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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.

Fanti F.[1*], Bell, P.R.[2], Vavrek, M.[3], Larson, D[4]., Koppelhus, E.[5], Sissons, R. L.[5], Langone, A.[6], Campione, N.E.[2], Sullivan C.[4,7]

[1]Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Alma Mater Studiorum, Università di Bologna, 40126 Bologna, Italy; federico.fanti@unibo.it

[2] Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2351, Australia; pbell23@une.edu.au; ~~nicolas.campione@gmail.com~~ncampion@une.edu.au

[3]Grande Prairie, T8W 2L5, Canada; matthew@matthewvavrek.com

[4]Royal BC Museum, Victoria, British Columbia V8W 9W2, Canada; dlarson@royalbcmuseum.bc.ca

[5]Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; ebk@ualberta.ca; robin.sissons@gmail.com; corwin1@ualberta.ca

[6]Istituto di Geoscienze e Georisorse, Consiglio Nazionle delle Ricerche, 27100 Pavia, Italy; langone@crystal.unipv.it

[7]Philip J. Currie Dinosaur Museum, Wembley, Alberta T0H 3S0, Canada

*corresponding author. Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Alma Mater Studiorum, Università di Bologna, 40126 Bologna, Italy; federico.fanti@unibo.it

29 **Abstract**

30 Patterns of Late Cretaceous terrestrial vertebrate diversity across North America have been

31 interpreted primarily in terms of biogeographic provincialism driven by latitude ~~and/~~or coastal-

32 inland habitat gradients. A major difficulty in determining the influence of these two gradients is the

33 existence of some large gaps in the terrestrial fossil record, notably the 'Bearpaw gap' caused by a

34 transgression of the inland Bearpaw Seaway during the latter part of the Campanian. In this context,

35 the terrestrial fauna preserved in the Campanian deposits of the Wapiti Formation (west-central

36 Alberta, Canada) ~~provides~~ is ~~unequalled~~ crucial ~~contribution to~~for addressing the information

37 deficit. Deposited at the edge of the palaeo-circumpolar region, Unit 3 of the strictly terrestrial

38 Wapiti Formation (WU3) is coeval with the 'Bearpaw gap', a ~~crucial~~ period when the terrestrial

39 record from better-sampled areas elsewhere in Canada and the U.S.A. gives way to marine

40 sediments. Here we show, based largely on evidence from the recently -discovered DC (Dinosaur-

41 Chelonian) Bonebed locality, that the diverse WU3 vertebrate fauna share similarities with lowland

42 to marginal marine ecosystems in the Oldman and Dinosaur Park formations which were deposited

43 in southern Alberta prior to the Bearpaw gap. ~~shares striking similarities with lowland to marginal~~

44 ~~marine ecosystems recording the initial phases of the Bearpaw transgression in the older Dinosaur~~

45 ~~Park Formation and with the onset of the Dinosaur Park Formation over the Oldman Formation in~~

46 ~~southern Alberta~~. In addition, a major change in faunal composition demarcates the upper boundary

47 of WU3, related to the disappearance of the Bearpaw Sea in Canada. Data presented here help, first

48 and foremost, to bridge a~~n~~ ~1.2-million-year gap in the North American record of Campanian

49 terrestrial vertebrates. Resemblances between the WU3 vertebrate fauna and slightly older

50 assemblages from southern Alberta ~~underline~~ underscore the importance ~~in~~ of determining the

51 spatiotemporal evolution of environmental factors (e.g., coastal proximity). The occurrence of

52 endemic forms and differences in relative taxon abundance ~~may~~ suggest ~~that~~ additional latitude-

53 correlated factors, implicating both latitudinal and coastal-inland habitat gradients ~~also exerted an~~

54 ~~important influence on~~ in driving the taxonomic composition of Late Cretaceous terrestrial faunas.

55

58

1. Introduction

The Late Cretaceous terrestrial faunas of western North America provide one of the ~~richest availablebest~~ 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~~Groups, both renowned for the information their remarkable fossil records provide on vertebrate evolution and diversity ~~in~~ from the

81   Late Cretaceous (Currie and Koppelhus, 2005; Eberth and Braman, 2012; Eberth et al., 2013;

82   Cullen and Evans, 2016; Gilbert and Bamforth, 2017). Here we refer to this terrestrial fossil record

83   hiatus ~~in the terrestrial fossil record~~ as the 'Bearpaw gap'.

84   Environmental gradients (e.g., between coastal and more inland environments) have an

85   important influence, alongside latitudinal gradients and many other abiotic factors, on the

86   distribution and diversity of modern faunas (Whittaker 1975; Hillebrand, 2004; Drakare et al.,

87   2006) and therefore must be ~~taken into account~~ considered when interpreting species distribution in

88   the fossil record. For example, (palaeo)latitudinal climatic gradients may explain observed north-

89   south faunal variations, including ~~instances of~~ endemism, whereas environmental gradients may

90   explain the existence of disparate, yet contemporaneous, ecological communities in strata deposited

91   in different settings. ~~Therefore, b~~Both latitudinal and environmental gradients have previously been

92   interpreted ~~represent potentially important influences~~as important ~~factors driving~~determinants of ~~on~~

93   ~~the composition of the faunas that existed in the Late Cretaceous~~the ~~faunal~~ composition~~during the~~

94   ~~evolution of across~~of faunas existing near the Western Interior Seaway during the Late Cretaceous

95   (e.g., Brinkman 1990; Lehman 1987, 2001; Sampson et al. 2010; Sampson and Loewen 2010;

96   Burgener et al., 2021; though also *see* Sullivan and Lucas, 2006; Vavrek and Larsson 2010; and

97   Lucas et al., 2016 for critical views). However, the current literature contains few well-constrained

98   studies of the ~~interaction~~ interplay between latitudinal and depositional gradients during the Late

99   Cretaceous and~~that show~~ *how* such interactions ~~may~~ could have shaped the vertebrate communities

100   of the time. Furthermore, the dynamics and ecological consequences of complex, large-scale Earth

101   system events (e.g., major transgressions and regressions), capable of reshaping the geography and

102   environment of entire depositional basins, have been addressed only at a conceptual level

103   (Weishampel and Horner, 1987; Horner et al., 1992; Upchurch et al., 2002; Brinkman, 2003; Bell

104   and Snively, 2008; Butler and Barrett, 2008; Fanti and Miyashita, 2009; Mannion et al., 2012, 2014;

105   Lucas et al., 2016; Chiarenza et al., 2019). This dearth of information is primarily due to the lack of

106   geographic and temporal continuity among fossil-bearing localities, combined with difficulties in

107 tracing time-representative surfaces across multiple ~~non-marine~~terrestrial sedimentary units

108 (Sullivan and Lucas, 2006; Holland and Loughney, 2021).

109   The terrestrial fauna preserved in the Upper Cretaceous Wapiti Formation of west-central

110 Alberta, Canada, has emerged as a source of important palaeontological and geological information

111 that contributes significantly to addressing these shortfalls. The ~~Wapiti~~ formation's clastic wedge

112 extends from the city of Edmonton, Alberta, to easternmost British Columbia, yet ~~virtually~~almost

113 all fossil localities known to date are in the vicinity of the city of Grande Prairie, where major and

114 minor drainage systems have provided the best exposures of this unit along the ~~banks of waterway~~

115 bankss of waterways (Fig. 1). As such, fossils collected from the Wapiti Formation are not only

116 geographically isolated within Alberta, but also, in the North American framework, located between

117 the world-renowned localities of southern Alberta (e.g., Currie and Koppelhus, 2005; Eberth et al.,

118 2013; Cullen and Evans, 2016) and the near-palaeopolar deposits of Alaska (e.g. Fiorillo, 2018).

119 The Wapiti Formation fossil record is also distinctive in two key respects. First, it comes

120 exclusively from ~~non-marine~~terrestrial (albeit potentially near-coastal, *see* Zubalich et al., 2021)

121 strata representing about 8 million years of Campanian–Maastrichtian time, critically including the

122 interval represented elsewhere in western North America by coastal and marine deposits of the

123 Bearpaw Formation. Second, the Wapiti Formation in the study area around Grande Prairie was

124 deposited at a palaeolatitude close to 60°N (Matthews et al., 2016), so its fossil assemblages are

125 unusual in representings multiple ~~a rare example of a~~ high-latitude Late Cretaceous ~~community, or~~

126 ~~rather multiple~~ communities that succeeded one another ~~over a period of~~across the 8 Ma timespan.

