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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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Filling the Bearpaw ~~Gap~~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 ~~and/~~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) ~~provides~~ is ~~unequalled~~ crucial ~~contribution to~~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 ~~crucial~~ 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 share 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. ~~shares striking similarities with lowland to marginal marine ecosystems recording the initial phases of the Bearpaw transgression in the older Dinosaur Park Formation and with the onset of the Dinosaur Park Formation over the Oldman Formation in southern Alberta~~. 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 ~~underline~~ underscore the importance ~~in~~ of determining the spatiotemporal evolution of environmental factors (e.g., coastal proximity). The occurrence of endemic forms and differences in relative taxon abundance ~~may~~ suggest ~~that~~ additional latitude-correlated factors, implicating both latitudinal and coastal-inland habitat gradients ~~also exerted an important influence on~~ in driving the taxonomic composition of Late Cretaceous terrestrial faunas.

Keywords: 6 -~~Microvertebrate~~; Campanian; Alberta; Bearpaw; Western Interior Seaway; Dinosaur Park Formation; Wapiti Formation

1. Introduction

The Late Cretaceous terrestrial faunas of western North America provide one of the ~~richest available~~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~~ref~~), 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 the Belly River Group) and late Campanian–-Maastrichtian Horseshoe Canyon Formation (hereafter ~~HSC~~HCHC 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' ~~inferred to have been~~ associated with ~~differing~~ 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 ~~break~~ 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 ~~between~~ from ~~approximately~~ ~~74~~76 ~~and~~ –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 g~~G~~roups, both renowned for the information their remarkable fossil records provide on vertebrate evolution and diversity ~~in~~ 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 ~~in the terrestrial fossil record~~ 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 ~~taken into account~~ considered when interpreting species distribution in the fossil record. For example, ~~(~~palaeo~~)~~latitudinal climatic gradients may explain observed north-south faunal variations, including ~~instances of~~ endemism, whereas environmental gradients may explain the existence of disparate~~,~~ yet contemporaneous~~,~~ ecological communities in strata deposited in different settings. ~~Therefore, b~~Both latitudinal and environmental gradients have previously been interpreted ~~represent potentially important influences~~as important ~~factors driving~~determinants of ~~on the composition of the faunas that existed in the Late Cretaceous~~the ~~faunal~~ composition~~during the evolution of~~ ~~across~~of faunas existing near the Western Interior Seaway during the Late Cretaceous (e.g., Brinkman 1990; Lehman 1987, 2001; 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 ~~interaction~~ interplay between latitudinal and depositional gradients during the Late Cretaceous and~~that show~~ *how* such interactions ~~may~~ 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 ~~non-marine~~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 ~~Wapiti~~ formation's clastic wedge extends from the city of Edmonton, Alberta, to easternmost British Columbia, yet ~~virtually~~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 waterway~~ banks~~s~~ 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 ~~non-marine~~terrestrial (albeit potentially near-coastal, *see* Zubalich 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~~s~~ multiple ~~a rare example of a~~ high-latitude Late Cretaceous ~~community, or rather multiple~~ communities that succeeded one another ~~over a period of~~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 ~~DC (~~Dinosaur-Chelonian (DC)~~)~~ Bonebed, which displays a high taxonomic diversity of well-preserved, ~~and~~ typically small (≤ 10 cm)~~,~~ plant ~~remains~~ and vertebrate ~~bones and teeth~~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 ~~further~~ 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.

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 ~~interval~~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 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 between ~74.3–73.1 Ma (Eberth and Kamo, 2020; Zubalich 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 ~~fossil content~~vertebrate

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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, ~~which was~~ 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; Zubalich 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; Zubalich 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; Zubalich 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 gGap.

