# UNIVERSITY OF BIRMINGHAM

# Deep-time biodiversity patterns and the dinosaurian fossil record of the Late Cretaceous Western Interior, North America

Maidment, Susannah; Dean, Christopher; Mansergh, Robert; Butler, Richard

*Document Version*
Peer reviewed version

[Link to publication on Research at Birmingham portal](Link to publication on Research at Birmingham portal)

1    Deep-time Biodiversity Patterns and the Dinosaurian Fossil Record of the Late

2    Cretaceous Western Interior, North America

3    Susannah C. R. Maidment[1,3], Christopher D. Dean[1], Robert I. Mansergh[1,2], Richard J. Butler[3]

4    [1]Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, United

5    Kingdom; susannah.maidment@nhm.ac.uk; christopher.dean@nhm.ac.uk;

6    [2]Department of Earth Sciences, 5 Gower Place, London WC1E 6BS; robert.mansergh.20@ucl.ac.uk;

7    [3]School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston,

8    Birmingham B15 2TT, United Kingdom; r.butler.1@bham.ac.uk.

1

9      **Abstract**

10     In order for palaeontological data to be informative to ecologists seeking to understand the causes

11     of today's diversity patterns, palaeontologists must demonstrate that actual biodiversity patterns

12     are preserved in our reconstructions of past ecosystems. During the Late Cretaceous, North America

13     was divided into two landmasses, Laramidia and Appalachia. Previous work has suggested strong

14     faunal provinciality on Laramidia at this time, but these arguments are almost entirely qualitative.

15     We quantitatively investigated faunal provinciality in ceratopsid and hadrosaurid dinosaurs using a

16     biogeographic network approach and investigated sampling biases by examining correlations

17     between dinosaur occurrences and collections. We carried out a model-fitting approach using

18     generalized least-squares regression to investigate the sources of sampling bias we identified. We

19     find that while the raw data strongly support faunal provinciality, this result is driven by sampling

20     bias. The data quality of ceratopsids and hadrosaurids is currently too poor to enable fair tests of

21     provincialism, even in this intensively sampled region, which probably represents the best-known

22     Late Cretaceous terrestrial ecosystem on Earth. To accurately reconstruct biodiversity patterns in

23     deep time, future work should focus on smaller scale, higher resolution case studies in which the

24     effects of sampling bias can be better controlled.

25

26     **Keywords:** faunal provincialism, endemicity, Laramidia, sampling bias, Ceratopsidae, Hadrosauridae.

**Introduction**

In order to predict how biodiversity patterns on today's Earth will respond to climate change, the factors that cause biodiversity distributions must be understood [1,2]. Deep-time perspectives can provide novel insights into the controls on biodiversity distribution. By examining biodiversity distributions at times in Earth's history when climate, continental arrangement, and oceanic currents were different than today, ecological hypotheses about the causative mechanisms behind biodiversity distribution and the establishment of modern patterns can be tested [3–7]. However, if palaeontologists wish their data to be informative to those working on the causative mechanisms of modern-day biodiversity patterns, we must first demonstrate that actual biodiversity patterns are preserved in our reconstructions of past ecosystems, and that we are able to overcome the many sampling biases that affect the fossil record [e.g., 8–10].

Dinosaurs are an exceptional model system for studying biodiversity and macroevolution in terrestrial vertebrates. For >150 million years, from the Late Triassic to the end of the Cretaceous, they dominated terrestrial ecosystems, occupied every continent, and radiated into a wide variety of ecological niches. Because of public interest, they are the best-sampled Mesozoic terrestrial vertebrate group, and their fossils have been collected for well over 150 years [11–14]. Arguably, the best-sampled part of the dinosaurian fossil record is the Late Cretaceous of the Western Interior region of North America [15–17]. During the Late Cretaceous, North America was divided into two landmasses, Laramidia to the west and Appalachia to the east, by the epicontinental Western Interior Seaway. In the latter stages of the Late Cretaceous (Campanian and Maastrichtian), large-bodied herbivorous niches in Laramidia were dominated by two groups of ornithischian dinosaurs, the hadrosaurs and ceratopsids. The body fossil record of the latter is entirely restricted to North America at this time, with the exception of a single taxon [18,19]. Study of these herbivorous dinosaurs has provided major insight into dinosaur behaviour, palaeoecology and biogeographic patterns [e.g., 20–32].

3

52    Numerous workers have argued for strong faunal provinciality in Laramidia throughout the

53    Campanian, and have divided the landmass into northern and southern faunal provinces [e.g., 33–

54    35]. This signal is particularly clear in chasmosaurine ceratopsids, where virtually all species are

55    recognised from either northern or southern Laramidia, but not both [34–36]. This endemicity in

56    ceratopsids is thought to have driven high levels of diversity, underpinning their radiation [34]. Since

57    no geological or geographical barrier has thus far been identified between northern and southern

58    Laramidia [37], the boundary between the northern and southern provinces has been suggested to

59    be related to latitudinal climate, temperature, or rainfall patterns [34, 35, 38] or was maintained due

60    to competition between local populations [39]. The patterns of apparent provincialism decrease in

61    the Maastrichtian, coincident with overall regression of the Western Interior Seaway [15, 17, 33, 36].

62    These hypotheses of biogeographic provincialism, however, remain controversial. With very

63    few exceptions [35, 36], studies that advocate for provincialism are based on qualitative

64    observations [e.g., 33, 34] and arise from comparisons of the fauna of specific geological formations

65    [e.g., 33–35]. Recent research has, however, suggested that some of the formations used in such

66    studies are not contemporaneous [17, 40] and that the length of time-intervals used results in the

67    amalgamation of multiple successive faunas [17, 37]. Many studies advocating faunal endemism are

68    based on taxonomic decisions that have proven controversial and the conclusions have been called

69    into question as a result [e.g., 37, 39]. Additionally, it remains a possibility that faunal provinces

70    within the Campanian are an artefact of sampling: most Campanian dinosaur occurrences are known

71    from Alberta, Montana, southern Utah and northern New Mexico, with far less sampling having

72    occurred in northern Utah and Wyoming [16].

