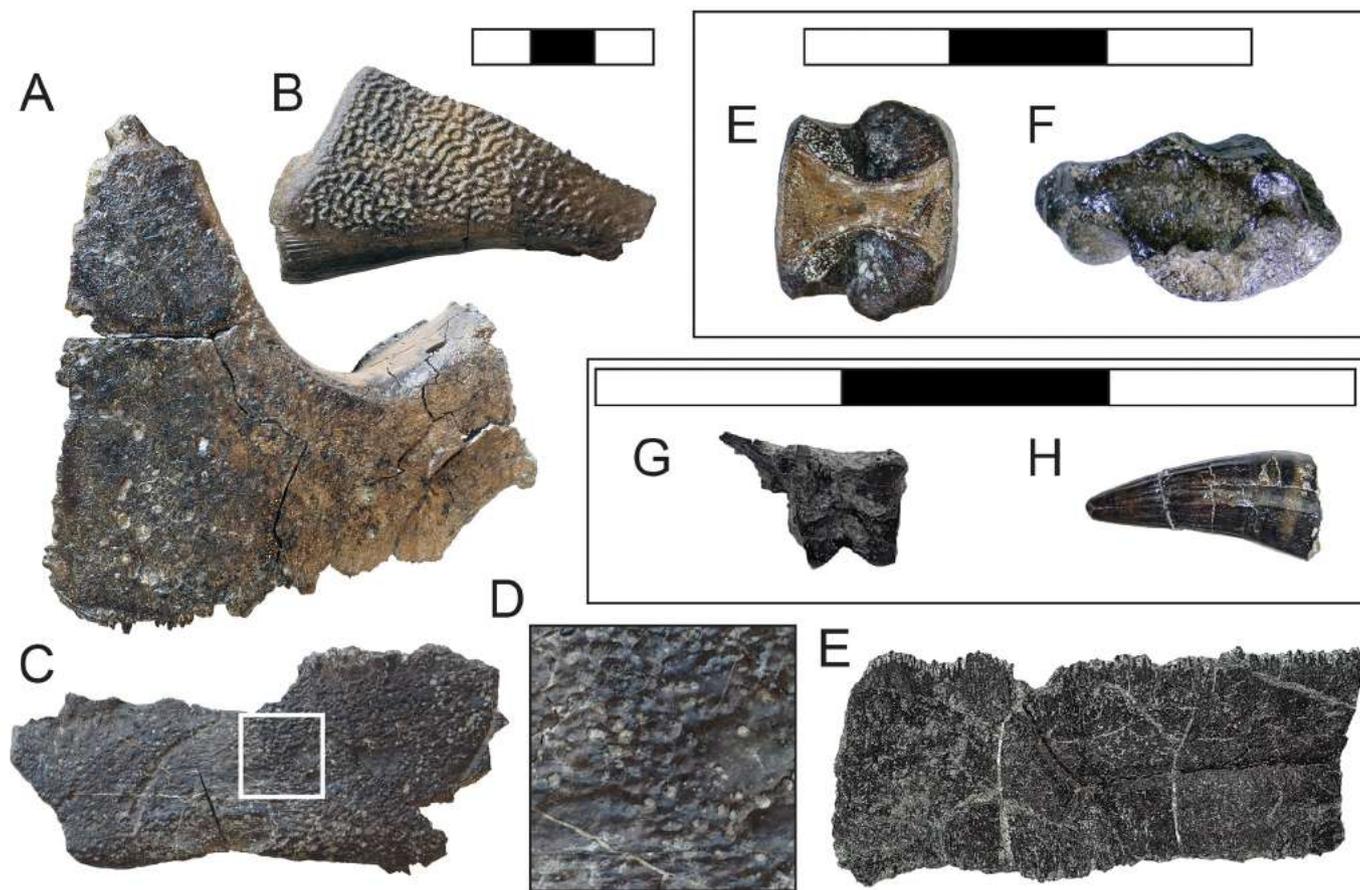


Fig. 6. Amphibian, turtle, squamate, *Champsosaurus*, and crocodyliform specimens from the DC Bonebed. A) *Plesiobaena antiqua* hypoplastron (UALVP 23092) in ventral view. B) Trionychnid right hypoplastron fragment (UALVP 23101), exhibiting typical trionychnid ornamentation. C) Baenidae indet. Fused hypoplastron and xiphiplastron (UALVP 59133) with D) inset of distinct, closely-pitted texture in area indicated by white box. E) Chelydrid costal (UALVP 59135), exhibiting deep sulci and subtle ornamentation. H) Amphicoelous *Hedronchus sternbergii* trunk vertebra (UALVP 59831) in right lateral view, exhibiting backswep neural spine. I) Conical crocodyliform tooth crown (UALVP 59811), with characteristic unserrated carinae. F) *Champsosaurus* centrum (UALVP 57408) in dorsal view, exhibiting distinct hourglass shaped neural canal groove. G) Squamate astragalocalcaneum (UALVP 59947) in dorsal view, exhibiting tibial and fibular facets at top of view. Note that each boxed panel has own scale bar. Scale bars 3 cm.

5. Ecological implications of the WU3 vertebrate assemblage

At present, the most ecologically informative samples of the WU3 vertebrate fauna are the diverse assemblage from the DC Bonebed and the smaller but similarly diverse one from Kleskun Hill (also WU3; Fanti and Miyashita, 2009; Nydam et al., 2010; Fox and Scott, 2010). Given that the WU3 sample corresponds stratigraphically to the Bearpaw gap—being younger than the Belly River assemblages of the Oldman and Dinosaur Park formations but older than the ‘Edmontonian’ assemblages of the HC Formation (excluding the subsurface Strathmore Member)—comparisons to both the Belly River and Edmontonian southern faunas are essential for understanding patterns of temporal and palaeolatitudinal variation in Alberta’s Late Cretaceous terrestrial vertebrate record. Microvertebrate samples are particularly significant in this regard, providing insights into the local (alpha) diversity of vertebrates and unique knowledge of the relative abundances of different vertebrate groups. Microvertebrates from the Oldman, Dinosaur Park, and HC formations have received considerable research attention (Brinkman, 1990; Gao and Fox, 1998; Beavan and Russell, 1999; Peng et al., 2001; Larson et al., 2010; Cullen and Evans, 2016; Oreska and Carrano, 2018), so extensive comparisons to the DC Bonebed and Kleskun Hill micro-samples are possible.

