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1 Large-scale stable isotope characterization of a Late Cretaceous
2 dinosaur-dominated ecosystem

3

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22

23 **ABSTRACT**

24 In the Cretaceous of North America, environmental sensitivity and habitat specialization have
25 been hypothesized to explain the surprisingly restricted geographic ranges of many large-bodied
26 dinosaurs. Understanding the drivers behind this are key to predicting broader trends of dinosaur
27 species and community response to climate change under greenhouse conditions. However,
28 previous studies of this question have frequently examined only small sub-components of the
29 paleoecosystem or operated without comparison to similar modern systems from which to
30 constrain interpretations. Here we perform a high-resolution multi-taxic $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ study of a
31 Cretaceous coastal floodplain ecosystem, focusing on species interactions and paleotemperature
32 estimation, and compare with similar data from extant systems. Bioapatite $\delta^{13}\text{C}$ preserves
33 predator-prey offsets between tyrannosaurs and ornithischians, and between aquatic reptiles and
34 fish. Large ornithischians had broadly overlapping stable isotope ranges, contrary to
35 hypothesized niche partitioning driven by specialization on coastal or inland subhabitat use.
36 Comparisons to a modern analogue coastal floodplain show similar patterns of ecological guild
37 structure and aquatic-terrestrial resource interchange. Multi-taxic oxygen isotope temperature
38 estimations yield results for the Campanian of Alberta consistent with the few other
39 paleotemperature proxies available, and are validated when applied for extant species from a
40 modern coastal floodplain, suggesting this approach is a simple and effective avenue for
41 paleoenvironmental reconstruction. Together, these new data suggest dinosaur niche-partitioning
42 was more complex than previously hypothesized, and provide a framework for future research on
43 dinosaur-dominated Mesozoic floodplain communities.

44

45 **INTRODUCTION**

46 The Cretaceous is a key interval of Earth history for understanding paleocommunity structure
47 and ecological dynamics in greenhouse systems, as it contains a rich and well-studied fossil
48 record from multiple continents, with those from the Campanian of Alberta, Canada, being
49 among the richest and most intensively collected (Brown et al., 2013). To thoroughly
50 characterize paleoecological dynamics at this time, however, we must build upon the inferences
51 obtained from broad-scale biodiversity meta-analyses (e.g. Butler et al., 2011; Sakamoto et al.,
52 2016) and examine species and communities at more ecologically sensitive spatial/temporal
53 scales (Price et al., 2018). Of particular interest is the testing of hypothesized subhabitat
54 partitioning, which has long been suggested to explain restricted distributions in coeval
55 Cretaceous dinosaurs (Fricke and Pearson, 2008; Horner et al., 1992; Lehman, 2001; Sampson et
56 al., 2010). These patterns are surprising given that large terrestrial tetrapods today commonly
57 have broad ranges and are relatively tolerant of changing environmental conditions (Lehman,
58 1987). The veracity of such patterns for dinosaur habitat zonation, however, remain debated (e.g.
59 Lucas et al., 2016), and are only variably recovered in studies of Cretaceous regional vertebrate
60 community dynamics (Brinkman et al., 1998; Cullen and Evans, 2016). Stable isotope analyses
61 provide a useful tool for testing these hypotheses, while simultaneously allowing assessment of
62 paleotemperature conditions in the terrestrial deposits of the Campanian of Alberta/Montana,
63 which remains relatively uncharacterized despite its densely-sampled and well-studied fossil
64 record (Barrick et al., 1999; Upchurch and Wolfe, 1987). Detailed assessments of
65 paleoecological and paleoenvironmental dynamics across both spatial and temporal gradients are
66 a key piece of data for patterns of biodiversity in greenhouse systems.

67

68 **APPROACH**

69 We perform the broadest multi-taxic stable isotope analysis to date of a vertebrate community in
70 the Mesozoic. We sample a phylogenetically, physiologically, and ecologically broad range of
71 vertebrate taxa from the Late Cretaceous of Alberta, so as to capture the isotopic range in this
72 ecosystem at a well-constrained spatial and temporal scale. Our analyses are used: (1) to
73 reconstruct paleocommunity structure from this ancient coastal floodplain and compare it with
74 stable isotope data from modern analogues, (2) to test the hypothesis of subhabitat specialization
75 amongst co-occurring large ornithischians, and (3) to estimate temperature(s) for the sampled
76 assemblage, with comparisons to the available data from regional samples obtained via other
77 proxies, and confirmatory tests of oxygen isotope-derived temperatures from modern analogues .

78

79 **LOCALITY & GEOLOGICAL SETTING**

80 We sampled a vertebrate microfossil bonebed, the ‘Rainy Day Site’, from the upper Oldman
81 Formation of Alberta (known as Judith River Fm. in Montana) (Figure 1) (Arbour and Evans,
82 2017; Cullen and Evans, 2016). Sedimentology in this locality is consistent with an active
83 channel belt with high aggradation and sediment support, grading into mud-dominated intervals
84 reflective of the wetter, more organic-rich settings of the uppermost Oldman Formation (Figure
85 1D). These deposits are constrained spatially, minimally time-averaged, represent local
86 deposition of wetland or similar materials in fluvial deposits in the broader coastal floodplain
87 environment, and, as the fossils were preserved together, were likely exposed to the same suite of
88 diagenetic/taphonomic effects (Rogers and Brady, 2010). This differs from many other isotopic
89 studies on Mesozoic dinosaur communities, which derive samples from multiple sites and
90 lithologies; that lack of control on diagenetic and other variation within a sample increases the

91 potential of significant analytical errors. Cretaceous data were compared to modern analogue
92 coastal floodplain stable isotope analyses of the Atchafalaya River Basin fauna of Louisiana
93 from Cullen et al. (2019). The Atchafalaya River Basin represents a useful analogue to the upper
94 Oldman Fm., as both are low-lying, seasonally flooded landscapes with warm temperate to
95 subtropical climates, contain relatively similar flora, and have numerous taxa that are
96 physiologically, ecologically, and phylogenetically similar (e.g. metatherian mammals,
97 crocodylians, lepisosteid fish, etc).