73    Three quantitative studies have investigated the provincialism hypothesis in dinosaurs of the

74    Late Cretaceous Western Interior. Gates *et al*. [35] used a variety of statistical techniques to assess

75    similarity between Campanian northern and southern faunas, and found evidence for either two

76    distinct provinces with a broad area of overlap between them, or a latitudinal diversity gradient. The

77   statistical techniques employed were unable to distinguish between these two hypotheses, and their

78   results regarding dinosaurs were inconclusive. They suggested further investigation into the causes

79   of dinosaur distribution in the Western Interior.  Berry [36] used a phylogenetic approach to assess

80   biogeography within the Campanian and found no evidence for endemic sub-clades of

81   chasmosaurine ceratopsids, arguing that this would be expected if there was a major barrier to

82   dispersal, or niche conservatism related to climate. Vavrek & Larsson [15] investigated faunal

83   endemism in the Maastrichtian of Laramidia using measures of beta-diversity. After correcting for

84   sampling biases they found little evidence of provincialism, instead suggesting a homogeneous

85   dinosaurian fauna across the Western Interior region at the very end of the Cretaceous; however,

86   they did not test to see whether apparent biogeographic patterns within the Campanian were also

87   caused by sampling.

88         Herein, we quantitatively test hypotheses of faunal endemism in both the Campanian and

89   Maastrichtian using biogeographic and multivariate statistical approaches. We focus our study on

90   ceratopsid and hadrosaurian dinosaurs, as these megaherbivores have well understood phylogenies

91   and taxonomies and have been at the centre of previous discussions of faunal provinciality in this

92   region. The distinctiveness of northern and southern Laramidian provinces are tested using

93   phylogenetically-corrected Biogeographic Connectedness (pBC). This quantitative method uses a

94   network approach to assess phylogenetic distances between taxa in different geographic areas,

95   resulting in a metric that quantifies the degree of faunal provinciality versus cosmopolitanism. It has

96   been used successfully to understand changes in faunal compositions through the Carboniferous–

97   Permian transition [41], and the Permian–Triassic and Triassic–Jurassic extinction events [42]. We

98   also introduce additions to the methodology that address concerns regarding variation in sampling

99   through time. To investigate the impact of sampling bias on our results, we examine correlations

100  between occurrences (records of specimens) and collections (sites where specimens have been

101  collected) with latitude, and use multivariate regression to examine which sources of sampling bias

102    best explain sampling patterns. We use our results to determine whether it is possible to identify

103    true geographic patterns of biodiversity on a continental scale in this very well-sampled area.

104

105    **Methods**

106         *Taxon sampling & phylogeny* —Since no complete phylogenetic analysis of all ceratopsids is

107    available, we built an informal supertree of all ceratopsid taxa considered valid in recent

108    phylogenetic analyses by combining the phylogenetic results of [18] for chasmosaurines and [19] for

109    centrosaurines. We resolved polytomies by removing *Nedoceratops*, a taxon some workers consider

110    to be invalid [43, but see 44], from the data matrix in [18] and re-analysing the dataset. This resolved

111    polytomies in the clade containing the common ancestor of *Eotriceratops, Triceratops* and all of its

112    descendants. The resulting supertree includes 67 taxa and represents a consensus of current views

113    on ceratopsian phylogeny (Fig. S1A).

114         The structure of the hadrosaurid tree is based on several key recent analyses [45–47]. We

115    resolved polytomies and added taxa considered valid but not included in those references using

116    other recent phylogenetic analyses [48–51]. The resulting supertree includes 55 taxa and represents

117    a current reasonable estimate of hadrosaur phylogeny (Fig. S1B).

118         *Stratigraphic age and geographic data*—Age for North American hadrosaur and ceratopsid

119    species was obtained from the primary literature. The formations in which taxa occurred were found

120    from the Paleobiology Database (PBDB; www.paleobiodb.org), and the most recent absolute age

121    estimate of those formations was obtained from the primary literature (see Online Supplementary

122    Material, OSM, for sources). The age and geographic data for taxa outside of North America was

123    obtained from the Paleobiology Database. pBC requires a *priori* assignment of geographic regions to

124    test hypotheses of biogeographic connectedness, so we assigned dinosaurs to either northern

125    Laramidia or southern Laramidia. Northern Laramidia includes taxa found in Wyoming and further

6

126    north; southern Laramidia includes taxa found in Utah and further south, following previous studies.

127    Age data was used to time-calibrate the phylogenetic trees using the 'timePaleoPhy' function of the

128    Strap package [52] in R version 3.5.2 [53] with the minimum branch length option specified

129    (type='mbl'). Whilst it would be ideal to use high-resolution bins to test patterns of biogeography

130    through the Late Cretaceous [17], too few taxa would be present in each bin to permit the use of

131    pBC. Consequently, we divided taxa into Campanian and Maastrichtian time bins, which also has the

132    benefit of allowing for comparison between previous studies of faunal provincialism in this area.

133    Where a taxon's stratigraphic range/uncertainty crossed the Campanian–Maastrichtian boundary, it

134    was included in both time intervals.

135        *pBC*—We calculated pBC for Campanian ceratopsids, Maastrichtian ceratopsids, and

136    Campanian hadrosaurs. Sampling of Maastrichtian hadrosaurs was too sparse, particularly in

137    southern Laramidia, to calculate meaningful pBC values. Trees were pruned to exclude taxa from

138    timeslices other than the one being analysed, and were made ultrametric prior to analysis. pBC was

139    calculated using the function BC of the package 'dispeRse' (available at

140    github.com/laurasoul/disperse). We initially varied the constant $\mu$ [see 41] from 1–15 million years;

141    subsequent analyses used a constant $\mu$ of 10. Data were jack-knifed 1000 times to produce a

142    distribution of possible pBC values. To address concerns about the potential for a relationship

143    between pBC and taxon sample size [54], we calculated rarefaction curves for pBC for the

144    ceratopsian data (to facilitate comparisons between the Campanian and Maastrichtian). Sample

145    sizes were rarefied down to a minimum number of five taxa. 95% confidence intervals for the

146    rarefaction curves were generated using 1000 replicates at each sampling level.

147        *Randomization of data (null model)*—In order to determine whether pBC for each clade and

148    time interval was significantly different from random, we randomly permuted the geographic areas

149    in which taxa are found. We generated 1000 permutations of the data for each clade and time

7

150     interval and calculated pBC for each permutation. The pBC for the unpermuted data was compared

151     to the distribution of permuted pBC values to establish statistical significance ($p<0.05$).