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 ~~HSC~~HC Formation. The Dinosaur Park and ~~HSC~~HC formations have ~~both~~ 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 ~~clearly~~ 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 ~~here~~ to deposits overlying the Dinosaur Park Formation and underlying the Drumheller Member of the ~~HCHSC~~HC Fm (*see* Rogers et al., 2016 and Zubalich 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, ~~non-marine~~terrestrial deposits of WU3 are correlative with the Bearpaw Formation of central Alberta (Fanti and Catuneanu, 2010; Zubalich et al., 2021). Sedimentological and palaeontological data also indicate that WU3 was deposited in extensive lowland environments located near (*i.e.*, within tens of kilometres of~~from)~~ the palaeo-shoreline (Fanti and Miyashita, 2009, Fanti and Catuneanu, 2010; Schröder-Adams, 2014; Koppelhus and Fanti, 2019, Chiarenza et al., 2019; Zubalich et al., 2021; this study).

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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 ~~have been~~ were primarily discussed by Fanti and Miyashita (2009), who described the WU3 fauna of the Kleskun Hill locality.~~;~~ ~~As~~ Wapiti Formation Unit 3 ~~described, WU3~~ is characterized by low-energy environments, fine-grained sediments and high accumulation rates, resulting in a high ~~n~~ ~~increased~~ preservation potential for vertebrate remains (Haubold, 1989; Butler et al., 2010; Fanti and Miyashita, 2009). ~~and in several conference abstracts focusing on~~The ~~the~~ newly discovered DC Bonebed ~~, which~~ 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)~~, also~~. It lies within ~~pertains to~~ WU3 and ~~is described herein. WU3 is also characterized by low-energy environments, fine-grained sediments and high accumulation rates, resulting in an increased preservation potential for vertebrate remains (Haubold, 1989; Butler et al., 2010; Fanti and Miyashita, 2009). The DC Bonebed~~ provides ~~further~~

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 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 being no thicker than< 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. Overall, wWe inferterpret that the deposits that include the DC Bonebed as having been laid down by an aggrading fluvial systemaan aggrading fluvial system in a distal/backswamp floodplain laid down the deposits that include the DC Bonebed in a distal/backswamp floodplain. 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 each other and 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 $^{206}Pb/^{238}U$ 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 ~~HSC~~HC Formation by Eberth and Braman (2012) and marks the transition from the *Pseudoaquilapollenites parallelus*-~~—~~*Parviprojectus leucocephalus* palynostratigraphic biozone to the *Wodehouseia gracile*-~~—~~*Mancicorpus 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 ~~that have~~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 ~~that is~~ common in the Upper Cretaceous of North America, but their known temporal ranges (Braman 2013, 2018) vary considerably. *Accuratipollis glomeratus* has the shortest range, cent~~e~~red at ~~about~~ ~75 Ma in southern Alberta (Braman 2018) and falling entirely within the *Aquilapollenites configuratus-Mancicorpus 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). Th~~e~~se results~~is~~ suggest~~s~~ that ~~the range of~~ *Accuratipollis glomeratus* might ~~in fact be~~ 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). Zygospores of presumed freshwater algae (*Botryococcus*, *Lecaniella*, *Pediastrum* and *Savitrina*) ~~which~~ 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 ~~therefore~~ corroborates the radiometric data presented ~~above, and~~above, ~~and~~ reinforcing~~es~~ the conclusion that WU3 and its ~~non-marine~~terrestrial vertebrate fauna are time-equivalent to the Bearpaw Formation of southern Alberta~~,~~, particularly ~~and most likely to~~

the Strathmore Member (~~HSC~~HC Formation) and the upper tongue of the Bearpaw Formation~~ in central Alberta~~.

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; Cocks 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 M~~y~~a, which would place it in the upper part of WU3; however, this age should be regarded ~~as uncertain~~with caution, as ~~they were~~it was based on few crystals and ~~proper~~ methodological ~~information~~details were ~~was~~ere not ~~never~~ 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~~ is here referred~~ to the basalmost deposits of Wapiti Formation Unit 4 (*see* also Cocks et al., 2020).