127 Over the last decade, an increasing number of papers have described the diverse vertebrate fossil

128 record of the Wapiti Formation, documenting some of the richest Cretaceous fossil sites in North

129 America (Currie et al., 2008; Fanti and Miyashita, 2009; Bell et al., 2014; Fanti et al., 2015; Bell

130 and Currie, 2016; Holland et al., 2021), remarkably preserved individual specimens (Nydam et al.,

131 2010; Bell et al., 2013a, 2014; Barbi et al., 2019), and diverse ichnofossil assemblages (Bell et al.,

132 2013b; Fanti et al., 2013; Enriquez et al., 2020, 2021, 2022).

133　　　　Here we introduce a new, highly informative multitaxic bonebed, referred to as the DC

134　(Dinosaur-Chelonian (DC)) Bonebed, which displays a high taxonomic diversity of well-preserved,

135　and typically small (≤ 10 cm), plant remains and vertebrate bones and teethremains. The bonebed is

136　situated within Wapiti Formation Unit 3 (*sensu* Fanti and Catuneanu, 2009, 2010; hereafter WU3),

137　a stratigraphic interval deposited in a lowland, terrestrial environment during the peak transgression

138　of the Bearpaw Formation. We provide new chronostratigraphic and palynological data to further

139　constrain the age of the Wapiti faunal assemblage from the DC Bonebed, and discuss its

140　significance in the context of western Canada's Campanian fossil record. Finally, we compare the

141　WU3 vertebrate fauna with other Late Cretaceous assemblages from Alberta and explore the

142　implications for interpreting palaeoenvironmental influences on patterns of faunal evolution in

143　northern Laramidia.

144

145　*Institutional abbreviations*: TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta,

146　Canada; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton,

147　Alberta, Canada.

148

2. Geographic and Geological Setting

150　　　　The diachronous and, complex, stratigraphic interval represented by the Bearpaw Formation

151　across the northern U.S. (Montana) and western Canada (Alberta and Saskatchewan) encompasses a

152　time intervalperiod of approximately 3 Ma during the Campanian (~76–73 Ma). In Montana, the

153　onset of transgressive conditions is documented at ~76 Ma in the contemporaneous deposits of the

154　Woodhawk Member of the Judith River Formation, whereas the base of the Bearpaw Formation is

155　dated at 75.2 Ma (Rogers, 1998; Rogers et al., 2016). In Alberta, the Bearpaw Formation represents

156　a reference marine interval that accumulated between ~74.3–73.1 Ma (Eberth and Kamo, 2020;

157　Zubalich et al., 2021; Figs. 1A, 2). It overlies the clastic deposits of the Belly River Group and

158　underlies the Edmonton Group, both renowned for their rich and diverse fossil contentvertebrate

159 faunas (Russell and Chamney, 1967; Dodson, 1971, 1990; Currie and Koppelhus, 2005; Larson et

160 al., 2010; Eberth et al., 2013; Cullen and Evans, 2016). The uppermost subunit of the Belly River

161 Group is the Dinosaur Park Formation, whose upper exposures constitute the Lethbridge Coal Zone,

162 which was deposited predominantly in poorly -drained, swampy environments associated with the

163 onset of the Bearpaw transgression (Eberth, 2005). The overlying Bearpaw Formation consists of

164 lower and upper tongues, bounding the Strathmore Member of the Horseshoe Canyon Formation

165 (Fig. 2). In central Alberta (*i.e.*, Drumheller–Calgary area), the coal-rich, paralic Strathmore

166 Member has been defined solely by subcrop geophysical (well-log) signatures as the stratigraphic

167 interval confined by the Maximum Flooding Surfaces (MFS) of the lower and upper Bearpaw

168 tongues (Eberth and Braman, 2012; Hathway, 2016; Zubalich et al., 2021). No exposures of the

169 Strathmore Member have been documented or sampled at the time of writing, but recent studies

170 suggest that deposits correlative with the Strathmore Member are represented in the WU3 beds

171 exposed in the Grande Prairie region (Fanti and Catuneanu, 2010; Zubalich et al., 2021). Given the

172 fact that the Strathmore Member has been traced using well-logs over much of central and western

173 Alberta (Hathway, 2016; Zubalich et al., 2021), correlative deposits within the Wapiti Formation

174 could provide crucial information in the future about the coastal and terrestrial fauna that existed

175 during the Bearpaw gGap.

176   Immediately overlying the upper Bearpaw tongue, the Drumheller Member, which includes

177 aggrading and prograding paralic and coal-rich deposits, marks the transition into the alluvial

178 deposits of the HSCHC Formation. The Dinosaur Park and HSCHC formations have both been

179 subjects of detailed stratigraphic and palaeontological studies focused on defining dinosaur

180 assemblage zones (Ryan and Evans, 2005; Mallon et al., 2012; Eberth et al., 2013). However, the

181 intervening Bearpaw gap represents a major interruption in the latest Cretaceous terrestrial fossil

182 record, limiting our comprehension of biogeography, evolution, and ecology during a part of the

183 Campanian clearly characterized by dynamic environmental and global change and, accordingly,

184 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 ~~off~~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).

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~~

211 insight into the sedimentology, facies analyses, and depositional architecture of WU3. Exposures

212 along the north bank of the Wapiti River near the DC Bonebed consist of tabular mudstone and

213 siltstone interbedded with minor channel sandstones and lenticular coal seams. The DC Bonebed

214 occurs at the base of a single-storey, laterally isolated channel deposit exposed approximately

215 transverse to the palaeo-flow direction (NE–SW; Fig. 3). The deposit contains point bars that are

216 vertically stacked, slightly asymmetric, and succession-dominated, suggesting a low rate of channel

217 migration/avulsion. The preservation of palaeochannel geometries permits discrimination of several

218 stages of point bar aggradation, and recognition of correlative overbank and inner levee surfaces.

219 The point bars are relatively thin, each ~~being no thicker than~~≤ 40 cm, and lack fine-grained

220 components but display slightly erosive bases with common clay- chips and rip-up clasts. The

221 sandstone of the channel deposit is organic-rich and contains rare leaf impressions, conifer cones,

222 and unidentified seeds. ~~Overall, w~~We in~~fer~~terpret that ~~the deposits that include the DC Bonebed as~~

223 ~~having been laid down by an aggrading fluvial system~~an aggrading fluvial system in a

224 distal/backswamp floodplain laid down the deposits that include the DC Bonebed ~~in a~~

225 ~~distal/backswamp floodplain~~. Sedimentological observations and facies associations indicate that

226 the sediments accumulated in the vicinity of a low-energy river system. For this study, additional

227 geological sections were measured along 18 km of the Wapiti River and integrated ~~with each other~~

228 ~~and~~ with those presented previously for Kleskun Hill (Fanti and Miyashita, 2009), Pipestone Creek

229 (Fanti and Currie, 2007; Currie et al., 2008), and other exposures in the Grande Prairie area (Fanti,

230 2009, Fanti and Catuneanu 2009). The new composite section of WU3 in the Grande Prairie area

231 documents the unit's major lithologies, facies distributions, and taxon occurrences. Mud-dominated

232 facies, frequent bentonitic layers, well- developed coal seams and peat deposits are present,

233 consistent with a water-saturated environment (*see* also Fanti and Miyashita, 2009; Koppelhus and

234 Fanti, 2019).

235

236   *3.1 U-Pb dating*

237   Samples were processed from three bentonite beds, respectively located stratigraphically 11

238   m below (Horizon B Lower bentonite, HBL), 10 m below (Horizon B Top bentonite, HBT), and 25

239   m above (Highway 40 bentonite, HW40) the DC Bonebed. Zircon grains provided a weighted

240   average age of 75.26±0.8 Ma for the HBL bentonite, 73.5±0.8 Ma for the HBT bentonite, and

241   72.4±0.7 Ma for the HW40 bentonite (*see* Suppl. Material). These new chronostratigraphic

242   constraints for WU3 are crucial for correlating the fossil sites discussed in this paper with the well-

243   sampled localities of central and southern Alberta (Fig. 2). Eberth and Kamo (2020) provided a

244   high-precision chronostratigraphy of the Bearpaw and Horseshoe Canyon Formations based on U-

245   Pb CA-ID-TIMS ages. They dated the base of the Bearpaw Formation in southern Alberta to 74.4 ±

246   0.1 Ma, and a bentonite situated 5.5 m above the base of the formation to 74.308 ± 0.031 Ma.