152          *Sampling bias*—To investigate whether biogeographic patterns we observed in the pBC

153     results were influenced by sampling bias, we downloaded raw occurrence data for ceratopsids and

154     hadrosaurs for the Campanian and Maastrichtian from the PBDB. We then downloaded North

155     American dinosaur-bearing collections and North American tetrapod-bearing collections for each

156     timeslice, and plotted occurrences and collections with latitude. We compared the curves using

157     Spearman's rho and Kendall's tau.

158          To investigate the possible causes of sampling bias we identified, we statistically examined

159     correlations between occurrences and outcrop area, depositional environment, and proxies for

160     exposure. First, we imported publicly available USGS state-level and Canadian Province digital

161     geological maps (www.ngmbd.usgs.gov; https://ags.aer.ca/publication/map-600;

162     https://geohub.saskatchewan.ca/datasets/bedrock-geology) into ArcMap 10 (www.esri.com),

163     identified Campanian and Maastrichtian strata, and assigned an environmental attribute

164     determining whether strata were deposited in a terrestrial, marine, or mixed setting (OSM). These

165     data, along with maximum green vegetation fraction (MGVF) and slope, both proxies for exposure,

166     were imported into R (version 3.5.0). Methods for generating MGVF and slope are provided in OSM.

167     Level plots of total outcrop area, terrestrial, mixed and marine outcrop area, slope, and MGVF were

168     produced using the levelplot() function of the rasterVis() package [55] (Fig. S2).

169          To investigate the power of each or a combination of these variables to explain the dinosaur

170     occurrence data, we carried out a model-fitting approach using generalized least-squares regression

171     (GLS). Ceratopsian and hadrosaur occurrences from the Paleobiology Database were counted in each

172     1-degree latitudinal bin (latitude is modern latitude, rather than palaeolatitude). Models compared

173     latitudinal changes in ceratopsian and hadrosaur occurrences to changes in four different measures

174     of outcrop area (see OSM), MGVF and slope. GLS autoregressive models were fitted to combinations

8

175     of potential explanatory variables. We used with a first order autoregressive model (corARMA) fitted

176     to the data to account for spatial autocorrelation using the function gls() in the R package nlme v.

177     3.1–150 [56]. GLS reduces the chance of overestimating statistical significance of regression lines

178     due to serial correlation in the latitudinal series.

179         Data series were ln-transformed prior to analysis to ensure normality and homoskedasticity

180     of residuals. We calculated likelihood-ratio based pseudo-$R^2$ values using the function r.squaredLR()

181     of the R package MuMIn [57]. Results were compared using Akaike's information criterion for small

182     sample sizes (AICc) and Akaike weights were calculated to identify the best combination of

183     explanatory variables from those tested. AICc was calculated using the function AICc() of the R

184     package qpcR [58], and Akaike weights calculated using the aic.w() function of the R package

185     phytools [59].

186         *Sampling bias and pBCs*

187         To test the impact of the Campanian bimodal sampling distribution on pBC results, we ran a

188     second pBC test where we randomly removed 95% of ceratopsian taxa from the Maastrichtian that

189     occurred between 35 and 50 degrees of latitude. We chose these latitudinal boundaries to enforce a

190     similar bimodal latitudinal diversity gradient on the Maastrichtian data as seen in the Campanian

191     (see Results). The remaining distribution of occurrences was used to re-run pBC analyses (with a $\mu$ of

192     10), and this process was repeated 1000 times for increased accuracy of results. pBC scores were

193     recorded for each run, and the resulting distribution was used to calculate the mean pBC to compare

194     against the original Maastrichtian ceratopsian pBC score and produce a probability density curve to

195     estimate the probability of different values of pBC scores.

196

197     **Results**

9

198         The observed value of pBC for Campanian ceratopsids was 0.05, while that for Campanian

199    hadrosaurs was 0.11, and for Maastrichtian ceratopsids the observed value was 0.16. pBC was

200    therefore lower for ceratopsids in the Campanian than in the Maastrichtian, and endemism was

201    correspondingly higher, in agreement with previous studies [33, 36]. Jack-knifed distributions of

202    ceratopsid pBC for the Campanian and Maastrichtian overlap (Fig. 1A–C), but their median values

203    are strongly significantly different from each other (Wilcox Test, W=60235, p=0.00). Rarefaction

204    curves for ceratopsids for the Campanian and Maastrichtian indicate a much higher pBC in the

205    Maastrichtian than in the Campanian at equivalent levels of sampling, although the confidence

206    intervals do overlap, particularly at lower sampling levels (Fig. 1D). This demonstrates that the higher

207    pBC of the Maastrichtian is not a consequence of sampling lower numbers of species in that interval

208    in comparison to the Campanian. Higher pBC equates to more cosmopolitan faunas, and thus this

209    result supports lower endemism in Laramidia during the Maastrichtian when compared to the

210    Campanian.

211         Values for pBC for both Campanian and Maastrichtian ceratopsid data are statistically

212    significantly lower than for datasets in which the geographic areas are randomized (Campanian,

213    p=0.00; Maastrichtian, p=0.015; Fig. S3), and the same is true for the Campanian hadrosaur data

214    (p=0.00; Fig. S3). This indicates that endemism was statistically significantly higher than in all

215    randomized datasets across both time intervals, and supports previous qualitative hypotheses of

216    distinct northern and southern provinces in Laramidia [e.g., 33–35]

217         Curves of raw occurrence data with latitude for hadrosaurs and ceratopsids in both the

218    Campanian and the Maastrichtian correlate strongly and statistically significantly with both dinosaur-

219    bearing and tetrapod-bearing collections (Fig. 2; Fig. S4; OSM). During the Campanian, sampling and

220    occurrences are focused at two latitudes: 51-49 degrees north, which corresponds with the Dinosaur

221    Park, Oldman and, to a lesser extent, the Foremost formations, and 36-37 degrees north, which

222    corresponds primarily with the Kirtland/Fruitland, Aguja and Kaiparowits formations (Fig. 2A, B; Fig.