A complete ~~full~~ systematic review of the ~~WU3 vertebrate assemblage~~DC B~~b~~onebed 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 ~~two~~ WU3 microsites, namely ~~namely~~ Kleskun Hill and the new DC Bonebed locality,~~;~~ are ~~both~~ highly informative. Kleskun Hill is a well-known ~~has long been known as a~~ source of ~~a~~ ~~of the remains of a~~ diverse terrestrial and freshwater aquatic fossils~~ (include freshwater aquatic taxa)~~~~and to~~

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~~some extent freshwater~~ ~~palaeocommunity~~, notably ~~containing~~ including fish, squamates, *C~~e~~hampsosaur~~uids~~*, large and small theropods, hadrosaurids (~~including~~ both neonate and adult specimens), ceratopsids, ~~possible pachycephalosaurids,~~ thescelosaurids, ~~and~~ 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 assemblage.

A total of 364 identifiable (below the level of Gnathostomata) vertebrate specimens were recovered from the DC Bonebed during the ~~years~~ 2014~~-~~–2019 field seasons. Specimens described in this paper were collected from different spots within the accretionar~~l~~y 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 ~~have greatest dimensions~~measure ~~within~~between 25 and 60 mm in their greatest dimension, and 72% measure~~are~~ <50 mm: therefore, the DC Bonebed is considered a~~s~~ 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 sample, whereas the remainder ~~represent~~ are tetrapods, including lissamphibians (0.5% ~~of the total~~), 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~~2~~%) in the available sample could ~~be referred only to~~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

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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 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 Pal~~a~~eocene 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 postcranial 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).

~~Among~~ O~~terrestrial~~ ~~the dinosaurian~~ ~~taxa represented in the DC Bonebed, the vast majority of elements are dinosaurian, and~~most are ~~from~~ ornithischians specimens~~, which~~ ~~elements~~ 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 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 ~~has~~ 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. *Chirostenotes*. 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.

5. Ecological implications~~y and significance~~ of the WU3 vertebrate assemblage

At present, the most ecologically informative ~~single~~ samples of the WU3 vertebrate fauna are~~is~~ the diverse assemblage from the DC Bonebed. ~~This is supplemented by~~ and the smaller but similarly diverse sample 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 ~~HSC~~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, ~~because such samples are informative regarding not only~~providing insights into~~on~~ the local (alpha)~~total~~ diversity of ~~the~~ vertebrates ~~fauna~~ and unique knowledge of~~n~~ ~~but also~~ the relative abundances ~~of specimens~~ of different vertebrate groups. Microvertebrates from the Oldman, Dinosaur Park, and ~~HSC~~HC formations have received considerable research attention (Brinkman, 1990; Gao and Fox, 1996; 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 microsamples 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). ~~The three microsamples are referred to here as the UO, DP and LC microsamples, respectively.~~ Similarly, Larson et al. (2010) provided comprehensive data on a microsample~~s~~ from the Morrin and Tolman members of the ~~HSC~~HC Formation, which we refer to here as the Morrin-Tolman (MT) microsample, 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 ~~HSC~~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.

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Striking faunal differences exist between the contemporaneous DC Bonebed and Kleskun Hill microsamples (Fig. 8A).~~,~~ As both sites are from WU3 and only ~23 km apart, ~~and must reflect an environmental and/or taphonomic discrepancy rather than~~ it seems unlikely that these differences are the results of large-scale biogeographic variation or faunal change over time ~~(Fig. 8A)~~. Instead, the differences probably ~~lie in~~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 *C~~c~~hampsosaur~~u~~us*, and less rich in presumably terrestrial lizards and dinosaurs (Fig. 8B). Taken together, the ~~complementary~~ contemporaneous Kleskun Hill and DC Bonebed assemblages give a broad, if in most respects taxonomically ~~imprecise~~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 *Myledaphus* teeth reported by Larson et al. (2010) in the ~~HSC~~HC-Morrin and Tolman members (~~HSC~~HC Fm) microsample. Although determining numbers of individuals based solely on isolated scales, bones and/or teeth is problematic ~~(based solely on isolated scales and/or teeth)~~, 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 the DC Bonebed is the near-total absence ~~from the DC Bonebed~~ of scales attributable to 'Holostean A', which are overwhelmingly abundant in the ~~HSC~~ Morrin – Tolman members of the Horseshoe Canyon Formation microsample and intermediate in abundance between *Myledaphus*/*Pseudomyledaphus* and lepisosteids in the DP and UO microsamples. 'Holostean A' is also the most abundant identifiable fish taxon in the small aquatic