247   Similarly, Eberth et al. (2016) provided a $^{206}Pb/^{238}U$ date of 74.26 ± 0.03 Ma for the basalmost

248   deposits of the Bearpaw Formation in central Alberta. Eberth and Kamo (2020) revised the age of

249   the Dorothy Bentonite, which occurs near the base of the upper Bearpaw tongue in southern

250   Alberta, to 73.7 ± 0.1 Ma. This bentonite was used to mark the top of the Strathmore Member of the

251   ~~HSC~~HC Formation by Eberth and Braman (2012) and marks the transition from the

252   *Pseudoaquilapollenites parallelus*—*Parviprojectus leucocephalus* palynostratigraphic biozone to

253   the *Wodehouseia gracile*—*Mancicorpus glaber* biozone (Braman, 2018; Eberth and Kamo, 2020

254   and below).

255

256   *3.2 Palynology*

257   The palynological assemblage from the DC Bonebed includes abundant fern spores and

258   pollen from conifers and angiosperms. Eighteen species of fern spore, including microspores from

259   heterosporous aquatic ferns, are present in the DC Bonebed sample. In some cases, they are still

260   encased in the microsporangia (massulae) and have characteristic anchor-shaped glochidia.

261   Fragmentary megaspores, including identifiable examples of *Ariadnesporites, Azolla* and

262   *Ghoshispora*, are also present. Bisaccate conifer pollen grains are abundant but do not provide

263 meaningful chronostratigraphic information, as they represent morphotypes ~~that have~~with long

264 stratigraphic ranges. Approximately 25 species of angiosperm were identified (*see* Supplementary

265 Material), many of which are represented by only a few specimens. A few of these species have

266 relatively short stratigraphic ranges (Fig. 4). The angiosperm palynomorphs are mostly of the

267 triprojectate type ~~that is~~ common in the Upper Cretaceous of North America, but their known

268 temporal ranges (Braman 2013, 2018) vary considerably. *Accuratipollis glomeratus* has the shortest

269 range, cent~~e~~red at ~~about~~ ~75 Ma in southern Alberta (Braman 2018) and falling entirely within the

270 *Aquilapollenites configuratus-Mancicorpus tripodiformis* palyno-stratigraphic biozone, which

271 extends from 75.5 to 74.5 Ma. However, this zonation is based on samples from southern Alberta,

272 whereas very little is known about the palyno-stratigraphy of the Wapiti Formation. Other

273 angiosperm pollen types from the DC Bonebed have longer ranges that suggest the DC Bonebed

274 assemblage belongs to the *Pseudoaquilapollenites parallelus*~~-~~—*Parviprojectus leucocephalus*

275 palyno-stratigraphic biozone, which ranges from 74.5 to 73.7 Ma (Braman 2018; Fig. 4). Th~~is~~ese

276 results~~is~~ suggest~~s~~ that ~~the range of~~ *Accuratipollis glomeratus* might ~~in fact be~~ have a longer range

277 than previously proposed, extending into the *Pseudoaquilapollenites parallelus*—~~-~~*Parviprojectus*

278 *leucocephalus* biozone.

279   With regard to the depositional environment, the identified megaspores and microspores

280 (*Aridanesporites*, *Azolla*, *Ghoshispora*) are characteristic of fresh, quiet water environments

281 (Srivastava and Braman, 2013). Zygospores of presumed freshwater algae (*Botryococcus*,

282 *Lecaniella*, *Pediastrum* and *Savitrina*) ~~which~~ that occupy similar habitats are also relatively

283 common in the sample. Taken together, the data suggest that shallow, marginal lacustrine settings~~,~~

284 or other quiet water environment~~s~~ were prevalent near the channel belt in which the DC Bonebed

285 was deposited (Nagy,1966; Yi 1997; Head 1992; Worobiec 2014).

286   The palynological evidence ~~therefore~~ corroborates the radiometric data presented ~~above,~~

287 ~~and~~above, and reinforc~~ing~~es the conclusion that WU3 and its ~~non-marine~~terrestrial vertebrate fauna

288 are time-equivalent to the Bearpaw Formation of southern Alberta~~,~~, particularly ~~and most likely to~~

289 the Strathmore Member (~~HSC~~HC Formation) and the upper tongue of the Bearpaw Formation ~~in~~

290 ~~central Alberta~~.

291

292 **4. Vertebrate Palaeontology**

293   Fossil vertebrate localities representing WU3 in the Grande Prairie region include the

294 Kleskun Hill and DC Bonebed microfossil localities, the Spring Creek lambeosaurine Bonebed

295 (Holland et al., 2021), and, potentially, the well-known Pipestone Creek *Pachyrhinosaurus*

296 Bonebed (Fanti and Miyashita, 2009; Nydam et al., 2010; Currie et al., 2008; Bell and Currie, 2016;

297 Cocks et al., 2020; this paper). Regarding the age of the latter, Eberth (in Currie et al. 2008)

298 reported an age of 73.27±0.25 M~y~a, which would place it in the upper part of WU3; however, this

299 age should be regarded ~~as uncertain~~with caution, as ~~they were~~it was based on few crystals and

300 ~~proper~~ methodological ~~information~~details were ~~was~~ere not ~~never~~ formally published (David A.

301 Eberth *pers. comm. to F.F.*). The Pipestone Creek Bonebed preserves what appear to be the remains

302 of a herd of the centrosaurine ceratopsid dinosaur *Pachyrhinosaurus lakustai* interspersed with

303 much smaller numbers of other fossils (Currie et al. 2008). The depositional setting is consistent

304 with the overlying, high-energy fluvial deposits of Wapiti Unit 4, which is dominated by a mixture

305 of isolated dinosaur skeletons and massive, monospecific bonebeds (e.g., Bell et al., 2014; Fanti et

306 al. 2015), and from which no highly productive microsites are so far known. Therefore, pending

307 more accurate dating of this site, we refer the Pipestone Creek bonebed ~~is here referred~~ to the

308 basalmost deposits of Wapiti Formation Unit 4 (*see* also Cocks et al., 2020).

309   A complete ~~full~~ systematic review of the ~~WU3 vertebrate assemblage~~DC Bonebed

310 assemblage, with justifications for our taxonomic identifications, can be found in the

311 Supplementary Material, and only the most salient aspects of the assemblage are considered here.

312 The ~~two~~ WU3 microsites, namely ~~namely~~ Kleskun Hill and the new DC Bonebed locality, are ~~both~~

313 highly informative. Kleskun Hill is a well-known ~~has long been known as a~~ source of ~~a of the~~

314 ~~remains of a~~ diverse terrestrial and freshwater aquatic fossils ~~(include freshwater aquatic taxa)~~and to

315 some extent freshwater palaeocommunity, notably containing including fish, squamates,

316 Cehampsosauruids, large and small theropods, hadrosaurids (including both neonate and adult

317 specimens), ceratopsids, possible pachycephalosaurids, thescelosaurids, and mammals, and a

318 possible pachycephalosaurid (Fanti and Miyashita, 2009; Nydam et al., 2010; Fox and Scott, 2010).

319 However, the DC Bonebed provides important new complementary information regarding the

320 diversity of the WU3 vertebrate assemblage.

321 A total of 364 identifiable (below the level of Gnathostomata) vertebrate specimens were

322 recovered from the DC Bonebed during the years 2014–2019 field seasons. Specimens described in

323 this paper were collected from different spots within the accretionalry sequence of an individual

324 channel (Fig. 3). One specimen is a partly articulated skeleton, but the others represent small to

325 medium-sized individual bones and teeth, primarily collected from a restricted, mud-dominated,

326 area. Specimens discussed in this paper range in size from 2.,4 to 288 mm., although 92.5% of all

327 elements have greatest dimensionsmeasure withinbetween 25 and 60 mm in their greatest

328 dimension, and 72% measureare <50 mm: therefore, the DC Bonebed is considered as microfossil-

329 dominated bonebed (sensu Behrensmeyer, 2007; Eberth et al., 2007; see SI2). Abiotic processes

330 were most likely responsible for the pervasive disarticulation and size-based sorting observed at the

331 DC Bonebed.

332 Fish account for some 25.8% of the specimens in the sample, whereas the remainder

333 represent are tetrapods, including lissamphibians (0.5% of the total), turtles (17.6%),

334 Champsosaurus (6.6%), squamates (0.5%), eusuchian crocodyliforms (0.8%), dinosaurs (33.5%),

335 and mammals (0.5%). The remaining specimens (14.32%) in the available sample could be referred

336 only tonot be classified beyond indeterminate Archosauria, Reptilia, or Tetrapoda.