10

223    S4A, B). These two areas have been sampled orders of magnitude better than the surrounding

224    latitudinal bins [16], although there are tetrapod- and dinosaur-bearing formations across the

225    majority of the Western Interior at this time (Fig. 2A, B; Fig. S4A, B). In the Maastrichtian, sampling is

226    more evenly spread across the range of latitudes for which we have hadrosaur and ceratopsid body

227    fossils (Fig. 2C, D; Fig. S4; C, D; [16]). These data are strongly indicative that the provinciality

228    observed based on raw data in the Campanian could be due to intensive sampling in the Dinosaur

229    Park Formation and Kirtland/Fruitland Formations with a lack of sufficient sampling between, and

230    our observed increase in pBC (=reduced endemism) in the Maastrichtian is due to increased

231    latitudinal coverage of sampling.

232    The mean pBC score of Maastrichtian ceratopsians subjected to a Campanian-style sampling

233    distribution was 0.0351 with a standard deviation of 0.0476, significantly lower than the original pBC

234    score of 0.16.  The probability of a pBC score less than or equal to 0.8 was 0.78 (OSM and Fig. S5).

235    These results provide a further indication that sampling bias is driving pBC scores of Campanian

236    fauna

237        A lack of sampling in the area between 49 degrees north and 37 degrees north (the

238    'sampling peaks') in Campanian strata could be caused by a variety of factors. It has long been

239    known that rock outcrop area is strongly correlated with raw diversity [e.g., 60, 61,]; if there is less

240    outcrop, there are fewer opportunities for palaeontologists to sample the rocks, and fewer fossils

241    found as a consequence. As terrestrial organisms, the vast majority of dinosaur fossils are found in

242    formations that were deposited on land. If Campanian rocks between the sampling peaks are

243    primarily marine, there will be fewer opportunities for dinosaur fossils to be preserved, and thus

244    fewer opportunities for them to be sampled by palaeontologists. Fossils are primarily found where

245    bare rock is exposed at the surface. If less rock is exposed between the sampling peaks than in the

246    areas of the peaks themselves, there will be fewer opportunities for fossils to come to light.

11

247        GLS analyses recovered the following best models (highest AICc weights) for outcrop and

248    tetrapod occurrence masks (see OSM for additional results): Campanian hadrosaurs, summed

249    outcrop area + MGVF + slope; Campanian ceratopsians, non-marine total outcrop area;

250    Maastrichtian hadrosaurs, null model; Maastrichtian ceratopsians, null model. However, in nearly all

251    cases the correlations are non-significant (OSM) and only the Campanian hadrosaur model results

252    had a strong overall explanatory power (OSM). This indicates that the potential sampling bias with

253    latitude in the Campanian that we have identified cannot be fully explained by any of these variables

254    and other sources of sampling bias that are hard to quantify may additionally be responsible.

255

256    **Discussion**

257        Several authors have suggested that the apparent faunal provincialism in Laramidia during the

258    Late Cretaceous is an artefact, either because the formations in which dinosaurian taxa have been

259    found are not contemporaneous [17, 37, 40] or due to uneven sampling of the fossil record [15, 16].

260    Our results show that while the raw data clearly supports faunal endemicity, particularly in the

261    Campanian, this pattern is driven by a lack of sampling outside of two specific latitudinal belts on

262    Laramidia (51-49 degrees north, which corresponds with the Dinosaur Park, Oldman and Foremost

263    formations , and 36-37 degrees north, which corresponds primarily with the Kirtland/Fruitland,

264    Aguja and Kaiparowits formations). This sampling bias cannot be fully explained by differences in

265    outcrop area across the region, or by differences in slope or vegetation, which are factors that affect

266    rock exposure.

267        There are numerous other factors that can bias sampling, but these are very difficult to quantify.

268    Low sampling between the northern and southern sampling peaks could occur if palaeontologists

269    have yet to prospect the area to the same degree that they have in the north and south. The Late

270    Cretaceous of the Western Interior has been intensively sampled for dinosaur fossils for over 100

271   years, and it is now probably the best-known Late Cretaceous ecosystem anywhere on Earth [15,16].

272   It is therefore highly unlikely that large parts of it remain unexplored for dinosaurs, and the fact that

273   dinosaur fossils are known from the area between the sampling peaks during the Maastrichtian

274   suggest the area has been explored. Lack of exploration for fossils is therefore unlikely to be the

275   primary driver of the uneven sampling patterns we have observed.

276       The 'common cause hypothesis' [e.g., 62] suggests that correlations between raw diversity and

277   sampling proxies (e.g., numbers of formations) are driven by a third factor, usually sea level.

278   Although initially formulated for marine environments, the possibility of a sea-level driven common

279   cause on land has also been discussed [e.g., 63]. During sea-level high stands sediment flux to inner

280   shelves and marginal marine areas is high; this results in both high potential for the preservation of

281   fossils due to rapid burial and high diversity due to habitat fragmentation leading to endemism and

282   increased beta diversity. Conversely, sediment bypasses inner shelf environments during low stands,

283   reducing sediment flux and leading to poorer preservation of fossils due to a lower chance of rapid

284   burial, while diversity is lower due to cosmopolitanism. Although the effect of eustatic sea level

285   changes on the global terrestrial fossil record of vertebrates has been questioned [63], Chiarenza et

286   al. [16] demonstrated that the areas of our northern and southern sampling peaks correlated with

287   high sediment fluxes and low runoff rates during the Campanian. It is therefore possible that

288   reduced sampling between our sampling peaks is because this area was less suitable for fossil

289   preservation in the Campanian. Indeed, Chiarenza *et al*. [16] suggested that faunal provinicialism in

290   the Campanian was a sampling bias at least partially due to variation in climatic induced taphonomic

291   suitability between northern and southern regions.

292       Historical collecting practises and/or land ownership might also play a role in the sampling

293   patterns we have observed. If the proportion of outcrop on public land was reduced in the areas

294   outside of our sampling peaks, this might mean palaeontologists have less access to explore there

295   for fossils. Furthermore, if there is a particularly field-active palaeontological institution close to an

13

296    area of Campanian outcrop, or long-term agreements in place with landowners, this may have

297    allowed prospecting to occur more regularly over a longer period of time in specific areas. A bias

298    may also be introduced by uneven regional entry of data into online databases such as the PBDB.