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vertebrate component of the sample from Kleskun Hill ~~(refs?).~~. Lepisosteids are somewhat less abundant as a proportion of the fish fauna in the DP and UO microsamples than at the DC Bonebed, and are absent from the ~~HSC~~MT microsample, although they do occur in the ~~HSC~~HC Formation (Quinney, 2011). *Myledaphus*, by contrast, is almost twice as abundant in the DP microsample as at the DC Bonebed, but rare in the UO microsample and especially the ~~HSC~~MT microsample. *Myledaphus* is, however, abundant in the marine-influenced LC microsample, accounting for about 45% of all identifiable fish specimens. The LC microsample 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, ~~HSC~~MT and UO microsamples, but teleosts are well represented in all three, and in the UO microsample in particular. Amiid and *Belonostomus* specimens are rare in the UO, DP and ~~HSC~~MT microsamples, 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 et al., 2016).

Turtles and *Champsosaurus* make up a far higher percentage of the DC Bonebed sample, relative to fish, than in~~of any of~~ the UO, DP, LC and ~~HSC~~MT ~~southern Alberta~~ 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 designed 'BMC' by Cullen and Evans (2016). The strong numerical dominance of *Champsosaurus* elements over crocodyliform elements at the DC Bonebed is ~~reversed~~ opposite to the condition~~at~~ observed in the DP and UO microsamples, despite ~~in both of which~~ crocodyliform specimens ~~are~~ being relatively sparse in general ~~but still more abundant than those of *Champsosaurus*~~. The ~~HSC~~MT microsample contains ~~a few~~some *Champsosaurus* elements ~~and~~ but no crocodyliforms ~~material at all~~, although crocodyliforms are known from other parts of the ~~HSC~~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, m~~M~~aterial referred to *Aspideretoides* sp., and potentially representing *A. foveatus*, is known from the lower part of the ~~HSC~~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 et al., 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 ~~HSC~~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 ~~Phil's Knob~~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 ~~Phil's Knob~~PK crocodyliforms are even more abundant than *Champsosaurus*, and the most abundant turtle taxon is the helochelydrid *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

Commentato [CS1]: Reviewer 2 complained about this, but the *Aspideretoides* material is reported in older papers that just say it's from "Unit 1", so we don't have any easy way of determining whether it's from the Horsethief Member or the Drumheller Member. We might want to note this in our response letter.

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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 ~~HSC~~HC Formation. Two mammal teeth, representing a multituberculate and a pediomyid marsupial, were~~have been~~ 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 scincoid *Kleskunsaurus grandeprairiensis*, and multiple specimens of the chamopsiid *Socognathus unicuspis*. (Nydam et al., 2010). While *Kleskunsaurus grandeprairiensis* ~~may be endemic~~is currently ~~unique~~known only from ~~to~~ WU3, *Socognathus unicuspis* ~~is known from~~occurs in the Dinosaur Park and Oldman Formations, and possibly also in~~from~~ the upper Maastrichtian Hell Creek Formation of Montana (Gao and Fox, 1996; Nydam, 2013). A dentary from Kleskun Hill referred to *Champs* 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, 1996; 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, 1996; 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, 1996; 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 larger 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. Hadrosaurids are less proportionally abundant in the ~~HSC~~MT microsample than at the DC Bonebed, presumably at least to some extent because~~because~~ the dinosaur component of the former was collected in large part from an *Albertosaurus* bonebed (Larson et al., 2010)~~, which and is rich in tyrannosaurid teeth as a result~~. However, theropods are even more prevalent as a percentage of the total fauna at Kleskun Hill than in the ~~HSC~~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 ~~HSC~~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 ~~HSC~~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 ~~HSC~~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 ~~a single~~one ~~pachycephalosaurid~~ tooth ~~is known~~~~was interpreted~~ from Kleskun Hill has been referred to Pachycephalosauridae (Fanti and Miyashita, 2009).