98

99 **MATERIAL & METHODS**

100 Stable isotope analyses performed on 83 samples ($N_{\text{taxa}}=17$), measured via laser-ablation gas-
101 chromatography isotope-ratio-mass-spectrometry at the University of Western Ontario, reported
102 using standard isotopic practice ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$), following the methods of Cullen et al (2019,
103 and references therein). Stable isotope compositions for each specimen and associated data were
104 recorded (Table DR1 & 2), with tests assessing sampling biases, XRD examining mineral
105 alteration, and relative grouping of isotopic compositions of sampled taxa (sensu Fricke et al.,
106 2008 and references therein) finding no bias and a lack of pervasive alteration (Figure DR1). The
107 carbon isotope composition of diet ($\delta^{13}\text{C}_{\text{diet}}$) was calculated using trophic enrichment factors (or
108 TEF; $\Delta = \delta_{\text{bioapatite}} - \delta_{\text{diet}}$) obtained for extant relatives and/or physiological analogues of sampled
109 taxa (Table DR3). Given a lack of specific ecologically-relevant extant relatives, dinosaur
110 $\delta^{13}\text{C}_{\text{diet}}$ was reconstructed under three TEF scenarios, as birds, as reptiles, and as mammals, to
111 reveal potential effects of dietary-physiology differences. Stable isotope compositions and TEF-
112 applied $\delta^{13}\text{C}_{\text{diet}}$ compositions for Cretaceous and modern taxa are included as species-level
113 means in Table DR4.

114 Temperature calculations derived from oxygen isotope compositions ($\delta^{18}\text{O}$) were
115 performed using taxon-bioapatite-isotope geothermometers, and particularly the ectotherm-
116 endotherm combined mean (EECM) equation of Cullen et al. (2019) (modified from dual taxon
117 approach of Fricke and Wing, 2004, including species-specific methods of others from
118 references therein). This modified method calculates the combined mean of bioapatite
119 $\delta^{18}\text{O}_{\text{phosphate}}$ (in this case, modified by 1‰ from laser-produced total $\delta^{18}\text{O}$, or $\delta^{18}\text{O}_{\text{LPTO}}$, sensu
120 Larson and Longstaffe, 2007) from each sampled ectotherm taxon, as well as the combined
121 mean of $\delta^{18}\text{O}_{\text{water}}$ determined for each sampled endotherm taxon, and uses them in the equation:
122 $T = 111.4 - (4.3)(\text{combined mean bioapatite } \delta^{18}\text{O}_{\text{ecto phosphate}} - \text{combined mean } \delta^{18}\text{O}_{\text{endo water}})$
123

124 PALEOCOMMUNITY STRUCTURE

125 Stable carbon compositions for Cretaceous taxa show offsets in $\delta^{13}\text{C}$ of ~1-3‰ present between
126 megacarnivorous tyrannosaurids and their large-bodied ornithischian prey, as well as between
127 aquatic reptiles and fish (Figure 2), consistent with expectations from predator-prey pairs known
128 for extant systems (Bocherens, 2000). There is considerable overlap in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$
129 among sampled bulk-feeding herbivores (hadrosaurids, ceratopsians, ankylosaurs) (Figures 2 and
130 3, Figure DR1C). While the full extent of plant isotopic heterogeneity in the Late Cretaceous of
131 this region of North America is not known, there is sufficient evidence to suggest that coastal vs.
132 inland signals should be detectable (Fricke and Pearson, 2008). This overlap thus challenges the
133 hypothesis that, at least in this model Campanian ecosystem, these taxa significantly partitioned
134 isotopic niches (a proxy for ecological niche, see Newsome et al., 2007) via subhabitat
135 specialization. Our results suggest instead that habitat use and dietary differences (if present) are
136 either not detectable using bioapatite $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, or that they partitioned niches via other

137 means, such as temporal or feeding-height stratification, across a broad range of plant sources
138 (Byerly et al., 2017; Mallon et al., 2013). The lack of apparent canopy effects in these data
139 provide some evidence against the latter, but this requires further study (Kohn, 2010, and
140 references therein). As well, it should be noted that species-level niche-partitioning also may
141 exist in these systems (Farlow and Planka, 2002; Mallon, 2019), and these results primarily
142 inform hypotheses of subhabitat niche partitioning among broader groups like hadrosaurids and
143 ceratopsids. It is also conceivable that these greenhouse environments were ecologically
144 unsaturated, facilitating a greater degree of shared resource use and weaker niche partitioning
145 (Pinto-Sanchez et al., 2014).