The Oldman Formation underlies the Dinosaur Park Formation in the Dinosaur Provincial Park area, but upper Oldman strata exposed in the vicinity of Manyberries in southeastern Alberta appear to have been

deposited contemporaneously with the Dinosaur Park Formation of Dinosaur Provincial Park, albeit in a more inland environment (Eberth and Hamblin, 1993; Cullen and Evans, 2016; Fanti, pers. obs.). Furthermore, the uppermost part of the Dinosaur Park Formation, called the Lethbridge Coal Zone, shows a strong marine influence and is faunally and lithologically distinct from the main portion of the formation, which is predominantly fluvial in origin (Brinkman, 1990; Beavan and Russell, 1999; Cullen and Evans, 2016). We interpret the voluminous data compiled by Cullen and Evans (2016) as defining three microsamples pertinent to our study: one from the upper Oldman strata in the Manyberries area (UO), one from the main, fluvial component of the Dinosaur Park Formation (DP), and one from the Lethbridge Coal Zone (LC). Similarly, Larson et al. (2010) provided comprehensive data on a microsample from the Morrin and Tolman members of the HC Formation, which we refer to here as the Morrin-Tolman (MT) micro-sample, and Fanti and Miyashita (2009) on a microsample from Kleskun Hill. These various samples have undoubtedly been influenced by different sets of taphonomic, environmental and ecological biases. For example, much of the MT microsample described by Larson et al. (2010) comes from a bonebed dominated by the tyrannosaurid *Albertosaurus*, guaranteeing high abundance of tyrannosaurid teeth. Nevertheless, comparisons among them are informative when undertaken with due caution.

Striking faunal differences exist between the contemporaneous DC Bonebed and Kleskun Hill microsamples (Fig. 8A). As both sites are from

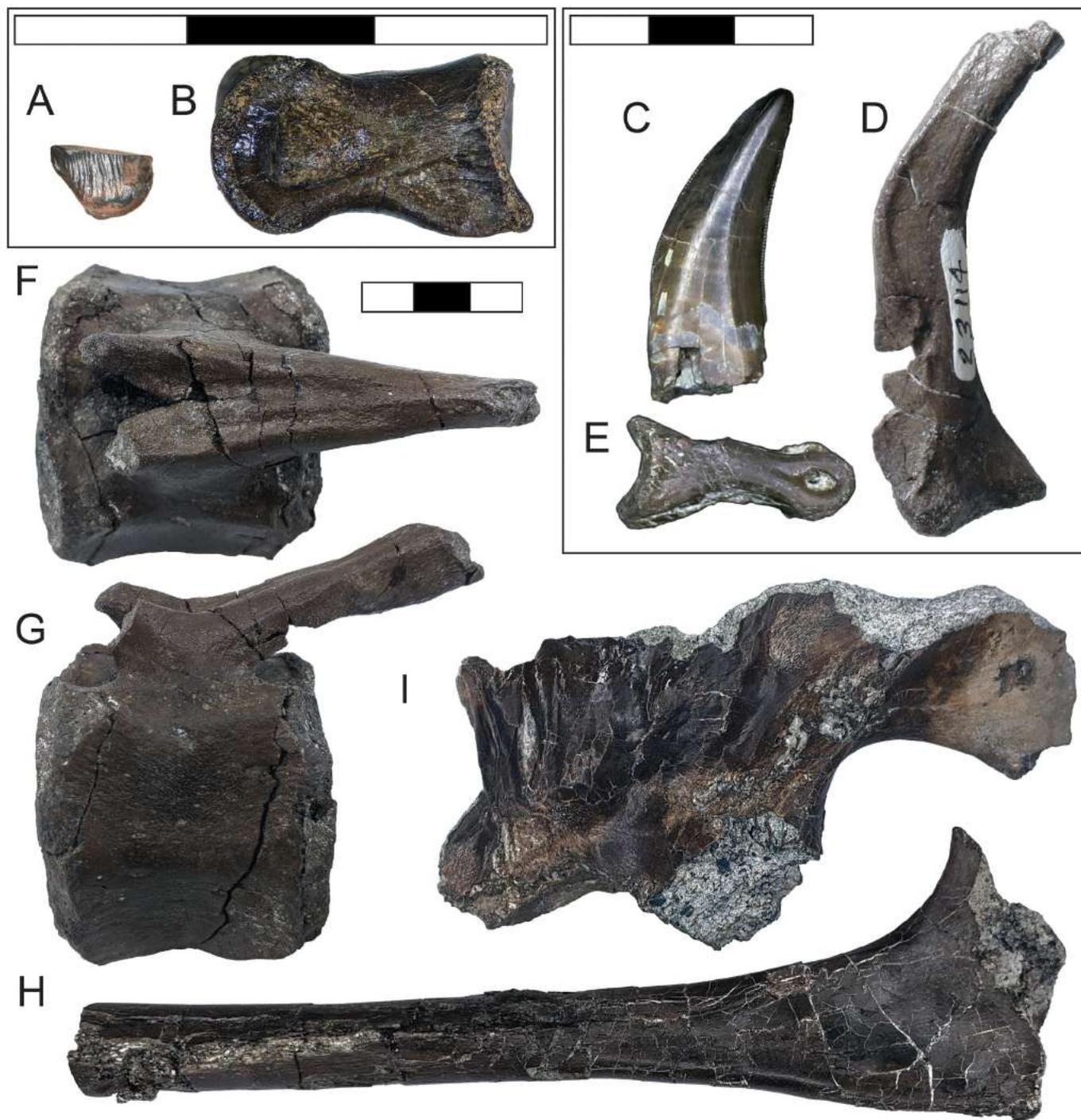


Fig. 7. Dinosaur specimens from the DC Bonebed. A) Ankylosaurid tooth crown (UALVP 59,116), exhibiting wear facet, constricted root, apicobasal ridges, and weak cingulum. B) Troodontid right pedal phalanx IV-1 in medial view (UALVP 60748), exhibiting depression on the proximoplantar corner (at lower right). C) Tyrannosaurid tooth crown (UALVP 57805). D) Thescelosaurid left quadrate (UALVP 23114) in lateral view, exhibiting distinct notch for the quadrate foramen. E) Dromaeosaurid pedal phalanx (UALVP 59507). Hadrosaurid caudal centrum (UALVP 61239) in F) dorsal and G) left lateral views. H) Partial ornithomimid left pubis (UALVP 59798) in medial view, with damaged pubic apron visible at left. I) Caenagnathid left ilium (UALVP 60800) in medial view. A sacral rib facet can be seen near the broken dorsal margin, roughly above the pubic peduncle. Note that each boxed panel has own scale bar. Scale bars 3 cm.