337 Lepisosteid (gar) remains (Fig. 5H–J) are the most abundant fish elements at the DC

338 Bonebed, with acipenserid (sturgeon) shoulder girdle bones and osteoderms (Fig. 5M) as a distant

339 second. Less abundant still are the distinctive hexagonal teeth (Fig. 5E, -F) and centra (Fig. 5C, -D)

340 of the rhinobatoid (guitarfish) Myledaphus bipartitus. A number of additional osteichthyan skeletal

341 elements not referable to Lepisosteidae or Acipenseridae are also present, notably including a

342 premaxilla of the aspidorhynchid *Belonostomus* (Fig. 5N‚-O), three amiid centra (Fig. 5A‚-B), a

343 single scale of the Holostean 'A' morphotype known from southern Alberta (Fig. 5K‚-L), and a

344 dentary referable to the osteoglossomorph *Coriops* (Fig. 5G).

345   Among tetrapods, the only amphibian elements from the DC Bonebed are two vertebrae

346 (Fig. 6H) referable to the scapherpet<u>ont</u>id salamander *Hedronchus* (= *Scapherpeton*; *see* Dubois and

347 Frétey, 2019). Turtles are remarkably abundant and diverse at the DC Bonebed, with three major

348 clades represented in the sample (Fig. 6A–E). Nearly half of the turtle elements that can be

349 identified below the level of Testudines pertain to Trionychidae, and many of these specimens are

350 shell fragments referable to *Aspideretoides foveatus* on the basis of their ornamentation. A partial

351 trionychid skull from the bonebed is reminiscent of the large trionychid *Axestemys* from the Upper

352 Cretaceous and Palaeocene of western North America (Vitek, 2012; Joyce et al., 2019). Baenid

353 turtle elements are also relatively abundant, and most—including a nearly complete skull—appear

354 referable to *Plesiobaena antiqua*, a species known from the Campanian of Montana and southern

355 Alberta (Brinkman, 2003; Lyson and Joyce, 2009). Chelydridae are represented by several partial

356 shell elements.

357   Squamates are represented by two large elements, namely a monstersaurian right frontal and

358 an astragalocalcaneum of indeterminate affinities (Fig. 6G). Specimens of the choristodere

359 *Champsosaurus* are relatively common at the site and include isolated cranial and postcranial

360 elements (Fig. 6F) that are indeterminate at the specific level. Crocodyliforms are extremely rare in

361 the Wapiti Formation, although a single osteoderm has been previously reported from the Pipestone

362 Creek Bonebed (Currie et al., 2008). The DC Bonebed sample includes three small eusuchian teeth

363 (Fig. 6I).

364   ~~Among O~~terrestrial ~~the dinosaurian taxa represented in the DC Bonebed, the vast majority~~

365 ~~of elements are dinosaurian, and~~most are ~~from~~ ornithischian<u>s specimens, which</u> ~~elements~~

366 predominate overwhelmingly <u>in the DC Bonebed</u> over theropod ones. Some 12 thescelosaurid

367 elements, representing at least two individuals, are known from the DC Bonebed (Fig. 7D).

368 Unexpectedly, a partial skeleton of an immature lambeosaurine hadrosaurid (UALVP 57103) was

369 collected from a sandstone (pointbar) deposit almost immediately adjacent, in the upstream

370 direction, to the DC Bonebed proper. The taxonomy of this specimen and its implications will be

371 detailed elsewhere. Indeterminate hadrosaurid material accounts for nearly half of all elements from

372 the bonebed that can be identified below the level of Dinosauria (Fig. 7F, G). The bonebed has

373 yielded a single ankylosaurid tooth (Fig. 7A). Non-avian theropods are represented by four

374 tyrannosaurid teeth (Fig. 7C), several dromaeosaurid bones (Fig. 7E), an ornithomimid metacarpal

375 and pubis (Fig. 7H), a troodontid pedal phalanx (Fig. 7B), and three small caenagnathid elements,

376 including an ilium (Fig. 7I), a pubis, and a pair of fused dentaries that we refer to Caenagnathidae

377 cf. *Chirostenotes*. The only avian specimen is the tarsometatarsus of an undoubtedly aquatic

378 hesperornithiform.

379 The only mammalian specimens from the DC Bonebed are a stagodontid marsupial

380 premolar referable to *Eodelphis* cf. *E. browni*, and a partial, indeterminate therian left mandible

381 with the tooth crowns broken away.

382

383 **5. Ecological implicationsy and significance of the WU3 vertebrate assemblage**

384 At present, the most ecologically informative single samples of the WU3 vertebrate fauna

385 areis the diverse assemblage from the DC Bonebed. This is supplemented by and the smaller but

386 similarly diverse sample from Kleskun Hill (also WU3; Fanti and Miyashita, 2009; Nydam et al.,

387 2010; Fox and Scott, 2010). Given that the WU3 sample corresponds stratigraphically to the

388 Bearpaw gap—being younger than the Belly River assemblages of the Oldman and Dinosaur Park

389 formations but older than the 'Edmontonian' assemblages of the HSCHC Formation (excluding the

390 subsurface Strathmore Member)—comparisons to both the Belly River and Edmontonian southern

391 faunas are essential for understanding patterns of temporal and palaeolatitudinal variation in

392 Alberta's Late Cretaceous terrestrial vertebrate record. Microvertebrate samples are particularly

393 significant in this regard, ~~because such samples are informative regarding not only~~providing

394 insights into~~on~~ the local (alpha)~~total~~ diversity of ~~the~~ vertebrate~~s fauna~~ and unique knowledge of~~n~~

395 ~~but also~~ the relative abundances ~~of specimens~~ of different vertebrate groups. Microvertebrates from

396 the Oldman, Dinosaur Park, and ~~HSC~~HC formations have received considerable research attention

397 (Brinkman, 1990; Gao and Fox, 1996; Beavan and Russell, 1999; Peng et al., 2001; Larson et al.,

398 2010; Cullen and Evans, 2016; Oreska and Carrano, 2018), so extensive comparisons to the DC

399 Bonebed and Kleskun Hill microsamples are possible.

400 The Oldman Formation underlies the Dinosaur Park Formation in the Dinosaur Provincial

401 Park area, but upper Oldman strata exposed in the vicinity of Manyberries in southeastern Alberta

402 appear to have been deposited contemporaneously with the Dinosaur Park Formation of Dinosaur

403 Provincial Park, albeit in a more inland environment (Eberth and Hamblin, 1993; Cullen and Evans,

404 2016; Fanti, pers. obs.). Furthermore, the uppermost part of the Dinosaur Park Formation, called the

405 Lethbridge Coal Zone, shows a strong marine influence and is faunally and lithologically distinct

406 from the main portion of the formation, which is predominantly fluvial in origin (Brinkman, 1990;

407 Beavan and Russell, 1999; Cullen and Evans, 2016). We interpret the voluminous data compiled by

408 Cullen and Evans (2016) as defining three microsamples pertinent to our study: one from the upper

409 Oldman strata in the Manyberries area (UO), one from the main, fluvial component of the Dinosaur

410 Park Formation (DP), and one from the Lethbridge Coal Zone (LC). ~~The three microsamples are~~

411 ~~referred to here as the UO, DP and LC microsamples, respectively.~~ Similarly, Larson et al. (2010)

412 provided comprehensive data on a microsample~~s~~ from the Morrin and Tolman members of the

413 ~~HSC~~HC Formation, which we refer to here as the Morrin-Tolman (MT) microsample, and Fanti and

414 Miyashita (2009) on a microsample from Kleskun Hill. These various samples have undoubtedly

415 been influenced by different sets of taphonomic, environmental and ecological biases. For example,

416 much of the ~~HSC~~MT microsample described by Larson et al. (2010) comes from a bonebed

417 dominated by the tyrannosaurid *Albertosaurus*, guaranteeing high abundance of tyrannosaurid teeth.