146 The small theropod *Troodon*, hypothesized as omnivorous or herbivorous (Holtz Jr et al.,
147 1998; Sankey, 2008), is shown here to be isotopically similar to the faunivorous small theropods
148 *Saurornitholestes* and *Dromaeosaurus*, as well as indeterminate mammals, suggesting a mixed-
149 feeding omnivorous or faunivorous diet (Figures 2 and 3). The data for the enigmatic
150 *Richardoestesia*, known only from a pair of jaws and isolated teeth, are more difficult to
151 interpret; our results do not strongly support hypothesized piscivory (Sankey, 2008), as $\delta^{13}\text{C}$
152 compositions could support feeding on fish and/or terrestrial resources (Figures 2 and 3). The
153 aquatic reptile *Champsosaurus* and the ray *Myledaphus* have more negative bioapatite $\delta^{13}\text{C}$
154 compared to other aquatic taxa, similar to the that observed between otters and other aquatic taxa
155 in the Atchafalaya (Figure 3). This may suggest a larger dietary proportion from aquatic
156 invertebrates (e.g. crustaceans, molluscs) when compared to crocodylians and large predatory fish
157 (Cullen et al., 2019). Relative isospace structure is similar between Cretaceous and modern
158 systems, regardless of which TEF is used to reconstruct dinosaur $\delta^{13}\text{C}_{\text{diet}}$. This suggests that at
159 the guild-level both modern and Cretaceous coastal floodplains are ecologically similar in terms

160 of relative structure and composition, and that, despite some differences, the Atchafalaya
161 provides a robust community and paleoenvironmental analogue for the Campanian of Alberta, and
162 more generally, coastal plain ecosystems from the latest Cretaceous of North America.

163 Overall, where overlap exists our results are in line with stable isotope compositions
164 recorded from other Late Cretaceous vertebrates (Amiot et al., 2015; Fricke and Pearson, 2008),
165 though our combination of broader taxon sampling and extant comparisons facilitate a greater
166 degree of ecological resolution for reconstruction and hypothesis testing. However, we recover
167 distinct results from those of Ostrom et al (1993), the only other broad multi-taxic stable isotope
168 study to attempt to reconstruct these ecosystems. Their analyses of high-molecular-weight
169 organic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ extracted from a mix of fossil bones and teeth sampled from multiple
170 sites throughout the Dinosaur Park Formation (formerly Judith River Formation) of Alberta
171 produced somewhat equivocal results, with many compositions at odds with expectations (e.g.
172 putatively herbivorous ornithomimids with higher $\delta^{15}\text{N}$ than faunivorous tyrannosaurs,
173 faunivorous lizards with lower $\delta^{15}\text{N}$ than herbivorous dinosaurs, etc). $\delta^{13}\text{C}$ compositions for their
174 samples were ~ -27 to -23‰ , rather than the ~ -10 to -3‰ compositions recorded here and in
175 other stable isotope studies of Cretaceous dinosaurs (Amiot et al., 2015; Fricke et al., 2008). The
176 differing sources of the material and distinct analytical methods may account for this disparity,
177 and it is also possible that their results may be reflective of a sediment bulk organic carbon
178 signal, as the latter has a nearly identical $\delta^{13}\text{C}$ range in the Late Cretaceous of western North
179 America (Fricke et al., 2008).

180

181 **PALEOTEMPERATURE RECONSTRUCTION**

182 Individual taxon oxygen isotope temperature estimates produce variable results, though the mean
183 paleotemperature estimate for the Late Campanian of Alberta derived from the multi-taxic
184 EECM method is 18°C (Figure 4, Table DR5). This is consistent with independent mean annual
185 paleotemperature proxies from the broader region, including leaf physiognomy (Upchurch and
186 Wolfe, 1987), clumped isotope analysis of paleosol carbonate nodules (Burgener et al., 2019),
187 and paired taxon oxygen isotope temperature estimates (Barrick et al., 1999), and produces
188 distinct results from the single taxon temperature estimate approaches (Figure 4, Amiot et al.,
189 2004, and references therein; Kohn, 1996)). Applying EECM to extant taxa from the modern
190 system produced a temperature estimate within ~2 °C of mean annual temperature, providing an
191 important independent check that the method produces useful results and may moderate some of
192 the variation introduced by individual taxon physiologies when using the single-taxon or ‘single
193 ectotherm, single endotherm’ variations of the approach (Figure 4). Our modified EECM method
194 is therefore a robust and simple tool for estimating paleotemperature in conjunction with multi-
195 taxic paleoecological stable isotope datasets.

196

197 **CONCLUSIONS**

198 Stable isotope analyses of a spatially and temporally constrained Mesozoic vertebrate ecosystem
199 reveals evidence of predator-prey offsets in $\delta^{13}\text{C}$ compositions and ecological guild distributions
200 that meet predictions derived from extant analogue ecosystems. The overlapping isotopic ranges
201 of bioapatite from large ornithischians argues against a long-held hypothesis that these groups
202 were strongly partitioning their niches based on subhabitat sensitivities. The bioapatite oxygen-
203 isotope EECM approach for paleotemperature estimation represents a and simple and robust
204 technique for paleoclimate reconstruction. Our combined fossil + modern combined approach

205 provides a framework for future paleocommunity analyses in these abundantly preserved coastal
206 plain systems.

207

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224

225 **REFERENCES CITED**

226 Amiot, R., Lécuyer, C., Buffetaut, E., Fluteau, F., Legendre, S., and Martineau, F., 2004,
227 Latitudinal temperature gradient during the Cretaceous Upper Campanian-Middle

228 Maastrichtian: $\delta^{18}\text{O}$ record of continental vertebrates: *Earth and Planetary Science*
229 *Letters*, v. 226, p. 255-272.

230 Amiot, R., Wang, X., Zhou, Z., Wang, X., Lécuyer, C., Buffetaut, E., Fluteau, F., Ding, Z.,
231 Kusuhashi, N., and Mo, J., 2015, Environment and ecology of East Asian dinosaurs
232 during the Early Cretaceous inferred from stable oxygen and carbon isotopes in apatite:
233 *Journal of Asian Earth Sciences*, v. 98, p. 358-370.