WU3 and only ~23 km apart, it seems unlikely that these differences are the results of large-scale biogeographic variation or faunal change over time. Instead, the differences probably reflect environmental, taphonomic, and/or sampling discrepancies. The DC Bonebed sample is proportionally much richer in aquatic to semi-aquatic taxa, namely fish, turtles, crocodyliforms and *Champsosaurus*, and less rich in presumably terrestrial lizards and dinosaurs (Fig. 8B). Taken together, the contemporaneous Kleskun Hill and DC Bonebed assemblages give a broad, if in

most respects taxonomically ambiguous, picture of the aquatic and terrestrial taxa that existed in northern Alberta during the late Campanian.

Based on the DC Bonebed, the fish component of the WU3 assemblage was dominated by lepisosteids, acipenserids, and *Myledaphus*, in descending order of abundance. The *Myledaphus* species present, *M. bipartitus*, occurs in the Dinosaur Park Formation (Neuman and Brinkman, 2005) but is distinct in dental ornamentation from the

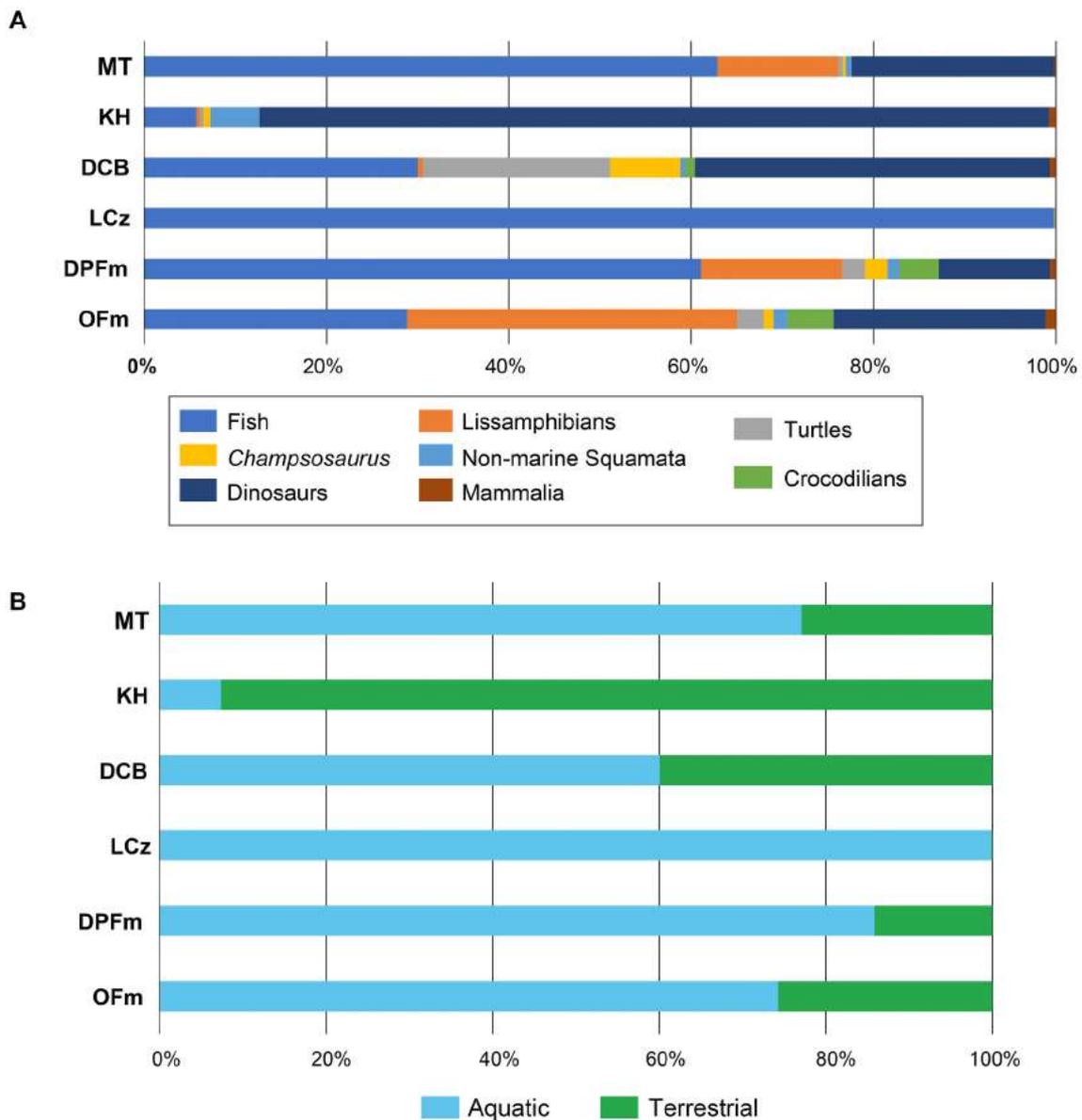


Fig. 8. A) Relative abundances of vertebrate groups for various sites and stratigraphic units in the Campanian of Alberta. Combined relative abundances total 100% in each case. B) Relative abundances of aquatic and terrestrial taxa. OFm, Oldman Formation; DPFm, Dinosaur Park Formation; LCz, Lethbridge Coal Zone; DCB, Dinosaur-Chelonian Bonebed; KH, Kleskun Hill; HCFm, Horseshoe Canyon Formation. See Supplementary Material for detailed abundance data.