299    Such a bias could stem from monographs on specific formations or museums whose collections

300    focus on specific areas that also have online databases. Data from these sources are comparatively

301    easy to enter into the PBDB and thus could be contributing to the sampling patterns we observed.

302       It seems highly likely that a combination of available outcrop area, rocks suitable for the

303    fossilization of vertebrate remains, and an interplay between climate, topography and historical

304    collection and data entry practises is responsible for variations in sampling across the Western

305    Interior, which have resulted in apparent northern and southern faunal provinces on Laramidia.

306    *Taxonomic differences in northern and southern Laramidia*

307       Despite the fact that we find faunal provincialism in the Late Cretaceous Western Interior to

308    mostly likely be due to sampling bias based on currently available data, it is clear that different taxa

309    are found in the northern and southern areas of Laramidia [33–35]. This is especially clear in

310    chasmosaurine ceratopsids, where there is almost no overlap at all between taxa found in the north

311    and those found in the south [34, but see 36, 39]). It has been demonstrated that many of these taxa

312    were not contemporaneous [40], which would at least partially explain taxonomic differences. But,

313    in addition, the study area covers 12 degrees of latitude and climate would have varied significantly

314    over that area, even in a greenhouse world where latitudinal temperature gradients were reduced

315    relative to today [39, 64]. General circulation models for the Campanian show significant variation in

316    mean annual temperature and rainfall patterns with latitude across Laramidia [16] and recent

317    research has suggested elevated temperature gradients in a climatic transition zone between the

318    northern and southern faunal provinces [38]. Given that there is evidence for both spatial [26] and

319    functional [29] niche partitioning in Laramidia's large herbivores, taxonomic differences between the

320    north and south could be related to climatic preference, and there may well have been a latitudinal

14

321    biodiversity gradient across the area. Unfortunately, we have demonstrated here that that raw data

322    is currently too influenced by sampling biases for such biodiversity patterns to be reconstructed.

323

324    **Conclusion**

325         We show that data quality of Campanian and Maastrichtian ceratopsids and hadrosaurs, two

326    of the most abundant clades of dinosaurs in the Late Cretaceous of North America, is currently too

327    poor to enable fair tests of endemicity and provincialism. In order to effectively test hypotheses

328    regarding the causative mechanisms of biodiversity distribution, palaeontologists must demonstrate

329    either that the fossil record preserves true biodiversity patterns at high levels of temporal

330    resolution, or that methods exist that can adequately overcome sampling biases. The Western

331    Interior region represents probably the most densely-sampled Late Cretaceous terrestrial region

332    worldwide [15, 16], but even in this intensively-sampled area, it is not currently possible to

333    reconstruct diversity patterns at the regional scale. In order for palaeontologists to make a

334    meaningful contribution to ecological hypotheses about future biodiversity change, we must focus

335    our efforts on smaller-scale case studies, where temporal resolution is high, stratigraphic correlation

336    is well-established, and where sampling biases are likely to be more homogenous and can be more

337    easily quantified. A good example of a recent such study is [65]. The results of multiple high-

338    resolution case studies can then be compared globally to establish the rules that governed past

339    biodiversity distributions.

340

341    **Acknowledgements**

15

345   Tyrrell Museum of Palaeontology) and an anonymous reviewer provided detailed and thoughtful

346   comments that improved this manuscript. This is Paleobiology Database official publication XXX.

347

348   **Author contributions**

349   SCRM & RJB designed the study. SCRM, RJB & CDD wrote the manuscript. RIM & SCRM collected

350   data and generated supertrees. SCRM, RJB and CDD ran analyses. All authors provided critical

351   comments on the manuscript.

352

353   **References**

354

355   1.  Gaston KJ. 2000. Global patterns in biodiversity. Nature 405: 220–227.

356   2.  Willig MR, Kaufman DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: pattern,

357       process, scale, synthesis. Ann. Rev. Ecol. Evol. Syst. 34: 273–309.

358   3.  Jablonski D, Roy K, Valentine JW. 2006. Out of the tropics: evolutionary dynamics of the

359       latitudinal diversity gradient. Science 314: 102–106.

360   4.  Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space

361       and time. Nature 491: 444–448.

362   5.  Dornelas M, Magurran AE, Buckland ST, Chao A, Chazdon RL, Colwell RK, Curtis T, Gaston KJ,

363       Gotelli NJ, Kosnick MA *et al.* 2013. Quantifying temporal change in biodiversity: challenges and

364       opportunities. Proc. R. Soc. B. 280: 20121931.

365   6.  Mannion PD, Upchurch P, Benson RJB, Goswami A. 2014. The latitudinal biodiversity gradient

366       through deep time. TREE 29: 42–50.

367   7.  Price SA, Schmitz L. 2016. A promising future for integrative biodiversity research: an increased

368       role of scale-dependency and functional biology. Phil. Trans. R. Soc. B. 371: 30150228.

16

369   8.   Fraser D. 2017. Can latitudinal richness gradients be measured in the terrestrial fossil record?

370        Paleobiology 43: 479–494.

371   9.   Jones LA, Dean CD, Mannion PD, Farnsworth A, Allison PA. 2021. Spatial sampling heterogeneity

372        limits the detectability of deep time latitudinal biodiversity gradients. Proc. R. Soc. B. 288:

373        20202762.

374   10.  Darroch SAF, Fraser D, Casey MM. 2021. The preservation potential of terrestrial biogeographic

375        patterns. Proc. R. Soc. B. 288: 20202927.

376   11.  Brusatte SL, Benton MJ, Ruta M, Lloyd GT. 2008. Superiority, competition, and opportunism in

377        the evolutionary radiation of dinosaurs. Science 321: 1485–1488.

378   12.  Lloyd GT, Davis KE, Pisani D, Tarver JE, Ruta M, Sakamoto M, Hone DWE, Jennings R, Benton MJ.

379        2008. Dinosaurs and the Cretaceous terrestrial revolution. Proc. R. Soc. B. 275: 2483–2490.

380   13.  Benson RBJ, Hunt G, Carrano MT, Campione N. 2017. Cope's rule and the adaptive landscape of

381        dinosaur body size evolution. Palaeontology 61: 13–48.