234 Arbour, V. M., and Evans, D. C., 2017, A new ankylosaurine dinosaur from the Judith River
235 Formation of Montana, USA, based on an exceptional skeleton with soft tissue
236 preservation: *Royal Society open science*, v. 4, no. 5, p. 161086.

237 Barrick, R. E., Fischer, A. G., and Showers, W. J., 1999, Oxygen isotopes from turtle bone:
238 applications for terrestrial paleoclimates?: *Palaios*, p. 186-191.

239 Bocherens, H., 2000, Preservation of isotopic signals (^{13}C , ^{15}N) in Pleistocene mammals, *in*
240 Ambrose, S. H., and Katzenberg, M. A., eds., *Biogeochemical approaches to paleodietary*
241 *analysis*, Volume 5: New York, Kluwer Academic Publishers, p. 65-88.

242 Brinkman, D. B., Ryan, M. J., and Eberth, D. A., 1998, The paleogeographic and stratigraphic
243 distribution of ceratopsids (Ornithischia) in the Upper Judith River Group of Western
244 Canada: *Palaios*, v. 13, no. 2, p. 160-169.

245 Brown, C. M., Evans, D. C., Campione, N. E., O'Brien, L. J., and Eberth, D. A., 2013, Evidence
246 for taphonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model
247 Mesozoic terrestrial alluvial-paralic system: *Palaeogeography, Palaeoclimatology,*
248 *Palaeoecology*, v. 372, p. 108-122.

249 Burgener, L., Hyland, E., Huntington, K. W., Kelson, J. R., and Sewall, J. O., 2019, Revisiting
250 the equable climate problem during the Late Cretaceous greenhouse using paleosol

251 carbonate clumped isotope temperatures from the Campanian of the Western Interior
252 Basin, USA: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 516, p. 244-267.

253 Butler, R. J., Benson, R. B., Carrano, M. T., Mannion, P. D., and Upchurch, P., 2011, Sea level,
254 dinosaur diversity and sampling biases: investigating the ‘common cause’ hypothesis in
255 the terrestrial realm: *Proceedings of the Royal Society of London B: Biological Sciences*,
256 v. 278, no. 1709, p. 1165-1170.

257 Byerly, P. A., Lonsinger, R., Gese, E., Kozlowski, A. J., and Waits, L., 2017, Resource
258 partitioning between kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*): a
259 comparison of historical and contemporary dietary overlap: *Canadian Journal of Zoology*,
260 no. ja.

261 Cullen, T. M., and Evans, D. C., 2016, Palaeoenvironmental drivers of vertebrate community
262 composition in the Belly River Group (Campanian) of Alberta, Canada, with implications
263 for dinosaur biogeography: *BMC Ecology*, v. 16, no. 52, p. 1-35.

264 Cullen, T. M., Longstaffe, F. J., Wortmann, U. G., Goodwin, M. B., Huang, L., and Evans, D. C.,
265 2019, Stable isotopic characterization of a coastal floodplain forest community: a case
266 study for isotopic reconstruction of Mesozoic vertebrate assemblages: *Royal Society*
267 *Open Science*, v. 6, no. 2, p. 181210.

268 Farlow, J. O., and Planka, E. R., 2002, Body size overlap, habitat partitioning and living space
269 requirements of terrestrial vertebrate predators: implications for the paleoecology of large
270 theropod dinosaurs: *Historical Biology*, v. 16, no. 1, p. 21-40.

271 Fricke, H. C., and Pearson, D. A., 2008, Stable isotope evidence for changes in dietary niche
272 partitioning among hadrosaurian and ceratopsian dinosaurs of the Hell Creek Formation,
273 North Dakota.: *Paleobiology*, v. 34, no. 4, p. 534-552.

274 Fricke, H. C., Rogers, R. R., Backlund, R., Dwyer, C. N., and Echt, S., 2008, Preservation of
275 primary stable isotope signals in dinosaur remains, and environmental gradients of the
276 Late Cretaceous of Montana and Alberta: *Palaeogeography, Palaeoclimatology,*
277 *Palaeoecology*, v. 266, no. 1-2, p. 13-27.

278 Fricke, H. C., and Wing, S. L., 2004, Oxygen isotope and paleobotanical estimates of
279 temperature and $\delta^{18}\text{O}$ -latitude gradients over North America during the early Eocene:
280 *American Journal of Science*, v. 304, p. 612-635.

281 Holtz Jr, T. R., Brinkman, D. L., and Chandler, C. L., 1998, Denticle morphometrics and a
282 possibly omnivorous feeding habit for the theropod dinosaur *Troodon*: *Gaia*, v. 15, p.
283 159-166.

284 Horner, J. R., Varricchio, D. J., and Goodwin, M. B., 1992, Marine transgressions and the
285 evolution of Cretaceous dinosaurs.: *Nature*, v. 358, p. 59-62.

286 Kohn, M. J., 1996, Predicting animal $\delta^{18}\text{O}$: accounting for diet and physiological adaptation:
287 *Geochimica et Cosmochimica Acta*, v. 60, no. 23, p. 4811-4829.

288 Kohn, M. J., 2010, Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)
289 ecology and (paleo) climate: *Proceedings of the National Academy of Sciences*, v. 107,
290 no. 46, p. 19691-19695.

291 Larson, T. E., and Longstaffe, F. J., 2007, Deciphering seasonal variations in the diet and
292 drinking water of modern White-Tailed deer by in situ analysis of osteons in cortical
293 bone: *Journal of Geophysical Research: Biogeosciences*, v. 112, no. G4, p. n/a-n/a.

294 Lehman, T. M., 1987, Late Maastrichtian paleoenvironments and dinosaur biogeography in the
295 western interior of North America: *Palaeogeography, Palaeoclimatology, Palaeoecology*,
296 v. 60, p. 189-217.