Myledaphus teeth reported by Larson et al. (2010) in the MT micro-sample. Although determining numbers of individuals based solely on isolated scales, bones and/or teeth is problematic, the prominence of acipenserid specimens within the fish fauna is a highly unusual feature of the DC Bonebed. It is notable that acipenseriforms (considered as a whole) did not outnumber *Myledaphus* (considered together with the similar *Pseudomyledaphus*, which does not occur at the DC Bonebed) at a single one of the dozens of Upper Cretaceous microsites in southern Alberta included in the analysis of Cullen and Evans (2016). Another peculiarity of the DC Bonebed is the near-total absence of scales attributable to 'Holostean A', which are overwhelmingly abundant in the MT micro-sample and intermediate in abundance between *Myledaphus/Pseudomyledaphus* and lepisosteids in the DP and UO micro-samples. 'Holostean A' is also the most abundant identifiable fish taxon in the small aquatic vertebrate component of the sample from Kleskun Hill. Lepisosteids are somewhat less abundant as a proportion of the fish fauna in the DP and UO micro-samples than at the DC Bonebed, and are absent from the MT micro-sample, although they do occur in the HC

Formation (Quinney, 2011). *Myledaphus*, by contrast, is almost twice as abundant in the DP micro-sample as at the DC Bonebed, but rare in the UO micro-sample and especially the MT micro-sample. *Myledaphus* is, however, abundant in the marine-influenced LC micro-sample, accounting for about 45% of all identifiable fish specimens. The LC micro-sample is also rich in other chondrichthyan material, as well as in identifiable teleost elements. Chondrichthyan taxa other than *Myledaphus* are minimally represented in the DP, MT and UO micro-samples, but teleosts are well represented in all three, and in the UO micro-sample in particular. Amiid and *Belonostomus* specimens are rare in the UO, DP and MT micro-samples, as they are at the DC Bonebed. At the Phil's Knob (PK) microsite, situated within the Foremost Formation that underlies the Oldman Formation in the Belly River Group, Lepisosteidae accounts for nearly half of all fish material recovered, and *Pseudomyledaphus* for nearly a third, while Acipenseriformes and 'Holostean A' are absent (Cullen and Evans, 2016).

Turtles and *Champsosaurus* make up a far higher percentage of the DC Bonebed sample, relative to fish, than in the UO, DP, LC and MT

microsamples, whereas lissamphibians make up a much lower percentage (Fig. 8A). The relative abundance of lissamphibians is particularly high in the UO microsample, with lissamphibians accounting for about 71% of aquatic vertebrates at a UO site designated 'BMC' by Cullen and Evans (2016). The strong numerical dominance of *Champsosaurus* elements over crocodyliform elements at the DC Bonebed is opposite to the condition observed in the DP and UO microsamples, despite crocodyliform specimens being relatively sparse in general. The MT microsample contains some *Champsosaurus* elements but no crocodyliforms, although crocodyliforms are known from other parts of the HC Formation (Wu et al., 1996; Quinney, 2011; Wu and Brinkman, 2015). The DC Bonebed turtle assemblage resembles the UO and DP microsamples in that baenid elements account for approximately one third of all identifiable turtle specimens, a similarity reinforced by the presence of the baenid *Plesiobaena antiqua* at the DC Bonebed and in the Dinosaur Park and Oldman formations (Brinkman, 2003). Trionychids are substantially more abundant than baenids at the DC Bonebed in the UO microsample, and especially in the DP microsample. Like *Plesiobaena antiqua*, the trionychid *Aspideretoides foveatus* is shared among the DC Bonebed and the Dinosaur Park and Oldman formations (Brinkman, 2003). However, material referred to *Aspideretoides* sp., and potentially representing *A. foveatus*, is known from the lower part of the HC Formation, as part of a relatively diverse turtle assemblage that includes chelydrids but lacks baenids (Brinkman and Eberth, 2006). A trionychid cf. *Axestemys* from the DC Bonebed is even less informative, given the wide stratigraphic distribution of *Axestemys* itself (Vitek, 2012). However, it should be noted that the DC turtle specimens include the northernmost examples of *P. baena*, *A. foveatus*, and any *Axestemys*-like form. The few turtle elements in the MT microsample are all referable to Chelydridae. Chelydrids are relatively uncommon at the DC Bonebed and in the DP microsample, but more abundant in the UO microsample. The DC Bonebed is missing some additional turtle taxa known from southern Alberta, including the nanhsiungchelyid *Basilemys*, the baenid *Boremys*, and the large aquatic form *Adocus* (Brinkman, 2003; Brinkman and Eberth, 2006), but these are comparatively rare taxa whose absence from the DC Bonebed might be an artifact of small sample size. The upper Maastrichtian Scollard Formation notably contains a high diversity of turtles, including but not limited to baenids, trionychids and chelydrids (Brinkman and Eberth, 2006). At the PK site, turtles and *Champsosaurus* make up about the same respective proportions of the aquatic vertebrate sample as at the DC Bonebed, but at PK crocodyliforms are even more abundant than *Champsosaurus*, and the most abundant turtle taxon is the helochelyid *Naomichelys*.

Combining information from the DC Bonebed and Kleskun Hill provides some valuable insights into the terrestrial component of the WU3 fauna. The most diagnostic mammal specimen so far reported from WU3 is the *Eodelphis* cf. *E. browni* tooth from the DC Bonebed. *Eodelphis browni* proper has previously been documented in the Oldman and Dinosaur Park formations (Fox and Naylor, 2006; Scott and Fox, 2015; Brannick and Wilson, 2020), but not in the HC Formation. Two mammal teeth, representing a multituberculate and a pediomyid marsupial, were reported from Kleskun Hill (Fanti and Miyashita, 2009; Fox and Scott, 2010), but these are less useful in establishing faunal correlations.

Squamates from Kleskun Hill include the only known specimen of the scinoid *Kleskunsaurus grandepriariensis*, and multiple specimens of the chamopsiid *Socognathus unicuspis*. (Nydam et al., 2010). While *Kleskunsaurus grandepriariensis* is currently known only from WU3, *Socognathus unicuspis* occurs in the Dinosaur Park and Oldman Formations, and possibly also in the upper Maastrichtian Hell Creek Formation of Montana (Gao and Fox, 1998; Nydam, 2013). A dentary from Kleskun Hill referred to *Chamops* cf. *C. segnis* by Sternberg (1951) has the historical distinction of being the first vertebrate fossil from the Wapiti Formation to be formally described, but displays some clear differences from the Lancian taxon *C. segnis* (Gao and Fox, 1998; Nydam, 2013), and its identification must be considered uncertain pending a re-evaluation of the specimen. The large monstersaur frontal from the DC Bonebed

represents the northernmost definitive record of Monstersauria in the Upper Cretaceous of western North America and provides an additional point of faunal similarity to the Oldman and Dinosaur Park formations, both of which have yielded multiple monstersaur taxa (Gao and Fox, 1998; Nydam, 2013). Currie et al. (2008: p. 11) briefly reported "a varanid cf. *Palaeosaniwa* [sic] vertebra" from the Pipestone Creek Bonebed, which may be a second monstersaur from the Wapiti Formation given that the large lizard *Palaeosaniwa canadensis* from the Dinosaur Park Formation and the Lance Formation of Wyoming (Estes, 1964; Gao and Fox, 1998; Nydam, 2013) is now considered a monstersaur (Yi and Norell, 2013). The astragalocalcaneum from the DC Bonebed is uninformative but could come from the same taxon as the frontal, judging by its large size.