382   14.  Benson RBJ. 2018. Dinosaur macroevolution and macroecology. Ann. Rev. Ecol. Evol. Syst. 49:

383        379–408.

384   15.  Vavrek MJ, Larsson HCE. 2010. Low beta diversity of Maastrichtian dinosaurs of North America.

385        PNAS 107: 8265–8268.

386   16.  Chiarenza AA, Mannion PD, Lunt DJ, Farnsworth A, Jones LA, Kelland S-J, Allison PA. 2019.

387        Ecological niche modelling does not support climatically-driven dinosaur diversity decline before

388        the Cretaceous/Paleogene mass extinction. Nat. Comm. 10. DOI: 10.1038/s41467-019-08997-2.

389   17.  Dean CD, Chiarenza AA, Maidment SCR. 2020. Formation binning: a new method for increased

390        temporal resolution in regional studies, applied to the Late Cretaceous dinosaur fossil record of

391        North America. Palaeontology 63: 881–901.

392   18.  Mallon JC, Ott C, Larson PL, Iuliano EM, Evans DC. 2016. *Spiclypeus shipporum* gen. et sp. nov., a

393        boldly audacious new chasmosaurine ceratopsid (Dinosauria: Ornithischia) from the Judith River

394        Formation (Upper Cretaceous: Campanian) of Montana, USA. PLOS One 11(5): e0154218.

17

395   19. Chiba K, Ryan MJ, Fanti F, Loewen MA, Evans DC. 2018. New material and systematic re-

396        evaluation of *Medusaceratops lokii* (Dinosauria, Ceratopsidae) from the Judith River Formation

397        (Campanian, Montana). J. Paleontol. 92: 272–288.

398   20. Carrano MT, Janis CM, Sepkoski JJ. 1999. Hadrosaurs as ungulate parallels: lost lifestyles and

399        deficient data. Acta Palaeontol. Pol. 44: 237–261.

400   21. Horner JR, Goodwin MB. 2006. Major cranial changes during *Triceratops* ontogeny. Proc. R. Soc.

401        B. 273: 2757–2761.

402   22. Witmer LM, Ridgely RC. 2008. Structure of the brain cavity and inner ear of the centrosaurine

403        ceratopsid dinosaur *Pachyrhinosaurus* based on CT scanning and 3D visualization. Pp 117–144 in

404        Currie PJ, Langston W, Tanke DH (eds) *A New Horned Dinosaur from an Upper Cretaceous Bone*

405        *Bed in Alberta*. NRC Research Press, Ottawa.

406   23. Bell PR, Snively E, Schychoski L. 2009. A comparison of jaw mechanics in hadrosaurid and

407        ceratopsid dinosaurs using finite element analysis. Anat. Rec. 292: 1338–1351.

408   24. Evans DC, Ridgely R, Witmer LM. 2009. Endocranial anatomy of Lambeosaurine hadrosaurids

409        (Dinosauria: Ornithischia): a sensorineural perspective on cranial crest function. Anat. Rec. 292:

410        1315–1337.

411   25. Schweitzer MH, Zhen W, Organ CL, Avci R, Suo Z, Freimark LM, Lebleu VS, Duncan MB, Vander

412        Heiden MG, Neveu JM *et al.* 2009. Biomolecular characterization and protein seqences of the

413        Campanian hadrosaur *B. canadensis.* Science 324: 626–631.

414   26. Lyson TR, Longrich NR. 2011. Spatial niche partitioning in dinosaurs from the latest Cretaceous

415        (Maastrichtian) of North America. Proc. R. Soc. B. 278: 1158–1164.

416   27. Prieto-Márquez A. 2010. Global historical biogeography of hadrosaurid dinosaurs. Zoo. J. Linn.

417        Soc. 159: 503–525.

418   28. Mallon JC, Evans DC, Ryan MJ, Anderson JS. 2012. Megaherbivorous dinosaur turnover in the

419        Dinosaur Park Formation (upper Campanian) of Alberta, Canada. Palaeogeog. Palaeoclimat.

420        Palaeoecol. 350–352: 124–138.

421   29. Mallon JC, Anderson JS. 2013. Skull ecomorphology of megaherbivorous dinosaurs from the

422       Dinosaur Park Formation (upper Campanian) of Alberta, Canada. PLOS One 8(7): e67182.

423   30. Knapp A, Knell RJ, Farke AA, Loewen MA, Hone DWE. 2018. Patterns of divergence in the

424       morphology of ceratopsian dinosaurs: sympatry is not a driver of ornament evolution. Proc. R.

425       Soc. B. 285: 20180312.

426   31. Terrill DF, Henderson CM, Anderson JS. 2020. New application of strontium isotopes reveals

427       evidence of limited migratory behaviour in Late Cretaceous hadrosaurs. Biol. Lett. 16: 20190930.

428   32. Lehman TM. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the

429       Western Interior of North America. Palaeogeog. Palaeoclimat. Palaeoecol. 60: 187–217.

430   33. Lehman TM 2001. Late Cretaceous dinosaur provinciality. Pp. 310–328 in Tanke DH, Carpenter K

431       (eds) *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington.

432   34. Sampson SD, Loewen MA, Farke AA, Roberts EM, Forster CA, Smith JA, Titus AL. 2010. New

433       horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism. PLOS

434       One 5(9): e12292.

435   35. Gates TA, Sampson SD, Zanno LE, Roberts EM, Eaton JG, Nydam RL, Hutchinson JH, Smith JA,

436       Loewen MA, Getty MA. 2010. Biogeography of terrestrial and freshwater vertebrates from the

437       Late Cretaceous (Campanian) Western Interior of North America. Palaeogeog. Palaeoclimat.

438       Palaeoecol. 291: 371–387.

439   36. Berry K. 2018. Paleontological evidence against a major geographic barrier at about the

440       paleolatitude of Colorado, USA, during the Late Campanian (Late Cretaceous): the conspicuous

441       absence of endemic subclades of chamosaurine ceratopsid (horned) dinosaurs and its

442       significance. The Mountain Geologist 55: 5–18.

443   37. Lucas SG, Sullivan RM, Lichtig AJ, Dalman SG, Jasinski SE. 2016. Late Cretaceous dinosaur

444       biogeography and endemism in the Western Interior Basin, North America: a critical re-

445       evaluation. Pp 195–215 in Khosla A, Lucas SG (eds) *Cretaceous Period: Biotic Diversity and*

446       *Biogeography*. New Mexico Museum of Natural History Science Bulletin 71.