The only theropod element from the DC Bonebed that is ~~potentially~~ identifiable at ~~the specific~~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. ~~Even~~ F~~f~~inding evidence of even a single individual caenagnathid among the 122 dinosaur bones and teeth available from the DC Bonebed is remarkable~~, however, given the rarity of caenagnathids at other sites~~, given that not ~~a single~~one caenagnathid~~e~~ bone~~s~~ was ~~found~~reported to occur in ~~.~~ t~~T~~he DP, Kleskun Hill, ~~HSC~~MT, and UO microsamples~~, in fact, have not been reported to contain caenagnathid material at all~~. 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 ~~microsample~~ and, especially, in the ~~HSC~~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 ~~HSC~~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

~~HSC~~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).

~~As a whole, and~~At least at face value, the WU3 vertebrate fauna more closely resembles ~~more closely~~ that of the Dinosaur Park Formation, and to a large extent also that of the Oldman Formation, ~~more closely~~ than that of the ~~HSC~~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 ~~the turtle *Aspideretoides foveatus*,~~ an indeterminate monstersaur~~,~~ 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 endemic squamate *Kleskunsaurus grandeprairiensis*, 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~~a single~~ general characteristics of the WU3 fauna, namely the rarity of crocodyliforms and the high abundance of theropods, represent~~s~~ even ~~an~~ arguable points of distinctive similarity to the vertebrate assemblage of the ~~HSC~~HC Formation. Moreover, the richness of theropods in the ~~HSC~~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 ~~HSC~~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 ~~HSC~~HC Formation. These distinctive survivors, including *Plesiobaena antiqua*, *Socognathus unicuspis*, and possibly *Chirostenotes pergracilis, Eodelphis browni* and *Aspideretoides foveatus*, 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 ~~HSC~~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 grandeprairiensis*, 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 neochoristodere possibly referable to *Champsosaurus* is even known from ~~the~~ Turonian–Coniacian deposits on ~~of~~ 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 Maastrichtian 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 towards 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 ~~HSC~~MT microsample, which is from the part of the ~~HSC~~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 ~~HSC~~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~~, from the perspective of non-marine fauna, from the entirety of~~, along with the Kleskun Hill locality, represent the only terrestrial fauna from the Bearpaw gap in western North America. The complementary and contemporaneous faunas from the DC Bonebed and Kelskun Hill (both WU3) show demonstrable affinities with the Belly River fauna of southern Alberta, including

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the shared presence of the baenid *Plesiobaena antiqua*, the trionychid *Aspideretoides foveatus*, and the chamopsiid *Socognathus unicuspis*. The identification of a monstersaur, *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 turtles and *Champsosaurus*. The scincoid *Kleskunsaurus grandeprairiensis* 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*, *Eodelphis browni* and *Aspideretoides foveatus*) survived throughout Bearpaw times by following suitable ~~tracking appropriate~~ habitats to the north in the Grande Prairie region. Given ~~the number of~~its evident peculiarities, however, the WU3 fauna is not simply a northerly, late-surviving Belly River fauna, but ~~one that was~~must have also been influenced ~~also~~ by the localized effects of climate and latitude, as well as by faunal turnover.