The relative abundance of hadrosaurid bones and teeth at the DC Bonebed is matched in the Kleskun Hill microsample, in which hadrosaurid specimens also make up nearly half of all dinosaur elements identifiable below the level of Dinosauria, but is considerably exceeded in the DP and UO microsamples, in which hadrosaurids account for a large majority of identifiable dinosaur specimens. At two particularly dinosaur-rich UO sites, designated 'PLS' and 'RDS' by Cullen and Evans (2016), more than 70% of all dinosaur specimens recovered represent hadrosaurids, and the figure for the UO microsample as a whole is about 80%. Hadrosaurids are less proportionally abundant in the MT microsample than at the DC Bonebed, presumably at least to some extent because the dinosaur component of the former was collected in large part from an *Albertosaurus* bonebed (Larson et al., 2010). However, theropods are even more prevalent as a percentage of the total fauna at Kleskun Hill than in the MT microsample, despite the provenance of the latter. The rarity of ceratopsid elements from the DC Bonebed is unusual, given the abundance of ceratopsids in Wapiti Formation Unit 4 (Currie et al., 2008; Fanti et al., 2015). Ceratopsids are represented in the Kleskun Hill microsample, but only by a few teeth, whereas ceratopsid elements constitute several percent of the identifiable dinosaur elements in the DP, UO and MT microsamples. Still more unusual is the DC Bonebed's extremely high abundance of thescelosaurids. The ratio of thescelosaurid elements to hadrosaurid elements at the DC Bonebed is about 0.29, whereas the ratio of 'hypsilophodont' (presumably including thescelosaurid) elements to hadrosaurid elements does not exceed 0.06 at any of the individual Dinosaur Park or upper Oldman localities considered by Cullen and Evans (2016). Thescelosaurids are also poorly represented in the Kleskun Hill and MT microsamples, but Brown and Druckenmiller (2011) referred to Thescelosaurinae a total of eight teeth from two sites of early Maastrichtian age in the Prince Creek Formation of Alaska. The rarity of ankylosaurid elements at the DC Bonebed is shared with the Kleskun Hill, UO, and MT microsamples, but ankylosaurid remains are more abundant in the DP microsample, and more abundant at the PLS site than in the UO microsample as a whole. The absence of identifiable pachycephalosaurid specimens from the DC Bonebed is consistent with the rarity of this group in general, although one tooth from Kleskun Hill has been referred to Pachycephalosauridae (Fanti and Miyashita, 2009).

The only theropod element from the DC Bonebed that is identifiable at a low taxonomic level is the small fused pair of dentaries referred to Caenagnathidae cf. *Chirostenotes*. This bone is similar in some important respects to specimens of *Chirostenotes pergracilis* from the Dinosaur Park Formation of southern Alberta (Longrich et al., 2013; Funston and Currie, 2020), but is unusual enough in size and morphology that referral to *Chirostenotes pergracilis* seems unwarranted (see Supplementary Material). The caenagnathid ilium and pubis from the DC Bonebed are less diagnostic but could potentially belong to the same skeleton as the fused dentaries given their small size. Finding evidence of even a single individual caenagnathid among the 122 dinosaur bones and teeth available from the DC Bonebed is remarkable, given that not one caenagnathid bone was reported to occur in the DP, Kleskun Hill, MT, and UO microsamples. While the rarity of caenagnathids in the Alberta Cretaceous record may be due in part to the edentulous condition of this

group, given the large contribution of shed tooth crowns to theropod representation at microsites, their unmistakable presence in the DC Bonebed sample is nevertheless striking.

The DC Bonebed is fairly similar to the DP and UO microsamples in containing small numbers of dromaeosaurid and tyrannosaurid elements, although tyrannosaurid teeth are more abundant in the Kleskun Hill and, especially, in the MT microsamples. Curiously, dromaeosaurids are about twice as abundant, as a percentage of all dinosaurian specimens recovered, at the PLS and RDS sites as they are in the total UO microsample, showing that representation of this group can be highly variable across localities. The large number of tyrannosaurid teeth in the MT microsample again reflects, at least in large part, the fact that much of this sample comes from an *Albertosaurus* bonebed (Larson et al., 2010). The Kleskun and MT microsamples also contain rare ornithomimid elements, tallying with the occurrence of only two ornithomimid elements at the DC Bonebed. Similarly, the presence of only a single troodontid phalanx in the DC Bonebed is consistent with the rarity of troodontids in the southern Alberta microsamples, although teeth attributed to *Troodon* by Fanti and Miyashita (2009) account for about 14% of the dinosaur elements in the microsample from Kleskun Hill. The absence from the DC Bonebed of the widespread but typically rare theropod tooth morphotypes designated *Paronychodon* and *Richardoestesia* (both of which have been reported from Kleskun Hill) may be a result of small sample size. Following the reidentification of Dinosaur Park Formation specimens of another tooth-based taxon, *Zapsalis*, as premaxillary teeth of the velociraptorine *Saurornitholestes* (Currie and Evans, 2020), the single tooth reported from Kleskun Hill of the *Zapsalis*-like taxon *Paronychodon* (Fanti and Miyashita, 2009) probably represents a premaxillary tooth of a *Saurornitholestes*-like velociraptorine. The hesperornithiform element from the DC Bonebed is an unusual record in that hesperornithiforms are not documented in the southern Alberta microsamples considered in this study, and have not been found at Kleskun Hill. However, a small number of hesperornithiform bones have been collected from the uppermost Dinosaur Park Formation of Saskatchewan, at the marine-influenced Saskatchewan Landing site (Gilbert et al., 2018).