418 Nevertheless, comparisons among them are informative when undertaken with due caution.

419   Striking faunal differences exist between the contemporaneous DC Bonebed and Kleskun

420   Hill microsamples (Fig. 8A)., As both sites are from WU3 and only ~23 km apart, and must reflect

421   an environmental and/or taphonomic discrepancy rather than it seems unlikely that these differences

422   are the results of large-scale biogeographic variation or faunal change over time (Fig. 8A). Instead,

423   the differences probably lie inreflect environmental, taphonomic, and/or sampling discrepancies.

424   The DC Bonebed sample is proportionally much richer in aquatic to semi-aquatic taxa, namely fish,

425   turtles, crocodyliforms and *Cehampsosaurus*, and less rich in presumably terrestrial lizards and

426   dinosaurs (Fig. 8B). Taken together, the complementary contemporaneous Kleskun Hill and DC

427   Bonebed assemblages give a broad, if in most respects taxonomically impreciseambiguous, picture

428   of the aquatic and terrestrial taxa that existed in northern Alberta during the late Campanian.

429   Based on the DC Bonebed, the fish component of the WU3 assemblage was dominated by

430   lepisosteids, acipenserids, and *Myledaphus*, in descending order of abundance. The *Myledaphus*

431   species present, *M. bipartitus*, occurs in the Dinosaur Park Formation (Neuman and Brinkman,

432   2005) but is distinct in dental ornamentation from the *Myledaphus* teeth reported by Larson et al.

433   (2010) in the HSCHC Morrin and Tolman members (HSCHC Fm) microsample. Although

434   determining numbers of individuals based solely on isolated scales, bones and/or teeth is

435   problematic (based solely on isolated scales and/or teeth), the prominence of acipenserid specimens

436   within the fish fauna is a highly unusual feature of the DC Bonebed. It is notable that

437   acipenseriforms (considered as a whole) did not outnumber *Myledaphus* (considered together with

438   the similar *Pseudomyledaphus*, which does not occur at the DC Bonebed) at a single one of the

439   dozens of Upper Cretaceous microsites in southern Alberta included in the analysis of Cullen and

440   Evans (2016). Another peculiarity of the the DC Bonebed is the near-total absence from the DC

441   Bonebed of scales attributable to 'Holostean A', which are overwhelmingly abundant in the HSC

442   Morrin – Tolman members of the Horseshoe Canyon Formation microsample and intermediate in

443   abundance between *Myledaphus*/*Pseudomyledaphus* and lepisosteids in the DP and UO

444   microsamples. 'Holostean A' is also the most abundant identifiable fish taxon in the small aquatic

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445 vertebrate component of the sample from Kleskun Hill (refs?).. Lepisosteids are somewhat less

446 abundant as a proportion of the fish fauna in the DP and UO microsamples than at the DC Bonebed,

447 and are absent from the HSCMT microsample, although they do occur in the HSCHC Formation

448 (Quinney, 2011). *Myledaphus*, by contrast, is almost twice as abundant in the DP microsample as at

449 the DC Bonebed, but rare in the UO microsample and especially the HSCMT microsample.

450 *Myledaphus* is, however, abundant in the marine-influenced LC microsample, accounting for about

451 45% of all identifiable fish specimens. The LC microsample is also rich in other chondrichthyan

452 material, as well as in identifiable teleost elements. Chondrichthyan taxa other than *Myledaphus* are

453 minimally represented in the DP, HSCMT and UO microsamples, but teleosts are well represented

454 in all three, and in the UO microsample in particular. Amiid and *Belonostomus* specimens are rare

455 in the UO, DP and HSCMT microsamples, as they are at the DC Bonebed. At the Phil's Knob (PK)

456 microsite, situated within the Foremost Formation that underlies the Oldman Formation in the Belly

457 River Group, Lepisosteidae accounts for nearly half of all fish material recovered, and

458 *Pseudomyledaphus* for nearly a third, while Acipenseriformes and 'Holostean A' are absent (Cullen

459 et al., 2016).

460 Turtles and *Champsosaurus* make up a far higher percentage of the DC Bonebed sample,

461 relative to fish, than inof any of the UO, DP, LC and HSCMT southern Alberta microsamples,

462 whereas lissamphibians make up a much lower percentage (Fig. 8A). The relative abundance of

463 lissamphibians is particularly high in the UO microsample, with lissamphibians accounting for

464 about 71% of aquatic vertebrates at a UO site designed 'BMC' by Cullen and Evans (2016). The

465 strong numerical dominance of *Champsosaurus* elements over crocodyliform elements at the DC

466 Bonebed is reversed opposite to the conditionat observed in the DP and UO microsamples, despite

467 in both of which crocodyliform specimens are being relatively sparse in general but still more

468 abundant than those of *Champsosaurus*. The HSCMT microsample contains a fewsome

469 *Champsosaurus* elements and but no crocodyliforms material at all, although crocodyliforms are

470 known from other parts of the HSCHC Formation (Wu et al., 1996; Quinney, 2011; Wu and

471   Brinkman, 2015). The DC Bonebed turtle assemblage resembles the UO and DP microsamples in

472   that baenid elements account for approximately one third of all identifiable turtle specimens, a

473   similarity reinforced by the presence of the baenid *Plesiobaena antiqua* at the DC Bonebed and in

474   the Dinosaur Park and Oldman formations (Brinkman, 2003). Trionychids are substantially more

475   abundant than baenids at the DC Bonebed in the UO microsample, and especially in the DP

476   microsample. Like *Plesiobaena antiqua*, the trionychid *Aspideretoides foveatus* is shared among the

477   DC Bonebed and the Dinosaur Park and Oldman formations (Brinkman, 2003). However,

478   mMaterial referred to *Aspideretoides* sp., and potentially representing *A. foveatus*, is known from

479   the lower part of the HSCHC Formation, as part of a relatively diverse turtle assemblage that

480   includes chelydrids but lacks baenids (Brinkman and Eberth, 2006). A trionychid cf. *Axestemys*

481   from the DC Bonebed is even less informative, given the wide stratigraphic distribution of

482   *Axestemys* itself (Vitek et al., 2012). However, it should be noted that the DC turtle specimens

483   include the northernmost examples of *P. baena*, *A. foveatus*, and any *Axestemys*-like form. The few

484   turtle elements in the HSCMT microsample are all referable to Chelydridae. Chelydrids are

485   relatively uncommon at the DC Bonebed and in the DP microsample, but more abundant in the UO

486   microsample. The DC Bonebed is missing some additional turtle taxa known from southern

487   Alberta, including the nanhsiungchelyid *Basilemys*, the baenid *Boremys*, and the large aquatic form

488   *Adocus* (Brinkman, 2003; Brinkman and Eberth, 2006), but these are comparatively rare taxa whose

489   absence from the DC Bonebed might be an artifact of small sample size. The upper Maastrichtian

490   Scollard Formation notably contains a high diversity of turtles, including but not limited to baenids,

491   trionychids and chelydrids (Brinkman and Eberth, 2006). At Phil's Knobthe PK site, turtles and

492   *Champsosaurus* make up about the same respective proportions of the aquatic vertebrate sample as

493   at the DC Bonebed, but at Phil's KnobPK crocodyliforms are even more abundant than

494   *Champsosaurus*, and the most abundant turtle taxon is the helochelydrid *Naomichelys*.

495   Combining information from the DC Bonebed and Kleskun Hill provides some valuable

496   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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497 far reported from WU3 is the *Eodelphis* cf. *E. browni* tooth from the DC Bonebed. *Eodelphis*

498 *browni* proper has previously been documented in the Oldman and Dinosaur Park formations (Fox

499 and Naylor, 2006; Scott and Fox, 2015, Brannick and Wilson, 2020), but not in the ~~HSC~~HC

500 Formation. Two mammal teeth, representing a multituberculate and a pediomyid marsupial,

501 were~~have been~~ reported from Kleskun Hill (Fanti and Miyashita, 2009; Fox and Scott, 2010), but

502 these are less useful in establishing faunal correlations.