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6. Palaeoenvironmental implications

Historically considered as ~~representing~~ 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 ~~HSC~~HC Formation, and thus documents multiple sea level changes (Eberth and Braman, 2012; Hathway, 2016; Zubalich et al., 2021). Furthermore, the Drumheller Marine Tongue in the upper part of the ~~HSC~~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 ~~is~~ correlates updip ~~gradually~~ ~~replaced~~ with ~~by time-equivalent~~ 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 ~~Mbr~~Member. (Fanti and Catuneanu, 2009, 2010; Zubalich 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; Zubalich 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 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 low-land, waterlogged, low-energy depositional systems (*see* Zubalich et al., 2021) that reached their maximum geographic extent and sediment accumulation rate during the deposition of the Strathmore Member of the ~~HSC~~HC Formation. WU3 is similar from a palaeontological perspective to the Dinosaur Park Formation ~~whereas~~ but clearly differs both lithologically and palaeontologically from the overlying deposits of Wapiti Unit 4 and from correlative beds of the upper ~~HSC~~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, 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 ~~characterize~~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 environments of WU3, ~~deposited~~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 character~~s~~istics of the Belly River Group assemblage, during ~~at~~ 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. ~~and require f~~Further exploration will be required in order to ~~examine~~understand the ~~timing and dispersal~~broader history of this fauna in the Grande Prairie region.

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

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continuous terrestrial deposits of the Wapiti Formation, and in particular Unit 3, offer an opportunity to begin filling the 'Bearpaw gap~~Gap~~'. The diverse WU3 vertebrate fauna documented here from the DC Bonebed, together with previously -described microvertebrates 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 ~~probable~~ possible endemic form (the scincoid *Kleskunsaurus grandeprairiensis*) 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 palaeocoastline. 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.

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784 people.
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789 CS, RLS, DL, EK; Resources: FF, PRB, MV, DL, RLS, NEC, CS; AL; Writing – original draft: FF,
790 CS, PRB; Writing – Review and Editing: FF, PRB, RLS, NEC, CS; Visualization: FF, RLS;
791 Funding acquisition: CS, FF, NEC, MV.
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Commentato [NC2]: Site was found under our DRI grant...

Commentato [C3R2]: Sounds like the DRI grant should be mentioned in the Acknowledgements.

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Figure Caption

Figure 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 ~~Bdonebed~~Bonebed.

Figure 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).

Figure 3: A) Field photograph of the Dinosaur-Chelonian (DC) B~~b~~onebed 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 ~~highlighted~~ dated bentonitic beds indicated.

Figure 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.

Figure 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, which 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. ~~Largely~~ Nearly complete *Belonostomus* ~~upper mandible~~fused premaxillae (UALVP 60781) in N) dorsal and O) ventral views~~,~~ ~~representing the left and right fused premaxillae~~, exhibiting two rows of closely packed tec~~oo~~th ~~rows~~, and delicate ganoine ornamentation on the dorsal surface. Note that each boxed panel has own scale bar. Scale bars 3 cm.

~~Chondrichthyan and osteichthyan specimens from the DC Bonebed. UALVP 60786 Amiid centrum in A) dorsal and B) anterior views. *Myledaphus bipartitus* centrum (UALVP 60802) in C) dorsal and D) anterior views. *Myledaphus bipartitus* shed crown (UALVP 59115) in E) lateral and F) occlusal view. G) Right *Coriops* dentary fragment (UALVP 60773) in lateral view. H) Lepisosteid scale (UALVP 23122). I) Lepisosteid caudal vertebra (UALVP 70744) in right lateral view. J) Lepisosteid tooth (UALVP 23117). 'Holostean A' scale (UALVP 60812) in K) external and L) internal views. M) Acipenserid dorsal scute (UALVP 59844) in dorsal view, anterior to the~~

~~left. *Belonostomus* upper mandible (UALVP 60781) in N) dorsal and O) ventral views. Note that each boxed panel has own scale bar. Scale bars 3 cm.~~