At least at face value, the WU3 vertebrate fauna more closely resembles that of the Dinosaur Park Formation, and to a large extent also that of the Oldman Formation, than that of the MT Formation. The WU3 fauna also displays some unusual features that may reflect high northern palaeolatitude, smaller-scale palaeoenvironmental factors, or perhaps in some cases limited sampling. The strongest faunal links to the Dinosaur Park and Oldman formations are provided by the presence at the DC Bonebed of the turtle *Plesiobaena antiqua*, and the presence at Kleskun Hill of the lizard *Socognathus unicuspis*. Corroborating evidence includes the occurrence at the DC Bonebed of an indeterminate monstrosaur and specimens comparable to the theropod *Chirostenotes pergracilis* and the marsupial *Eodelphis browni*, although these faunal correlations are less individually persuasive because they are less certain, taxonomically precise, and/or distinctive. Unusual features of the WU3 assemblage, relative to Late Cretaceous faunas from southern Alberta, include the presence of the seemingly endemic squamate *Kleskunsaurus grandeprairensis*, the surprisingly high relative abundance of acipenserids, turtles, *Champsosaurus*, thescelosaurids, *Troodon*, and perhaps lepisosteids and caenagnathids, and the unusual rarity of 'Holostean A' and lissamphibians. The WU3 fauna appears slightly closer to that of the Dinosaur Park Formation than that of the upper Oldman Formation in the relatively high abundance of *Myledaphus* and in containing many more trionychids than chelydrids, but closer to that of the upper Oldman Formation in the low abundance of ankylosaurids. Only two general characteristics of the WU3 fauna, namely the rarity of crocodyliforms and the high abundance of theropods, represent even arguable points of distinctive similarity to the vertebrate assemblage of the HC Formation. Moreover, the richness of theropods in the MT microsample of Larson et al. (2010) is clearly due in part to the origin of much of that sample in an *Albertosaurus* bonebed, and is unlikely to be truly representative even

of the Morrin and Tolman members of the HC Formation.

One major implication of these findings is that the WU3 vertebrate fauna has a partially Belly River character, containing a number of taxa that existed in southern Alberta prior to the Bearpaw gap but are not represented in the HC Formation. These distinctive survivors, including *Plesiobaena antiqua*, *Socognathus unicuspis*, and possibly *Chirostenotes pergracilis* and *Eodelphis browni*, presumably existed throughout Bearpaw times in continental ecosystems that are poorly documented in the Alberta fossil record. At least in most cases, their absence from the HC Formation may reflect evolutionary turnover around the end of the Campanian.

Nevertheless, the WU3 assemblage cannot simply be regarded as a northerly, late-surviving Belly River fauna, given the presence of a number of peculiarities. Only one potentially endemic species, the scincoid *Kleskunsaurus grandeprairensis*, has so far been documented in WU3 (Nydam et al., 2010), but the WU3 assemblage nevertheless has some unusual features pertaining to the abundance of certain groups and the rarity of others. Many of these patterns lack any obvious explanation, but the abundance of *Myledaphus* and the predominance of trionychids over chelydrids may reflect the coastal rather than inland character of the fauna given that they are shared with the Dinosaur Park microsample but not with the upper Oldman microsample. The single hesperornithiform element from the DC Bonebed is another likely indicator of coastal proximity, especially given the presence of hesperornithiforms at Saskatchewan Landing (Gilbert et al., 2018).

By contrast, the fact that *Champsosaurus* elements predominate over crocodyliform ones at the DC Bonebed—unlike in both the DP and UO microsamples—may be due to latitude. *Champsosaurus* is consistently present in the Campanian of southern Alberta and Montana, but absent from contemporaneous faunas in Utah, Texas, and Mexico (Larson et al., 2010). A neochoeristodere possibly referable to *Champsosaurus* is even known from Turonian–Coniacian deposits on Axel Heiberg Island in the Canadian Arctic, occurring with turtles, amiids, lepisosteids, and teleosts (Tarduno et al., 1998; Friedman et al., 2003; Vandermark et al., 2007). Crocodylians have previously been documented in Campanian strata from Mexico to southern Alberta (Markwick, 1998; Gates et al., 2010; Lucas et al., 2016; Rivera-Sylva et al., 2019), but Amiot et al. (2004) suggested the southern Alberta occurrence was near the northern limit of their range, defined by their inability to tolerate climates in which the mean temperature of the coldest month averaged below 5–10 °C. The presence of a small number of crocodyliform elements at the DC Bonebed alongside a much larger quantity of *Champsosaurus* material is consistent with the seemingly greater ability of *Champsosaurus* to thrive in high-latitude environments. However, *Champsosaurus* is also notably abundant in the vertebrate assemblage from Saskatchewan Landing, in which crocodyliforms do not occur (Gilbert et al., 2018). Acipenserids resemble champsosaurids in having a predominantly high-latitude record, with reported Campanian and Maastriichtian occurrences extending from the Northwest Territories to northern New Mexico (Hilton and Grande, 2006; Vavrek et al., 2014). Furthermore, they may have spread into the southern part of this range only as temperatures decreased toward the end of the Cretaceous (Vavrek et al., 2014). Accordingly, the numerous acipenserid elements recovered from the DC Bonebed may be another indication of the high-latitude character of the WU3 fauna.

The high abundance and moderately high diversity of turtles in WU3 suggests that they, like *Champsosaurus*, may have been resilient to high-latitude conditions despite being ectotherms. Brinkman and Eberth (2006) argued based on the Upper Cretaceous Alberta record for a link between turtle diversity and palaeotemperature, warmer conditions being conducive to greater species richness. Consistent with this hypothesis is the fact that the MT microsample, which is from the part of the HC Formation thought to have been deposited under cool conditions (Larson et al., 2010), contains only one turtle taxon. Cool temperatures may also explain why crocodyliform material is absent from the MT microsample while *Champsosaurus* is present, albeit in small numbers.

Wapiti Formation Unit 3 may have been laid down in a warmer environment despite the high palaeolatitude, given its greater turtle diversity and the presence of a few crocodyliform elements. The abundance of *Myledaphus* at the DC Bonebed arguably supports this interpretation, as extant rhinobatoids have circumtropical to warm temperate distributions (Wilson et al., 2013).

In the context of Late Cretaceous Albertan vertebrate communities, the WU3 assemblage suggests that evolutionary turnover, palaeolatitude, and proximity to the coastline of the Western Interior Seaway were all important influences on faunal composition (Fig. 9). However, knowledge of the assemblage rests overwhelmingly on specimens recovered from Kleskun Hill and the DC Bonebed, and broader sampling will be needed to build a more complete picture of the vertebrate fauna.