503   Squamates from Kleskun Hill include the only known specimen of the scincoid

504 *Kleskunsaurus grandeprairiensis*, and multiple specimens of the chamopsiid *Socognathus*

505 *unicuspis*. (Nydam et al., 2010). While *Kleskunsaurus grandeprairiensis* ~~may be endemic~~is

506 currently ~~unique~~known only from ~~to~~ WU3, *Socognathus unicuspis* ~~is known from~~occurs in the

507 Dinosaur Park and Oldman Formations, and possibly also in~~from~~ the upper Maastrichtian Hell

508 Creek Formation of Montana (Gao and Fox, 1996; Nydam, 2013). A dentary from Kleskun Hill

509 referred to *Chamops* cf. *C. segnis* by Sternberg (1951) has the historical distinction of being the first

510 vertebrate fossil from the Wapiti Formation to be formally described, but displays some clear

511 differences from the Lancian taxon *C. segnis* (Gao and Fox, 1996; Nydam, 2013), and its

512 identification must be considered uncertain pending a re-evaluation of the specimen. The large

513 monstersaur frontal from the DC Bonebed represents the northernmost definitive record of

514 Monstersauria in the Upper Cretaceous of western North America and provides an additional point

515 of faunal similarity to the Oldman and Dinosaur Park formations, both of which have yielded

516 multiple monstersaur taxa (Gao and Fox, 1996; Nydam, 2013). Currie et al. (2008: p. 11) briefly

517 reported "a varanid cf. *Palaeosaniwa* [sic] vertebra" from the Pipestone Creek Bonebed, which may

518 be a second monstersaur from the Wapiti Formation given that the large lizard *Palaeosaniwa*

519 *canadensis* from the Dinosaur Park Formation and the Lance Formation of Wyoming (Estes, 1964;

520 Gao and Fox, 1996; Nydam, 2013) is now considered a monstersaur (Yi and Norell, 2013). The

521 astragalocalcaneum from the DC Bonebed is uninformative but could come from the same taxon as

522 the frontal, judging by its large size.

523   The relative abundance of hadrosaurid bones and teeth at the DC Bonebed is matched in the

524   Kleskun Hill microsample, in which hadrosaurid specimens also make up nearly half of all dinosaur

525   elements identifiable below the level of Dinosauria, but is considerably exceeded in the DP and UO

526   microsamples, in which hadrosaurids account for a larger majority of identifiable dinosaur

527   specimens. At two particularly dinosaur-rich UO sites, designated 'PLS' and 'RDS' by Cullen and

528   Evans (2016), more than 70% of all dinosaur specimens recovered represent hadrosaurids.

529   Hadrosaurids are less proportionally abundant in the ~~HSC~~MT microsample than at the DC Bonebed,

530   presumably at least to some extent because~~because~~ the dinosaur component of the former was

531   collected in large part from an *Albertosaurus* bonebed (Larson et al., 2010)~~, which~~ and is rich in

532   ~~tyrannosaurid teeth as a result~~. However, theropods are even more prevalent as a percentage of the

533   total fauna at Kleskun Hill than in the ~~HSC~~MT microsample, despite the provenance of the latter.

534   The rarity of ceratopsid elements from the DC Bonebed is unusual, given the abundance of

535   ceratopsids in Wapiti Formation Unit 4 (Currie et al., 2008; Fanti et al., 2015). Ceratopsids are

536   represented in the Kleskun Hill microsample, but only by a few teeth, whereas ceratopsid elements

537   constitute several percent of the identifiable dinosaur elements in the DP, UO and ~~HSC~~MT

538   microsamples. Still more unusual is the DC Bonebed's extremely high abundance of

539   thescelosaurids. The ratio of thescelosaurid elements to hadrosaurid elements at the DC Bonebed is

540   about 0.29, whereas the ratio of "hypsilophodont" (presumably including thescelosaurid) elements

541   to hadrosaurid elements does not exceed 0.06 at any of the individual Dinosaur Park or upper

542   Oldman localities considered by Cullen and Evans (2016). Thescelosaurids are also poorly

543   represented in the Kleskun Hill and ~~HSC~~MT microsamples, but Brown and Druckenmiller (2011)

544   referred to Thescelosaurinae a total of eight teeth from two sites of early Maastrichtian age in the

545   Prince Creek Formation of Alaska. The rarity of ankylosaurid elements at the DC Bonebed is shared

546   with the Kleskun Hill, UO, and ~~HSC~~MT microsamples, but ankylosaurid remains are more

547   abundant in the DP microsample, and more abundant at the PLS site than in the UO microsample as

548   a whole. The absence of identifiable pachycephalosaurid specimens from the the DC Bonebed is

549 consistent with the rarity of this group in general, although ~~a single~~one ~~pachycephalosaurid~~ tooth ~~is~~

550 ~~known~~was interpreted from Kleskun Hill has been referred to Pachycephalosauridae (Fanti and

551 Miyashita, 2009).

552   The only theropod element from the DC Bonebed that is ~~potentially~~ identifiable at ~~the~~

553 ~~specific~~a low taxonomic level is the small fused pair of dentaries referred to Caenagnathidae cf.

554 *Chirostenotes*. This bone is similar in some important respects to specimens of *Chirostenotes*

555 *pergracilis* from the Dinosaur Park Formation of southern Alberta (Longrich et al., 2013; Funston

556 and Currie, 2020), but is unusual enough in size and morphology that referral to *Chirostenotes*

557 *pergracilis* seems unwarranted (see Supplementary Material). The caenagnathid ilium and pubis

558 from the DC Bonebed are less diagnostic but could potentially belong to the same skeleton as the

559 fused dentaries given their small size. ~~Even F~~finding evidence of even a single individual

560 caenagnathid among the 122 dinosaur bones and teeth available from the DC Bonebed is

561 remarkable~~, however, given the rarity of caenagnathids at other sites~~, given that not ~~a single~~one

562 caenagnathi~~de~~ bone~~s~~ was ~~found~~reported to occur in ~~. t~~The DP, Kleskun Hill, ~~HSC~~MT, and UO

563 microsamples~~, in fact, have not been reported to contain caenagnathid material at all~~. While the

564 rarity of caenagnathids in the Alberta Cretaceous record may be due in part to the edentulous

565 condition of this group, given the large contribution of shed tooth crowns to theropod representation

566 at microsites, their unmistakable presence in the DC Bonebed sample is nevertheless striking.

567   The DC Bonebed is fairly similar to the DP and UO microsamples in containing small

568 numbers of dromaeosaurid and tyrannosaurid elements, although tyrannosaurid teeth are more

569 abundant in the Kleskun Hill ~~microsample~~and, especially, in the ~~HSC~~MT microsample~~s~~. Curiously,

570 dromaeosaurids are about twice as abundant, as a percentage of all dinosaurian specimens

571 recovered, at the PLS and RDS sites as they are in the total UO microsample, showing that

572 representation of this group can be highly variable across localities. The large number of

573 tyrannosaurid teeth in the ~~HSC~~MT microsample again reflects, at least in large part, the fact that

574 much of this sample comes from an *Albertosaurus* bonebed (Larson et al., 2010). The Kleskun and

575 ~~HSC~~MT microsamples also contain rare ornithomimid elements, tallying with the occurrence of

576 only two ornithomimid elements at the DC Bonebed. Similarly, the presence of only a single

577 troodontid phalanx in the DC Bonebed is consistent with the rarity of troodontids in the southern

578 Alberta microsamples, although teeth attributed to *Troodon* by Fanti and Miyashita (2009) account

579 for about 14% of the dinosaur elements in the microsample from Kleskun Hill. The absence from

580 the DC Bonebed of the widespread but typically rare theropod tooth morphotypes designated

581 *Paronychodon* and *Richardoestesia* (both of which have been reported from Kleskun Hill) may be a

582 result of small sample size. Following the reidentification of Dinosaur Park Formation specimens of

583 another tooth-based taxon, *Zapsalis*, as premaxillary teeth of the velociraptorine *Saurornitholestes*

584 (Currie and Evans, 2020), the single tooth reported from Kleskun Hill of the *Zapsalis*-like taxon

585 *Paronychodon* (Fanti and Miyashita, 2009) probably represents a premaxillary tooth of a

586 *Saurornitholestes*-like velociraptorine. The hesperornithiform element from the DC Bonebed is an