Figure 6: Amphibia, turtle, squamate, *Champsosaurus*, and crocodyliform specimens from the DC Bonebed. A) *Plesiobaena antiqua* hypoplastron (UALVP 23092) in ventral view. B) Trionychid right hypoplastron fragment (UALVP 23101), exhibiting typical tryionychid ornamentation~~, though not referable to *Aspideretoides foveatus*~~. C) Baenidae indet. f~~F~~used 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 ~~relatively little~~subtle ornamentation. H) Amphicoelous *Hedronchus sternbergii* trunk vertebra (UALVP 59831) in right lateral view, exhibiting backswept neural spine. I) Conical crocodyliform tooth crown (UALVP 59811), with characteristic unserrated carinae ~~visible running lengthwise from base to apex at the center of this view~~. 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 ~~specimens inset in~~that each boxed panel has~~s~~ ~~at different~~own scale bar. Scale bars 3 cm.~~Amphibia, turtle, squamate, *Champsosaurus*, and crocodyliform specimens from the DC Bonebed. A) *Plesiobaena antiqua* hypoplastron (UALVP 23092) in ventral view. B) Trionychid right hypoplastron fragment (UALVP 23101). C) Baenidae indet. hypoplastron and xiphiplastron (UALVP59133) with D) inset of texture indicated by white box. E) Chelydrid costal (UALVP 59135). H) *Hedronchus sternbergii* trunk vertebra (UALVP 59831) in right lateral view. I) Crocodyliform tooth crown (UALVP 59811). F) *Champsosaurus* centrum (UALVP 57408) in dorsal view. G) Squamate astragalocalcaneum (UALVP 59947) in dorsal view. Note specimens inset in boxes at different scale. Scale bars 3 cm.~~

Figure 7: Dinosaur specimens from the DC Bonebed. A) Ankylosaurid tooth crown (UALVP

59116), 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~~ with typical centrum and neural arch morphology~~. H) Partial ornithomimid left pubis (UALVP 59798) in medial view, with ~~fragmentary~~ damaged pubic apron visible at left. I) Caenagnathid left ilium (UALVP 60800) in medial view. A, sacral rib facet can be ~~noted~~ seen ~~off-center of~~near the broken dorsal margin, roughly above the pubic pedunclee~~on the dorsal-most remaining area~~. Note ~~specimens inset in~~that each boxed panel has owns~~ at different~~ scale bar. Scale bars 3 cm.~~Dinosaur specimens from the DC Bonebed. A) Ankylosaurid tooth crown (UALVP 59116). B) Troodontid right pedal phalanx IV-1 in medial view (UALVP 60748). C) Tyrannosaurid tooth crown (UALVP 57805). D) Thescelosaurid left quadrate (UALVP 23114) in lateral view. E) Dromaeosaurid pedal phalanx (UALVP 59507). Hadrosaurid caudal centrum (UALVP 61239) in F) dorsal and G) left lateral views. H) Ornithomimid left pubis (UALVP 59798) in medial view. I) Caenagnathid left ilium (UALVP 60800) in medial view. Note specimens inset in boxes at different scale. Scale bars 3 cm.~~

Figure 8: A) Relative abundances ~~at family level~~ of vertebrate groups~~taxonomy~~ for various~~during the~~ sites and stratigraphic units in the Campanian of~~in~~ Alberta. Combined relative abundances total 100% ~~for~~ in each ~~individual stratigraphic unit~~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 SI for detailed ~~accounts~~abundance data.

Figure 9: Chart showing the documented stratigraphic distribution, in the Campanian of Alberta, ~~for the Campanian~~ 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 diversity of discussed microsite localities in Wapiti Unit 3 (in ascending order: DC bonebed, Kleskun Hill, and Red Willow River). C.z., coal zone

Supplementary material

SI 1: Supplementary data discussing U-Pb dating procedures, and Systematic Palaeontology~~,~~ of vertebrate fauna from the Dinosaur-Chelonian B~~b~~onebed (Wapiti Formation Unit 3, upper Campanian, Alberta, Canada).

SI 2: Detailed faunal counts for microvertebrate taxa representative of the Dinosaur-Chelonian Bonebed, Oldman, Dinosaur Park (including the Lethbridge Coal Zone), Wapiti Formation (including Dinosaur-Chelonian B~~b~~onebed and Kleskun Hill sites), and Horseshoe Canyon formations.