To summarise, the DC Bonebed is the most ecologically informative sample of the WU3 vertebrate fauna and, along with the Kleskun Hill locality, represents the only terrestrial fauna from the Bearpaw gap in western North America. The complementary and contemporaneous faunas from the DC Bonebed and Kleskun Hill (both WU3) show demonstrable affinities with the Belly River fauna of southern Alberta, including the shared presence of the baenid *Plesiobaena antiqua*, the trionychid *Aspideretoides foveatus*, and the chamopsiid *Socognathus unicuspis*. The identification of a monstrosaur, *Eodelphis* cf. *E. browni* and cf. *Chirostenotes* from the DC Bonebed provides additional potential links with the Belly River fauna. At the same time, the WU3 fauna differs from both the Belly River and Edmonton groups in the unusual abundance of acipenseriforms, near absence of 'Holostean A', and the abundance of

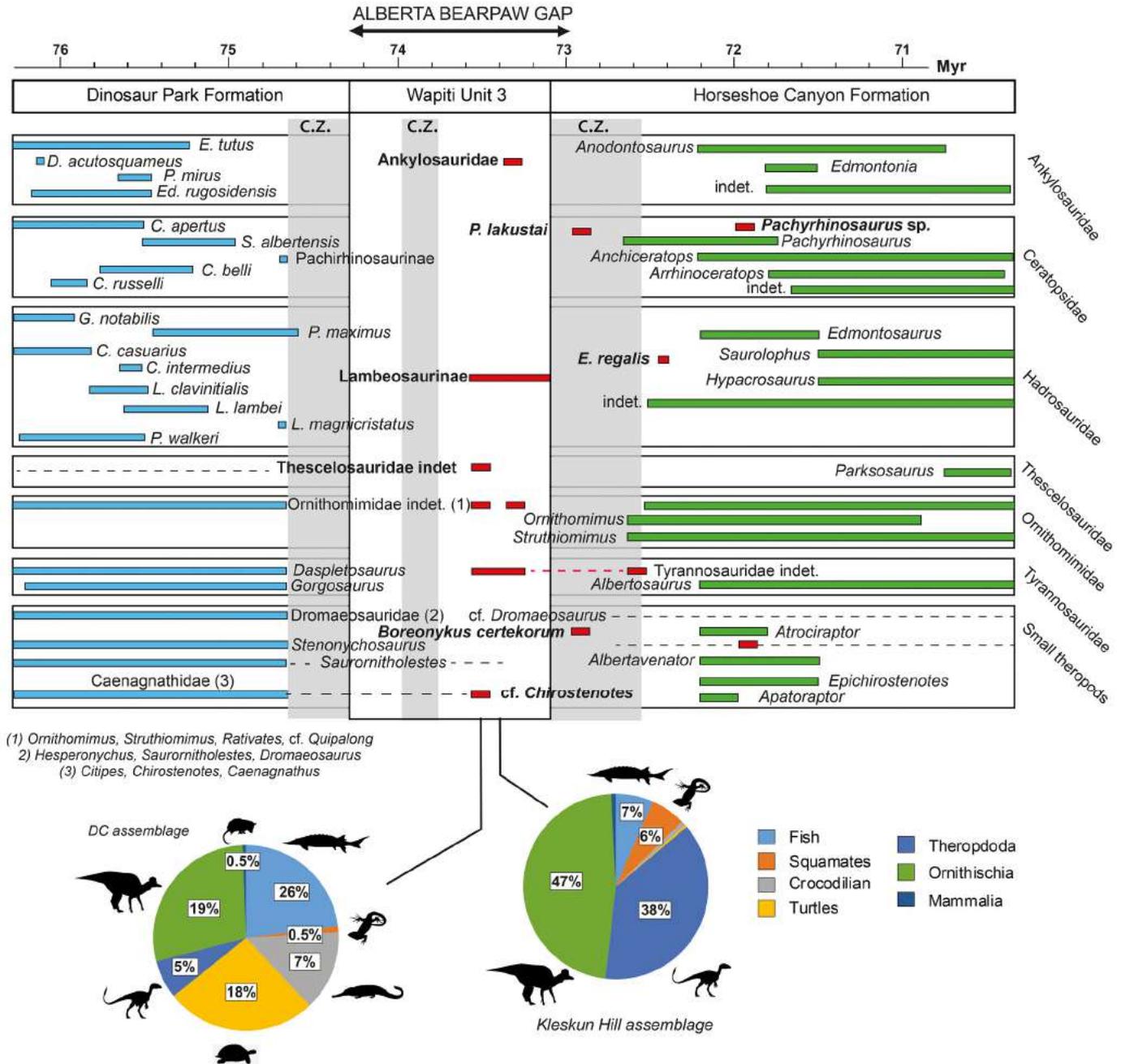


Fig. 9. Chart showing the documented stratigraphic distribution, in the Campanian of Alberta, of various vertebrate species and clades discussed in this paper (light blue boxes, Dinosaur Park Formation; red boxes, Wapiti Formation; green boxes, Horseshoe Canyon Formation). Pie diagrams represent the compositions of the fossil vertebrate assemblages from the DC Bonebed and Kleskun Hill. C.z., coal zone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

turtles and *Champsosaurus*. The scinoid *Kleskunsaurus grandepriariensis* remains the only taxon potentially endemic to WU3. The implication is that at least some 'typical' Belly River Group taxa (such as *Plesiobaena antiqua*, *Socognathus unicuspis*, and possibly *Chirostenotes pergracilis* and *Eodelphis browni*) survived throughout Bearpaw times by following suitable habitats to the north in the Grande Prairie region. Given its evident peculiarities, however, the WU3 fauna is not simply a northerly, late-surviving Belly River fauna, but must have also been influenced by the localized effects of climate and latitude, as well as by faunal turnover.