297 Lehman, T. M., 2001, Late Cretaceous dinosaur provinciality., *in* Tanke, D., and Carpenter, K.,
298 eds., *Mesozoic Vertebrate Life*, Indiana University Press, p. 310-328.

299 Lucas, S. G., Sullivan, C., Lichtig, A. J., Dalman, S., and Jasinski, S. E., 2016, Late Cretaceous
300 dinosaur biogeography and endemism in the western interior basin, North America: a
301 critical re-evaluation: *New Mexico Museum of Natural History and Science Bulletin*, v.
302 71, p. 195-213.

303 Mallon, J. C., 2019, Competition structured a Late Cretaceous megaherbivorous dinosaur
304 assemblage: *Scientific reports*, v. 9, no. 1, p. 1-18.

305 Mallon, J. C., Evans, D. C., Ryan, M. J., and Anderson, J. S., 2013, Feeding height stratification
306 among the herbivorous dinosaurs from the Dinosaur Park Formation (upper Campanian)
307 of Alberta, Canada: *BMC Ecology*, v. 13, no. 1, p. 1-15.

308 Newsome, S. D., Martinez del Rio, C., Bearhop, S., and Phillips, D. L., 2007, A niche for
309 isotopic ecology: *Frontiers in Ecology and the Environment*, v. 5, no. 8, p. 429-436.

310 Ostrom, P. H., Macko, S. A., Engel, M. H., and Russell, D. A., 1993, Assessment of trophic
311 structure of Cretaceous communities based on stable nitrogen isotope analyses: *Geology*,
312 v. 21, no. 6, p. 491.

313 Pinto-Sanchez, N. R., Crawford, A. J., and Wiens, J. J., 2014, Using historical biogeography to
314 test for community saturation: *Ecol Lett*, v. 17, no. 9, p. 1077-1085.

315 Price, G. J., Louys, J., Faith, J. T., Lorenzen, E., and Westaway, M. C., 2018, Big data little help
316 in megafauna mysteries: *Nature*, v. 558, no. 7708, p. 23.

317 Rogers, R. R., and Brady, M. E., 2010, Origins of microfossil bonebeds: insights from the Upper
318 Cretaceous Judith River Formation of north-central Montana: *Paleobiology*, v. 36, no. 1,
319 p. 80-112.

320 Sakamoto, M., Benton, M. J., and Venditti, C., 2016, Dinosaurs in decline tens of millions of
321 years before their final extinction: *Proceedings of the National Academy of Sciences*, v.
322 113, no. 18, p. 5036-5040.

323 Sampson, S. D., Loewen, M. A., Farke, A. A., Roberts, E. M., Forster, C. A., Smith, J. A., and
324 Titus, A. L., 2010, New horned dinosaurs from Utah provide evidence for
325 intracontinental dinosaur endemism: *PLoS One*, v. 5, no. 9, p. e12292.

326 Sankey, J. T., 2008, Small theropod teeth from the Lance Formation of Wyoming, USA, *in*
327 Sankey, J. T., and Baszio, S., eds., *Vertebrate Microfossil Assemblages: Their Role in*
328 *Paleoecology and Paleobiogeography*, Indiana University Press, p. 135-158.

329 Upchurch, G. R., and Wolfe, J. A., 1987, Mid-Cretaceous to Early Tertiary vegetation and
330 climate: evidence from fossil leaves and woods, *in* Friis, E. M., Chaloner, W. G., and
331 Crane, P. R., eds., *The Origins of Angiosperms and Their Biological Consequences:*
332 *Cambridge*, Cambridge University Press.