587 unusual record in that hesperornithiforms are not documented in the southern Alberta microsamples

588 considered in this study, and have not been found at Kleskun Hill. However, a small number of

589 hesperornithiform bones have been collected from the uppermost Dinosaur Park Formation of

590 Saskatchewan, at the marine-influenced Saskatchewan Landing site (Gilbert et al., 2018).

591 ~~As a whole, and~~At least at face value, the WU3 vertebrate fauna more closely resembles

592 ~~more closely~~ that of the Dinosaur Park Formation, and to a large extent also that of the Oldman

593 Formation, ~~more closely~~ than that of the ~~HSC~~MT Formation. The WU3 fauna also displays some

594 unusual features that may reflect high northern palaeolatitude, smaller-scale palaeoenvironmental

595 factors, or perhaps in some cases limited sampling. The strongest faunal links to the Dinosaur Park

596 and Oldman formations are provided by the presence at the DC Bonebed of the turtle *Plesiobaena*

597 *antiqua*, and the presence at Kleskun Hill of the lizard *Socognathus unicuspis*. Corroborating

598 evidence includes the occurrence at the DC Bonebed of ~~the turtle *Aspideretoides foveatus*,~~ an

599 indeterminate monstersaur~~,~~ and specimens comparable to the theropod *Chirostenotes pergracilis*

600 and the marsupial *Eodelphis browni*, although these faunal correlations are less individually

601 persuasive because they are less certain, taxonomically precise, and/or distinctive. Unusual features

602 of the WU3 assemblage, relative to Late Cretaceous faunas from southern Alberta, include the

603 presence of the endemic squamate *Kleskunsaurus grandeprairiensis*, the surprisingly high relative

604 abundance of acipenserids, turtles, *Champsosaurus*, thescelosaurids, *Troodon*, and perhaps

605 lepisosteids and caenagnathids, and the unusual rarity of 'Holostean A' and lissamphibians. The

606 WU3 fauna appears slightly closer to that of the Dinosaur Park Formation than that of the upper

607 Oldman Formation in the relatively high abundance of *Myledaphus* and in containing many more

608 trionychids than chelydrids, but closer to that of the upper Oldman Formation in the low abundance

609 of ankylosaurids. Only two~~a single~~ general characteristics of the WU3 fauna, namely the rarity of

610 crocodyliforms and the high abundance of theropods, represents even ~~an~~ arguable points of

611 distinctive similarity to the vertebrate assemblage of the ~~HSC~~HC Formation. Moreover, the richness

612 of theropods in the ~~HSC~~MT microsample of Larson et al. (2010) is clearly due in part to the origin

613 of much of that sample in an *Albertosaurus* bonebed, and is unlikely to be truly representative even

614 of the Morrin and Tolman members of the ~~HSC~~HC Formation.

615 One major implication of these findings is that the WU3 vertebrate fauna has a partially

616 Belly River character, containing a number of taxa that existed in southern Alberta prior to the

617 Bearpaw gap but are not represented in the ~~HSC~~HC Formation. These distinctive survivors,

618 including *Plesiobaena antiqua*, *Socognathus unicuspis*, and possibly *Chirostenotes pergracilis,*

619 *Eodelphis browni* and *Aspideretoides foveatus*, presumably existed throughout Bearpaw times in

620 continental ecosystems that are poorly documented in the Alberta fossil record. At least in most

621 cases, their absence from the ~~HSC~~HC Formation may reflect evolutionary turnover around the end

622 of the Campanian.

623 Nevertheless, the WU3 assemblage cannot simply be regarded as a northerly, late-surviving

624 Belly River fauna, given the presence of a number of peculiarities. Only one potentially endemic

625 species, the scincoid *Kleskunsaurus grandeprairiensis*, has so far been documented in WU3

626 (Nydam et al., 2010), but the WU3 assemblage nevertheless has some unusual features pertaining to

627 the abundance of certain groups and the rarity of others. Many of these patterns lack any obvious

628 explanation, but the abundance of *Myledaphus* and the predominance of trionychids over chelydrids

629 may reflect the coastal rather than inland character of the fauna given that they are shared with the

630 Dinosaur Park microsample but not with the upper Oldman microsample. The single

631 hesperornithiform element from the DC Bonebed is another likely indicator of coastal proximity,

632 especially given the presence of hesperornithiforms at Saskatchewan Landing (Gilbert et al., 2018).

633   By contrast, the fact that *Champsosaurus* elements predominate over crocodyliform ones at

634 the DC Bonebed—unlike in both the DP and UO microsamples—may be due to latitude.

635 *Champsosaurus* is consistently present in the Campanian of southern Alberta and Montana, but

636 absent from contemporaneous faunas in Utah, Texas, and Mexico (Larson et al., 2010). A

637 neochoristodere possibly referable to *Champsosaurus* is even known from the Turonian–Coniacian

638 deposits on of Axel Heiberg Island in the Canadian Arctic, occurring with turtles, amiids,

639 lepisosteids, and teleosts (Tarduno et al., 1998; Friedman et al., 2003; Vandermark et al., 2007).

640 Crocodylians have previously been documented in Campanian strata from Mexico to southern

641 Alberta (Markwick 1998; Gates et al., 2010; Lucas et al., 2016; Rivera-Sylva et al., 2019), but

642 Amiot et al. (2004) suggested the southern Alberta occurrence was near the northern limit of their

643 range, defined by their inability to tolerate climates in which the mean temperature of the coldest

644 month averaged below 5–10°C. The presence of a small number of crocodyliform elements at the

645 DC Bonebed alongside a much larger quantity of *Champsosaurus* material is consistent with the

646 seemingly greater ability of *Champsosaurus* to thrive in high-latitude environments. However,

647 *Champsosaurus* is also notably abundant in the vertebrate assemblage from Saskatchewan Landing,

648 in which crocodyliforms do not occur (Gilbert et al., 2018). Acipenserids resemble champsosaurids

649 in having a predominantly high-latitude record, with reported Campanian and Maastrichtian

650 occurrences extending from the Northwest Territories to northern New Mexico (Hilton and Grande,

651 2006; Vavrek et al., 2014). Furthermore, they may have spread into the southern part of this range

652 only as temperatures decreased towards the end of the Cretaceous (Vavrek et al., 2014).

653 Accordingly, the numerous acipenserid elements recovered from the DC Bonebed may be another

654 indication of the high-latitude character of the WU3 fauna.

655   The high abundance and moderately high diversity of turtles in WU3 suggests that they, like

656 *Champsosaurus*, may have been resilient to high-latitude conditions despite being ectotherms.

657 Brinkman and Eberth (2006) argued based on the Upper Cretaceous Alberta record for a link

658 between turtle diversity and palaeotemperature, warmer conditions being conducive to greater

659 species richness. Consistent with this hypothesis is the fact that the ~~HSC~~MT microsample, which is

660 from the part of the ~~HSC~~HC Formation thought to have been deposited under cool conditions

661 (Larson et al., 2010), contains only one turtle taxon. Cool temperatures may also explain why

662 crocodyliform material is absent from the ~~HSC~~MT microsample while *Champsosaurus* is present,

663 albeit in small numbers. Wapiti Formation Unit 3 may have been laid down in a warmer

664 environment despite the high palaeolatitude, given its greater turtle diversity and the presence of a

665 few crocodyliform elements. The abundance of *Myledaphus* at the DC Bonebed arguably supports

666 this interpretation, as extant rhinobatoids have circumtropical to warm temperate distributions

667 (Wilson et al., 2013).

668   In the context of Late Cretaceous Albertan vertebrate communities, the WU3 assemblage

669 suggests that evolutionary turnover, palaeolatitude, and proximity to the coastline of the Western

670 Interior Seaway were all important influences on faunal composition (Fig. 9). However, knowledge

671 of the assemblage rests overwhelmingly on specimens recovered from Kleskun Hill and the DC

672 Bonebed, and broader sampling will be needed to build a more complete picture of the vertebrate

673 fauna.

674   To summarise, the DC Bonebed is the most ecologically informative sample of the WU3

675 vertebrate fauna and~~, from the perspective of non-marine fauna, from the entirety of~~, along with the

676 Kleskun Hill locality, represent the only terrestrial fauna from the Bearpaw gap in western North

677 America. The complementary and contemporaneous faunas from the DC Bonebed and Kelskun Hill

678 (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 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.