6. Palaeoenvironmental implications

Historically considered to have been produced by a single, major marine transgressive event, the Bearpaw Formation in fact comprises two marine tongues divided by the coal-dominated deposits of the Strathmore Member of the HC Formation, and thus documents multiple sea level changes (Eberth and Braman, 2012; Hathway, 2016; Zupalich et al., 2021). Furthermore, the Drumheller Marine Tongue in the upper part of the HC Formation represents an additional, minor incursion of the Western Interior Seaway (Straight and Eberth, 2002). To the north and west of the main areas of Bearpaw deposition in central and southern Alberta, the Bearpaw shale correlates updip with coastal and terrestrial deposits that are dominated by coal seams and organic-rich, fine-grained sediments. In west-central Alberta, WU3 includes low-energy, mud-dominated, alluvial lowland deposits, and formed in a depositional setting consistent with the pattern of transgressive-regressive events recorded by the Bearpaw Formation and Strathmore Member (Fanti and Catuneanu, 2009, 2010; Zupalich et al., 2021). Measured sections in the Grande Prairie area document frequent coal seams and peat horizons, with widespread oxbow lakes, bogs and marshes (Fanti and Miyashita, 2009; Fanti and Catuneanu, 2009). The sedimentological evidence for a waterlogged landscape is consistent with the presence in the DC Bonebed palynomorph sample of megaspores and microspores characteristic of quiet freshwater environments, and zygospores apparently belonging to freshwater algae.

The Bearpaw Formation was deposited diachronously across Alberta, owing to a younger onset of paralic-marine conditions toward the north. Recent studies of Bearpaw palaeogeography have documented not only the geographic extent of coal zones at the bottom (Lethbridge Coal Zone) and top (Drumheller Member) of this interval, but also widespread coal-dominated areas to the west of Edmonton, similar to those found near Grande Prairie (Fanti and Miyashita, 2009; Zupalich et al., 2021). Therefore, the geographic extent of the ecological and environmental settings in which coal is typically deposited may represent the key to understanding the composition of vertebrate faunas in west-central Alberta during the time of relatively high sea levels that encompasses the Bearpaw Gap (Dawson et al., 1994; Catuneanu et al., 1997, 1999; Eberth and Braman, 2012; Hathway, 2016). The Bearpaw transgressive-regressive cycles resulted in a northward shift and expansion of lowland, waterlogged, low-energy depositional systems (see Zupalich et al., 2021) that reached their maximum geographic extent and sediment accumulation rate during the deposition of the Strathmore Member of the HC Formation. WU3 is similar from a palaeontological perspective to the Dinosaur Park Formation but clearly differs both lithologically and palaeontologically from the overlying deposits of Wapiti Unit 4 and from correlative beds of the upper HC Formation in central Alberta, which record terrestrial deposition during progressive falling stages of the Bearpaw Sea (Fanti and Catuneanu, 2010; Eberth and Braman, 2012; Eberth and Kamo, 2020).

Data presented here suggest that suitable habitat for continental vertebrate communities extended, during Bearpaw times, at least about 5° to the north of the Dinosaur Provincial Park area, and thus to the margin of the inferred Campanian polar regions (60° North palaeolatitude; Fig. 9). Further investigation of the vertebrate fauna of older deposits in the study area (i.e. Wapiti Unit 2, time-equivalent to the

Oldman and Dinosaur Park formations of southern Alberta) is needed in order to determine whether a fauna broadly resembling that of WU3 and the upper Belly River Group already existed in the region prior to the Bearpaw gap, or whether such a fauna dispersed into the region during the Bearpaw gap itself. Unquestionably, WU3 is crucial for testing recent models and hypotheses regarding the impact on vertebrate thanatocoenoses of both spatiotemporal biases and abiotic factors along the Western Interior Seaway (Lehman, 1987; Gates et al., 2010; Gates et al., 2012; Vavrek and Larsson, 2010; Loewen et al., 2013; Chiarenza et al., 2019). The fossil record discussed in this study represents the only known major source of evidence regarding continental vertebrate faunas inhabiting Alberta during this time interval.

In summary, the sedimentology and palynology of the DC Bonebed point to a quiet freshwater environment in the alluvial lowlands of WU3, contemporaneous with deposition of marine shales of the Bearpaw Formation in southern Alberta. The northerly terrestrial depositional environment of WU3, situated at the edge of the Campanian polar region (60° North palaeolatitude), provided suitable habitat that was colonized by a vertebrate fauna with at least some characteristics of the Belly River Group assemblage, during a time when much of southern Alberta was inundated by the Bearpaw Sea. The faunal compositions of parts of the Wapiti Formation that bracket WU3 are, however, still poorly known. Further exploration will be required in order to understand the broader history of this fauna in the Grande Prairie region.

7. Conclusions

The Bearpaw Formation in Alberta—a northerly expression of the final major incursions of the Western Interior Seaway—has stood as a substantial ~1.2-million-year-long gap separating the well-studied terrestrial faunas of the Belly River and Edmonton groups. In west-central Alberta, the continuous terrestrial deposits of the Wapiti Formation, and in particular Unit 3, offer an opportunity to begin filling the 'Bearpaw gap'. The diverse WU3 vertebrate fauna documented here from the DC Bonebed, together with previously described micro-vertebrates from Kleskun Hill, shows a distinctive Belly River signature similar to those of the older upper Oldman and Dinosaur Park formations, and demonstrates that a vertebrate community with this basic character existed in west-central Alberta well after the classic Dinosaur Park Formation ecosystem had been extirpated by the Bearpaw transgression. The presence of a possible endemic form (the scinoid *Kleskunsaurus grandepriariensis*) in the WU3 assemblage, and some unusual abundance patterns relative to southern Belly River faunas (e.g., abundance of *Myledaphus*, acipenserids, *Champsosaurus* and thescelosaurids; rarity of lissamphibians and crocodyliforms), likely reflect some combination of high palaeolatitude and close proximity to the palaeocoast-line. These findings imply faunal composition along the margins of the Western Interior Seaway was influenced by a complex, superimposed mosaic of palaeolatitudinal and palaeoenvironmental gradients, in addition to evolutionary turnover.

CRediT authorship contribution statement

F.Fanti: Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – Review and Editing, Visualization, Funding acquisition. **P.Bell:** Conceptualization, Resources, Writing – original draft, Writing – Review and Editing. **M.Wavrek:** Conceptualization, Resources, Funding acquisition. **D.Larson:** Methodology, Resources, Investigation. **E.Koppelhus:** Investigation. **R.Sissons:** Conceptualization, Investigation, Resources, Writing – Review and Editing, Visualization. **A.Langone:** Methodology, Resources. **N.Campione:** Conceptualization, Resources, Writing – Review and Editing, Funding acquisition. **C.Sullivan:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – Review and Editing, Funding acquisition.

Declaration of Competing Interest

I declare no conflict of interest related to this manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2022.110923>.

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