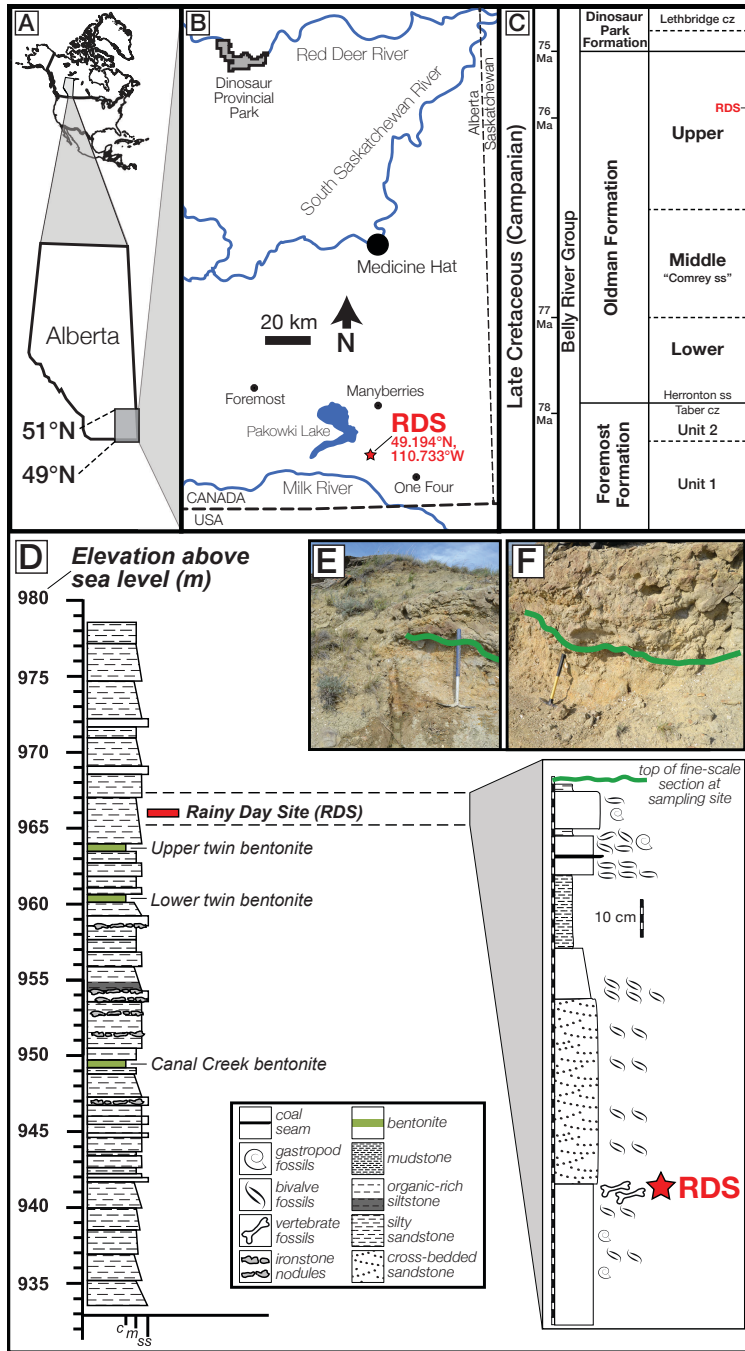
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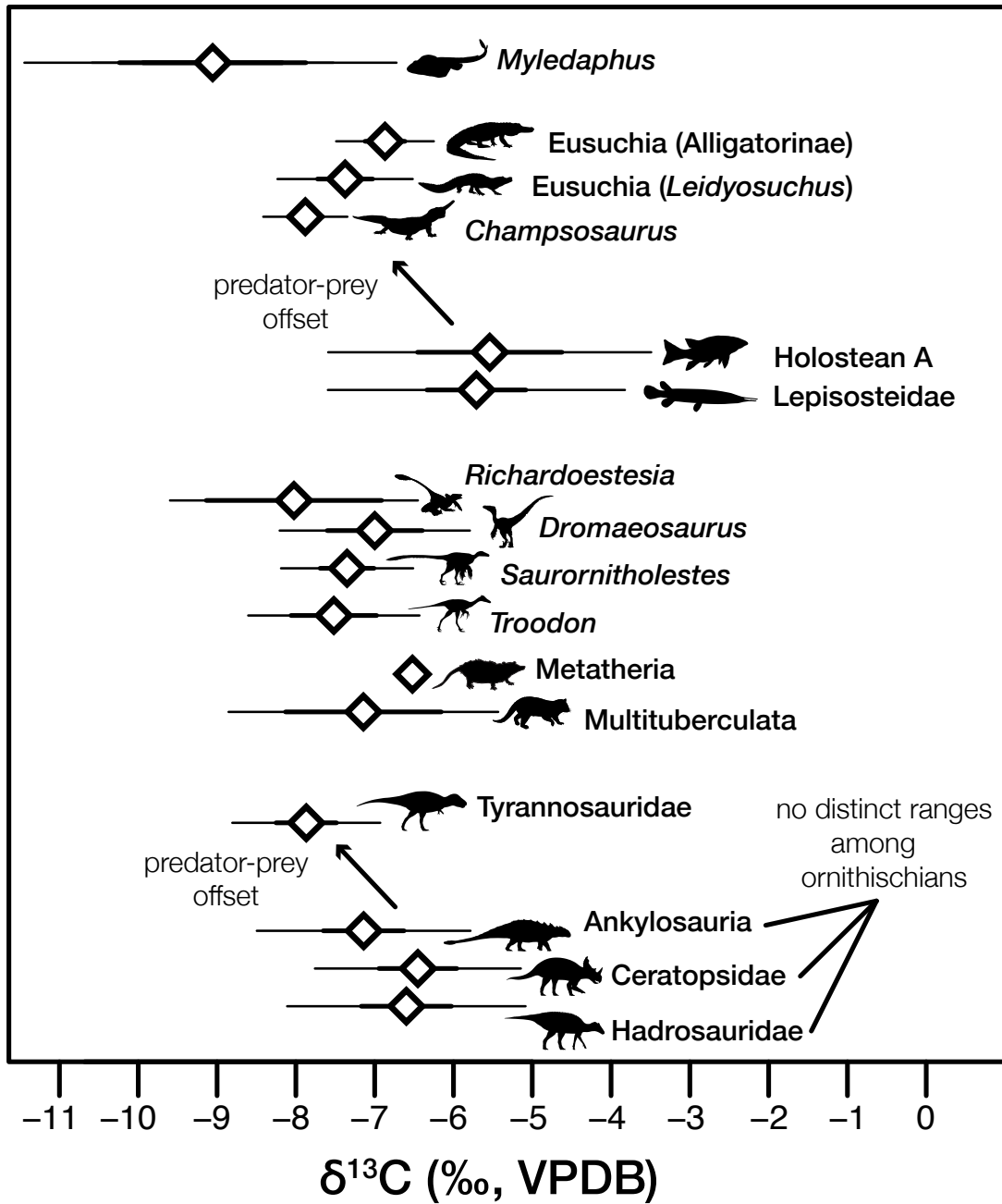
335 **FIGURES & FIGURE CAPTIONS**

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337 Figure 1. Geographic and
 338 stratigraphic position of
 339 Cretaceous locality ('Rainy Day
 340 Site', or RDS). A, position of
 341 study area in North America; B,
 342 position of RDS in southern
 343 Alberta (specific GPS coordinates
 344 on-file at Royal Tyrrell Museum
 345 and available upon request); C,
 346 Campanian stratigraphy of
 347 southern Alberta with
 348 stratigraphic position of RDS
 349 indicated; D, Stratigraphic section
 350 at RDS locality indicating
 351 location of RDS in respect to
 352 other nearby sites and marker
 353 beds; E, photograph of locality
 354 showing position of RDS and
 355 nearby sites and marker beds; F,



356 photograph of broader area stratigraphy. Green line in E & F indicates position relative to
 357 stratigraphic column in D inset. Abbreviations: c—clay; cz—coal zone; m—mud; ss—sandstone.