19

447    38. Burgener L, Hyland E, Griffith E, Mitášová H, Zanno LE, Gates TA. 2021. An extreme climate

448        gradient-induced ecological regionalization in the Upper Cretaceous Western Interior Basin of

449        North America. GSA Bull. DOI: 10.1130/B35904.1.

450    39. Longrich NR. 2014. The horned dinosaurs *Pentaceratops* and *Kosmoceratops* from the upper

451        Campanian of Alberta and implications for dinosaur biogeography. Cret. Res. 51:292–308.

452    40. Fowler DW. 2017. Revised geochronology, correlation and dinosaur stratigraphic ranges of the

453        Santonian-Maastrichtian (Late Cretaceous) formations of the Western Interior of North America.

454        PLOS One 12(11): e0188426.

455    41. Dunne EM, Close RA, Button DJ, Brocklehurst N, Cashmore DD, Lloyd GT, Butler RJ. 2018.

456        Diversity change during the rise of tetrapods and the impact of the 'Carboniferous rainforest

457        collapse'. Proc. R. Soc. B. 285: 20172730.

458    42. Button DJ, Lloyd GT, Ezcurra MD, Butler RJ. 2017. Mass extinctions drove increased faunal

459        cosmopolitanism on the supercontinent Pangaea. Nat. Comm. 8: 733.

460    43. Scannella JB, Horner JR. 2011. *"Nedoceratops"*: an example of a transitional morphology. PLoS

461        One 6: e28705.

462    44. Farke AA. 2011. Anatomy and taxonomic status of the chasmosaurine ceratopsid *Nedoceratops*

463        *hatcheri* from the Upper Cretaceous Lance Formation of Wyoming, USA. PLoS One 6: e16196.

464    45. Zhang J, Wang X, Wang Q, Jiang S, Cheng X, Li N, Qiu R. 2019. A new saurolophine hadrosaurid

465        (Dinosauria: Ornithopoda) from the Upper Cretaceous of Shandong, China. Ann. Brazil. Acad. Sci.

466        91: e20160920.

467    46. Cruzado-Caballero P, Powell J. 2017. *Bonapartesaurus rionegrensis*, a new hadrosaurine dinosaur

468        from South America: implications for phylogenetic and biogeographic relations with North

469        America. J. Vert. Palaeontol. 37: e1289381.

470    47. Mori H, Druckenmiller PS, Erickson GM. 2016. A new Arctic hadrosaurid from the Prince Creek

471        Formation (lower Maastrichtian) of northern Alaska. Acta Palaeontol. Pol. 61: 15–32.

472    48. Lehman TM, Wick SL, Wagner JR. 2016. Hadrosaurian dinosaurs from the Maastrichtian Javelina

473        Formation, Big Bend National Park, Texas. J. Paleontol. 90: 333–356.

474    49. Gates TA, Jinnah Z, Levitt C, Getty MA. 2014. New hadrosaurid (Dinosauria, Ornithopoda)

475        specimens from the lower-middle Campanian Wahweap Formation of southern Utah. Pp 156–

476        173 in Eberth DA, Evans DC (eds). *Hadrosaurs*. Indiana University Press, Bloomington.

477    50. Prieto-Márquez A, Dalla Vecchia FM, Gaete R, Galobart À. 2013. Diversity, relationships and

478        biogeography of the Lambeosaurine dinosaurs from the European Archipelago, with description

479        of the new aralosaurin *Canardia garonnensis*. PLOS One 8(7): e69835.

480    51. Godefroit P, Bolotsky YL, Bolotsky IY. 2012. Osteology and relationships of *Olorotitan arharensis*,

481        a hollow-crested hadrosaurid dinosaur from the latest Cretaceous of far eastern Russia. Acta

482        Palaeontol. Pol. 57: 526–560.

483    52. Bell MA, Lloyd GT. 2015. Strap: Stratigraphic Tree Analysis for Palaeontology. Available from:

484        cran.r-project.org/web/packages/strap.

485    53. R Core Team, 2019. R: a language and environment for statistical computing. R Foundation for

486        Statistical Computing, Vienna, Austria. www.R-project.org.

487    54. Kubo T. 2019. Biogeographic network analysis of Cretaceous terrestrial tetrapods: a phylogeny-

488        based approach. Syst. Biol. 68: 1034–1051.

489    55. Lamigueiro OP, Hijmans R. 2021. rasterVis: Visualization methods for Raster Data. Available

490        from: oscarperpinan.github.io/rastervis.

491    56. Pinheiro J, Bates D, DebRoy S, Sarkar D, ESIPACK authors, Hesiterkamp S, Van Willigen B, Ranke J,

492        R Core Team. 2018. nlme: Linear and nonlinear mixed effects models. Available from: cran.r-

493        project.org/web/packages/nlme.

494    57. Barton K. 2018. MuMIn: Multi-model inference. Available from: cran.r-

495        project.org/web/packages/MuMIn.

496    58. Spiess AN. 2018. qpcR: Modelling and analysis of real-time PCR data. Available from: cran.r-

497        project.org/web/packages/qpcR.

21

498    59. Revell LJ. 2017. phytools: Phylogenetic tools for comparative biology (and other things).

499        Available from: cran.r-project.org/web/packages/phytools.

500    60. Raup DM. 1976. Species diversity in the Phanerozoic: an interpretation. Paleobiology 2: 289–

501        297.

502    61. Smith AB, McGowan AJ. 2005. Cyclicity in the fossil record mirrors rock outcrop area. Biol. Lett.

503        1: 443–445.

504    62. Smith AB, Gale AS, Monks NEA. 2001. Sea-level change and rock-record bias in the Cretaceous: a

505        problem for extinction and biodiversity studies. Paleobiology 27: 241–253.

506    63. Butler RJ, Benson RJB, Carrano MT, Mannion PD, Upchurch P. 2011. Sea level, dinosaur diversity

507        and sampling biases: investigating the 'common cause' hypothesis in the terrestrial realm.