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 pala_e_ontological 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 characterizepoint 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, depositedsituated 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 charactersistics 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 fFurther exploration will be required in order to examineunderstand the timing and dispersalbroader 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

757 continuous terrestrial deposits of the Wapiti Formation, and in particular Unit 3, offer an

758 opportunity to begin filling the 'Bearpaw gapGap'. The diverse WU3 vertebrate fauna documented

759 here from the DC Bonebed, together with previously -described microvertebrates from Kleskun

760 Hill, shows a distinctive Belly River signature similar to those of the older upper Oldman and

761 Dinosaur Park formations, and demonstrates that a vertebrate community with this basic character

762 existed in west-central Alberta well after the classic Dinosaur Park Formation ecosystem had been

763 extirpated by the Bearpaw transgression. The presence of a probable possible endemic form (the

764 scincoid *Kleskunsaurus grandeprairiensis*) in the WU3 assemblage, and some unusual abundance

765 patterns relative to southern Belly River faunas (e.g., abundance of *Myledaphus*, acipenserids,

766 *Champsosaurus* and thescelosaurids; rarity of lissamphibians and crocodyliforms), likely reflect

767 some combination of high palaeolatitude and close proximity to the palaeocoastline. These findings

768 imply faunal composition along the margins of the Western Interior Seaway was influenced by a

769 complex, superimposed mosaic of palaeolatitudinal and palaeoenvironmental gradients, in addition

770 to evolutionary turnover.

771

situated is Treaty 8 territory, the traditional lands of the Cree, Beaver, Dene Tha' and the Métis

people.

Author Contributions

Conceptualization: FF, CS, MW, NC, PB, RS; Methodology: FF, AL, DL, CS; Investigation: FF,

CS, RLS, DL, EK; Resources: FF, PRB, MV, DL, RLS, NEC, CS; AL; Writing – original draft: FF,

CS, PRB; Writing – Review and Editing: FF, PRB, RLS, NEC, CS; Visualization: FF, RLS;

Funding acquisition: CS, FF, NEC, MV.

> **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 ~~Bdonconebed~~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

1189   Amphicoelous amiid centrum in A) dorsal and B) anterior views, with paired, elongate

1190   depressions for neural arch articulation visible in dorsal view. Deeply amphicoelous

1191   *Myledaphus bipartitus* centrum (UALVP 60802) in C) dorsal and D) anterior views.

1192   *Myledaphus bipartitus* shed crown (UALVP 59115) in E) lateral and F) occlusal views,

1193   which characteristic marginal vertical grooves seen in lateral view, and enamel folds (rather

1194   than tubercles seen in *M. pustulosus*) seen in occlusal view. G) Right *Coriops* dentary

1195   fragment (UALVP 60773) in lateral view, exhibiting deep ramus, lateral foramina, and one

1196   remaining conical tooth. H) Lepisosteid scale (UALVP 23122) exhibiting typical polygonal

1197   shape, enamelled surface, and weakly developed articular peg morphology. I) Anteriorly

1198   convex lepisosteid caudal vertebra (UALVP 70744) in right lateral view. Distinctive

1199   horizontal ridge, as in extant gar, is present on lateral surface. J) Conical, longitudinally

1200   striated lepisosteid tooth (UALVP 23117), with enameloid cap at apex. 'Holostean A' scale

1201   (UALVP 60812) in K) external and L) internal views, showing typical peg- and- depression

1202   morphology. M) Acipenserid dorsal scute (UALVP 59844) in dorsal view, (anterior to the

1203   left), showing characteristic pitted ornamentation. ~~Largely~~ Nearly complete *Belonostomus*

1204   ~~upper mandible~~fused premaxillae (UALVP 60781) in N) dorsal and O) ventral views,

1205   ~~representing the left and right fused premaxillae~~, exhibiting two rows of closely packed

1206   te~~e~~ooth ~~rows~~, and delicate ganoine ornamentation on the dorsal surface. Note that each

1207   boxed panel has own scale bar. Scale bars 3 cm.

1208   ~~Chondrichthyan and osteichthyan specimens from the DC Bonebed. UALVP 60786~~

1209   ~~Amiid centrum in A) dorsal and B) anterior views. *Myledaphus bipartitus* centrum (UALVP 60802)~~

1210   ~~in C) dorsal and D) anterior views. *Myledaphus bipartitus* shed crown (UALVP 59115) in E) lateral~~

1211   ~~and F) occlusal view. G) Right *Coriops* dentary fragment (UALVP 60773) in lateral view. H)~~

1212   ~~Lepisosteid scale (UALVP 23122). I) Lepisosteid caudal vertebra (UALVP 70744) in right lateral~~

1213   ~~view. J) Lepisosteid tooth (UALVP 23117). 'Holostean A' scale (UALVP 60812) in K) external~~

1214   ~~and L) internal views. M) Acipenserid dorsal scute (UALVP 59844) in dorsal view, anterior to the~~

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~~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 ~~relatively little~~subtle ornamentation. H) Amphicoelous *Hedronchus sternbergii* trunk vertebra (UALVP 59831) in right lateral view, exhibiting backswept neural spine. I) ~~C~~onical ~~c~~rocodyliform tooth crown (UALVP 59811), with characteristic unserrated carina~~e 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

1241 59116), exhibiting wear facet, constricted root, apicobasal ridges, and weak cingulum. B)

1242 Troodontid right pedal phalanx IV-1 in medial view (UALVP 60748), exhibiting depression

1243 on the proximoplantar corner (at lower right). C) Tyrannosaurid tooth crown (UALVP

1244 57805). D) Thescelosaurid left quadrate (UALVP 23114) in lateral view, exhibiting distinct

1245 notch for the quadrate foramen. E) Dromaeosaurid pedal phalanx (UALVP 59507).

1246 Hadrosaurid caudal centrum (UALVP 61239) in F) dorsal and G) left lateral views ~~with~~

1247 ~~typical centrum and neural arch morphology~~. H) Partial ornithomimid left pubis (UALVP

1248 59798) in medial view, with ~~fragmentary~~ damaged pubic apron visible at left. I)

1249 Caenagnathid left ilium (UALVP 60800) in medial view. A, sacral rib facet can be ~~noted~~

1250 seen ~~off-center of~~near the broken dorsal margin, roughly above the pubic peduncle~~on the~~

1251 ~~dorsal-most remaining area~~. Note ~~specimens inset in~~that each boxe~~d~~ panel has own~~s~~ ~~at~~

1252 ~~different~~ scale bar. Scale bars 3 cm.~~Dinosaur specimens from the DC Bonebed. A)~~

1253 ~~Ankylosaurid tooth crown (UALVP~~

1254 ~~59116). B) Troodontid right pedal phalanx IV-1 in medial view (UALVP 60748). C)~~

1255 ~~Tyrannosaurid tooth crown (UALVP 57805). D) Thescelosaurid left quadrate (UALVP~~

1256 ~~23114) in lateral view. E) Dromaeosaurid pedal phalanx (UALVP 59507). Hadrosaurid~~

1257 ~~caudal centrum (UALVP 61239) in F) dorsal and G) left lateral views. H) Ornithomimid left~~

1258 ~~pubis (UALVP 59798) in medial view. I) Caenagnathid left ilium (UALVP 60800) in~~

1259 ~~medial view. Note specimens inset in boxes at different scale. Scale bars 3 cm.~~

1260 **Figure 8:** A) Relative abundance~~s~~ ~~at family level~~ of vertebrate group~~s~~taxonomy for various~~during~~

1261 ~~the~~ sites and stratigraphic units in the Campanian ~~of~~~~in~~ Alberta. Combined relative

1262 abundances total 100% ~~for~~ in each ~~individual stratigraphic unit~~case. B)

1263 relative abundance~~s~~ of aquatic and terrestrial taxa. OFm, Oldman Formation; DPFm,

1264 Dinosaur Park Formation; LCz, Lethbridge Coal Zone; DCB, Dinosaur-Chelonian Bonebed;

1265 KH, Kleskun Hill; HCFm, Horseshoe Canyon Formation. See SI for detailed

1266 ~~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 Bonebed (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 Bonebed and Kleskun Hill sites), and Horseshoe Canyon formations.