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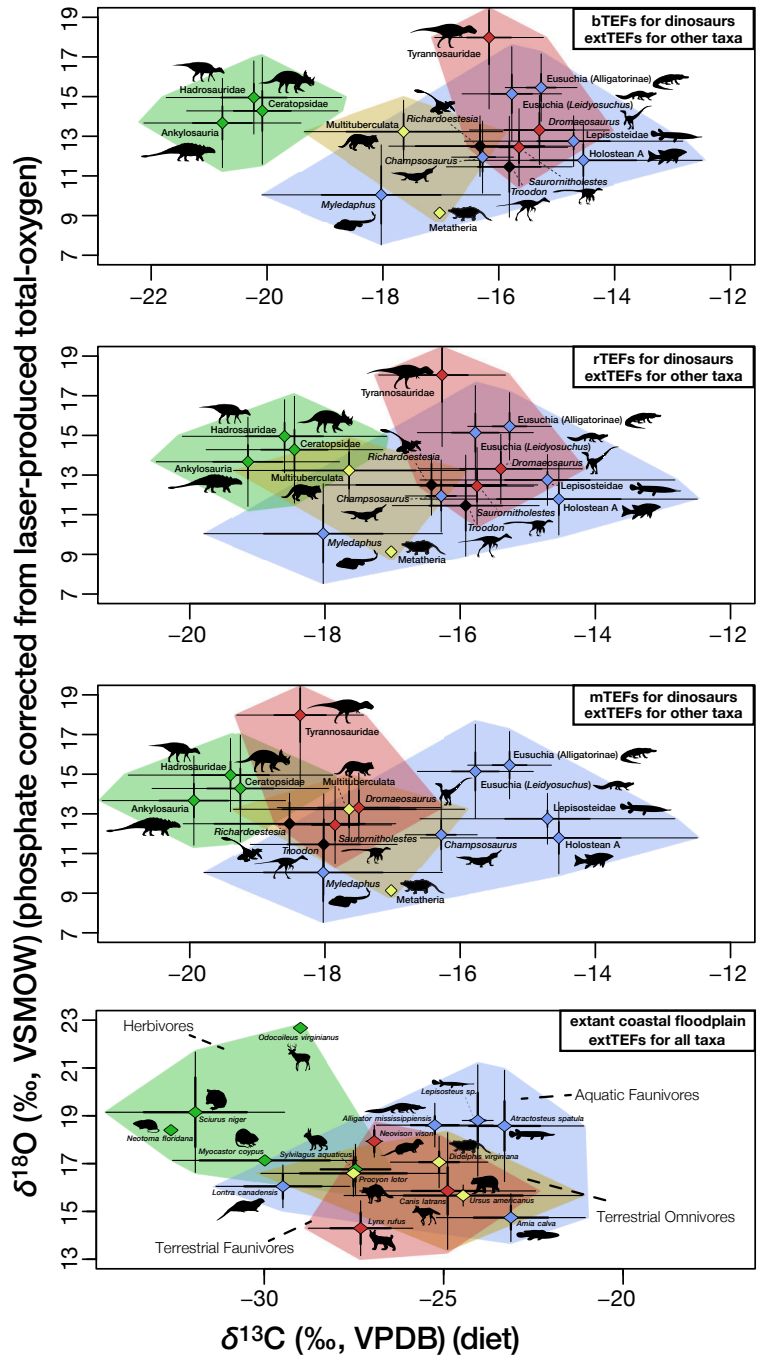
359 Figure 2. Stable carbon isotope compositions of analyzed fossil taxa. Expected predator-prey

360 isotopic offsets exist between tyrannosaurids and large ornithischians, and between aquatic