508        Proceedings of the Royal Society B 278: 1165–1170.

509    64. Huber BT, Norris RD, MacLeod KG. 2002. Deep-sea paleotemperature record of extreme warmth

510        during the Cretaceous. Geology 30: 123–126.

511    65. Cantalpiedra JL, Soledad Domingo M, Domingo L. 2018. Multi-scale interplays of biotic and

512        abiotic drivers shape mammalian sub-continental diversity over millions of years. Sci. Rep. 8:
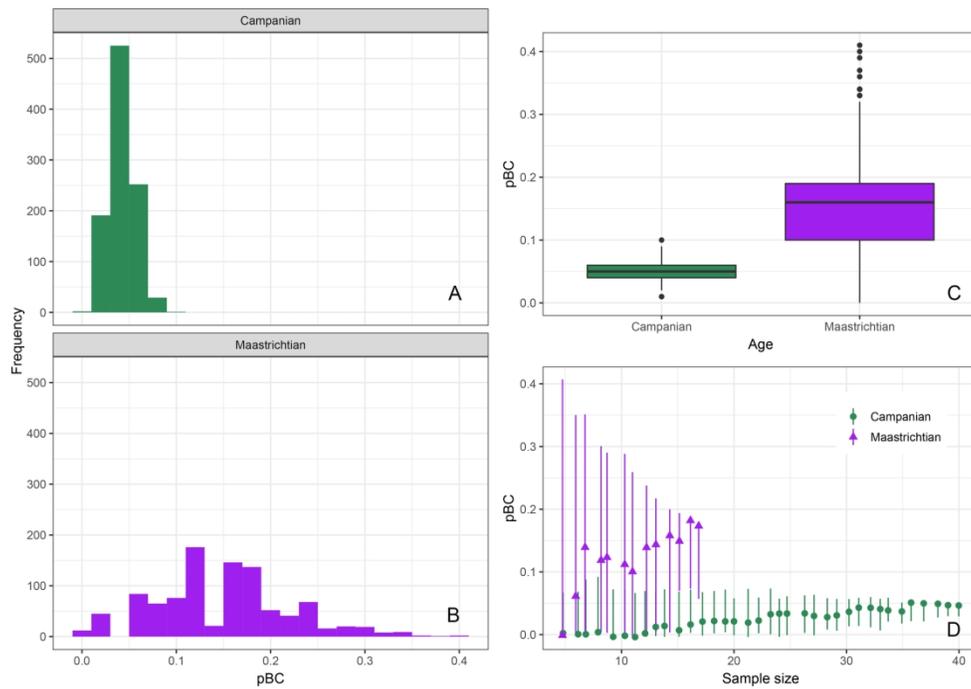
513        13413.

514

Figure 1. A–C. Jacknifed distributions of pBC values for Campanian (green) and Maastrichtian (purple) ceratopsids. D. Rarefaction curves for Campanian (green circles) and Maastrichtian (purple triangles) ceratopsids. Error bars show the 95% confidence intervals of values obtained during rarefaction.
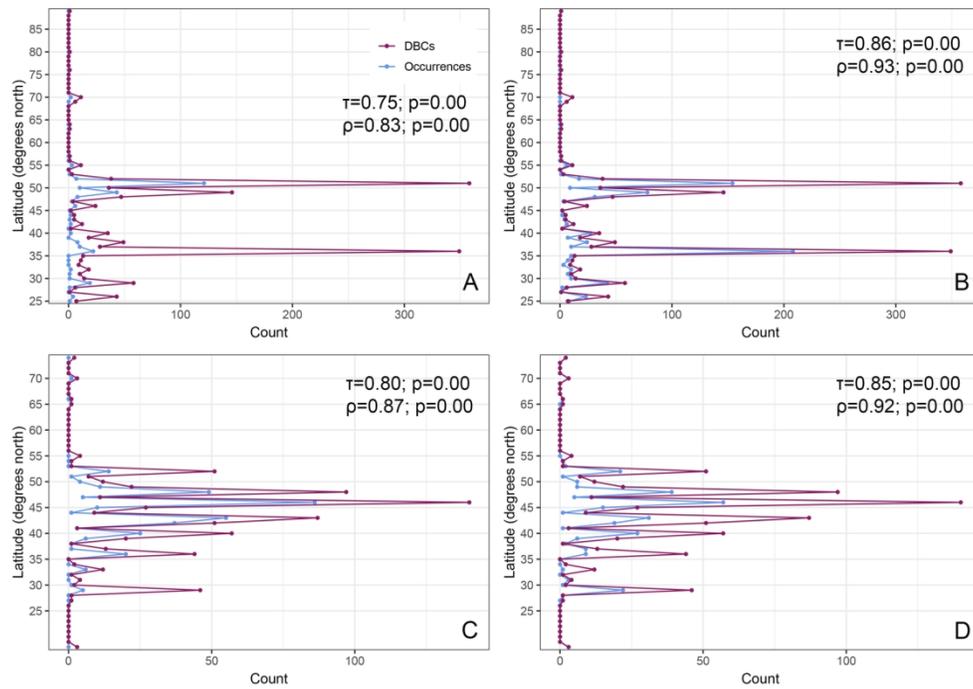
175x123mm (300 x 300 DPI)

Figure 2: A, C, ceratopsid occurrences and dinosaur-bearing collections with latitude in the A, Campanian and C, Maastrichtian. B, D, hadrosaurid occurrences and dinosaur-bearing collections with latitude in the B, Campanian and D, Maastrichtian. τ = Kendall's tau; ρ = Spearman's rho; DBCs, dinosaur-bearing collections.

148x104mm (300 x 300 DPI)

**Figure 1. A–C.** Jacknifed distributions of pBC values for Campanian (green) and Maastrichtian (purple) ceratopsids. **D**. Rarefaction curves for Campanian (green circles) and Maastrichtian (purple triangles) ceratopsids. Error bars show the 95% confidence intervals of values obtained during rarefaction.

**Figure 2: A, C,** ceratopsid occurrences and dinosaur-bearing collections with latitude in the **A**, Campanian and **C**, Maastrichtian. **B, D**, hadrosaurid occurrences and dinosaur-bearing collections with latitude in the **B**, Campanian and **D**, Maastrichtian. **τ** = Kendall's tau; **ρ** = Spearman's rho; **DBCs**, dinosaur-bearing collections.