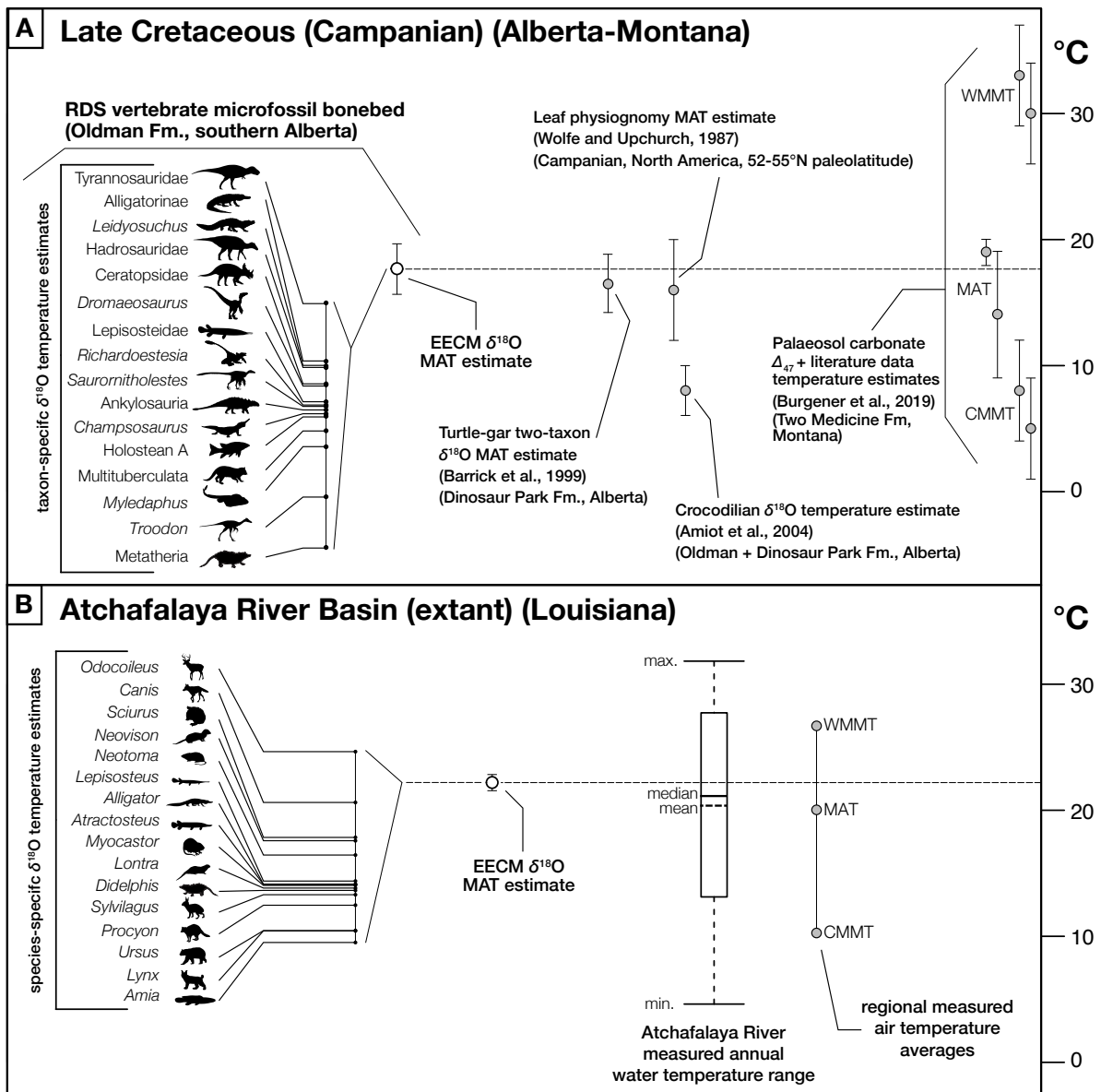
361 reptiles and fish. No distinct separation present in the isotopic ranges of sampled ornithischians.

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363 Figure 3: Stable carbon and oxygen
 364 isotope distributions of taxa in
 365 Cretaceous system, with $\delta^{13}\text{C}_{\text{diet}}$ of
 366 dinosaurs reconstructed using bird
 367 (bTEF), reptile (rTEF), and
 368 mammal (mTEF) carbon-isotope
 369 trophic enrichment factors (TEF).
 370 All other taxa in Cretaceous and
 371 modern Atchafalaya systems
 372 reconstructed using TEFs from
 373 extant relatives (extTEFs) (see
 374 Tables DR3 and DR4 for additional
 375 information). For broad ecological
 376 guilds reconstructed for Cretaceous
 377 and modern Atchafalaya
 378 comparisons, green = terrestrial
 379 herbivores, red = terrestrial
 380 faunivores, yellow = terrestrial
 381 omnivores, and blue = aquatic taxa.



382 Stable oxygen isotope compositions are 'phosphate-corrected' (i.e. modified to display only
 383 $\delta^{18}\text{O}_{\text{phosphate}}$, and remove the small fraction of $\delta^{18}\text{O}_{\text{carbonate}}$ and $\delta^{18}\text{O}_{\text{hydroxyl}}$ also measured in laser-
 384 produced total-oxygen) in order to facilitate comparisons with modern Atchafalaya data from
 385 Cullen et al. (2019). Full description of method contained in that reference.



386 Figure 4: Oxygen isotope-based temperature estimates. A, individual taxon isotope-temperature
 387 estimates from Cretaceous paleoecosystem compared to endotherm-ectotherm-combined-mean
 388 (EECM) estimate from same data, alongside temperature estimates from other proxies (MAT=
 389 mean annual temperature, WMMT= warm month mean temperature, and CMMT= cold month
 390 mean temperature). B, individual taxon isotope-temperature estimates from the modern
 391 Atchafalaya River Basin ecosystem compared to EECM estimate from same data, to measured
 392 temperatures from Atchafalaya River (taken multiple times per day during one full year), and to
 393 measured air temperatures for that region. All temperatures and $\delta^{18}\text{O}_{\text{water}}$ calculated from
 394 $\delta^{18}\text{O}_{\text{phosphate}}$ compositions. See Table DR5 for detailed information and original data sources.

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SUPPLEMENTARY INFORMATION

¹GSA Data Repository item 2020155. This contains the data, including Figure DR1 (tests of sampling bias and geochemical alteration), Table DR1 (mean $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and collection data for all specimens), Table DR2 ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements for all samples), Table DR3 (Trophic Enrichment Factors applied for $\delta^{13}\text{C}_{\text{diet}}$ comparisons between Cretaceous and modern faunal communities), Table DR4 (species mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for Cretaceous and modern taxa), Table DR5 (Calculated oxygen isotope-based temperature estimates for Cretaceous and Atchafalaya, other Campanian paleotemperature proxies, and modern Louisiana temperature data), and associated supplementary references mentioned within the included DR figures and tables. Data Repository available online at <http://www.geosociety.org/datarepository/2020/>, or on request from editing@geosociety.org