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

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ABSTRACT

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

INTRODUCTION

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

APPROACH

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

LOCALITY & GEOLOGICAL SETTING

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

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

MATERIAL & METHODS

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

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

$$T = 111.4 - (4.3)(\text{combined mean bioapatite } \delta^{18}\text{O}_{\text{ecto phosphate}} - \text{combined mean } \delta^{18}\text{O}_{\text{endo water}})$$

PALEOCOMMUNITY STRUCTURE

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

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

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

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

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

PALEOTEMPERATURE RECONSTRUCTION

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

CONCLUSIONS

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

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

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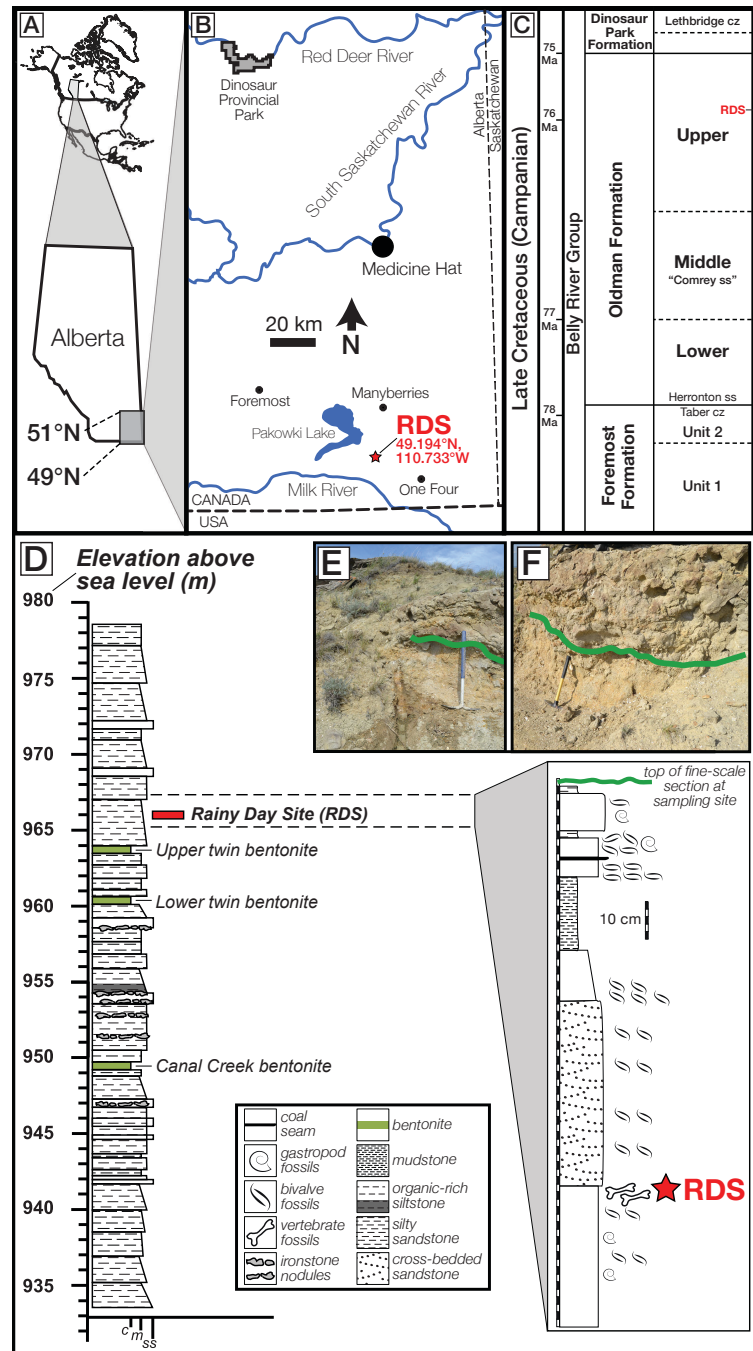
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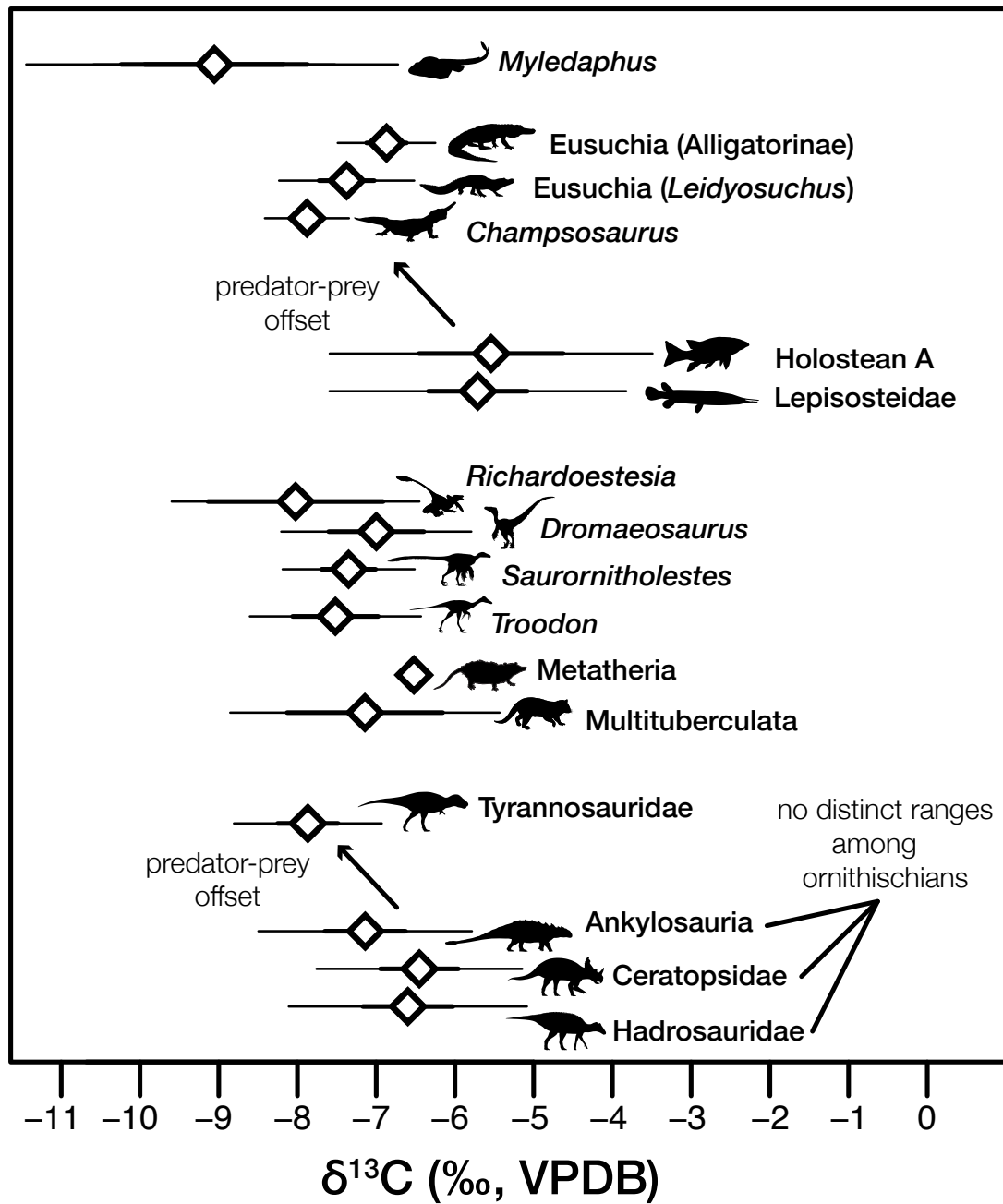
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FIGURES & FIGURE CAPTIONS

Figure 1. Geographic and stratigraphic position of Cretaceous locality ('Rainy Day Site', or RDS). A, position of study area in North America; B, position of RDS in southern Alberta (specific GPS coordinates on-file at Royal Tyrrell Museum and available upon request); C, Campanian stratigraphy of southern Alberta with stratigraphic position of RDS indicated; D, Stratigraphic section at RDS locality indicating location of RDS in respect to other nearby sites and marker beds; E, photograph of locality showing position of RDS and nearby sites and marker beds; F, photograph of broader area stratigraphy. Green line in E & F indicates position relative to stratigraphic column in D inset. Abbreviations: c—clay; cz—coal zone; m—mud; ss—sandstone.



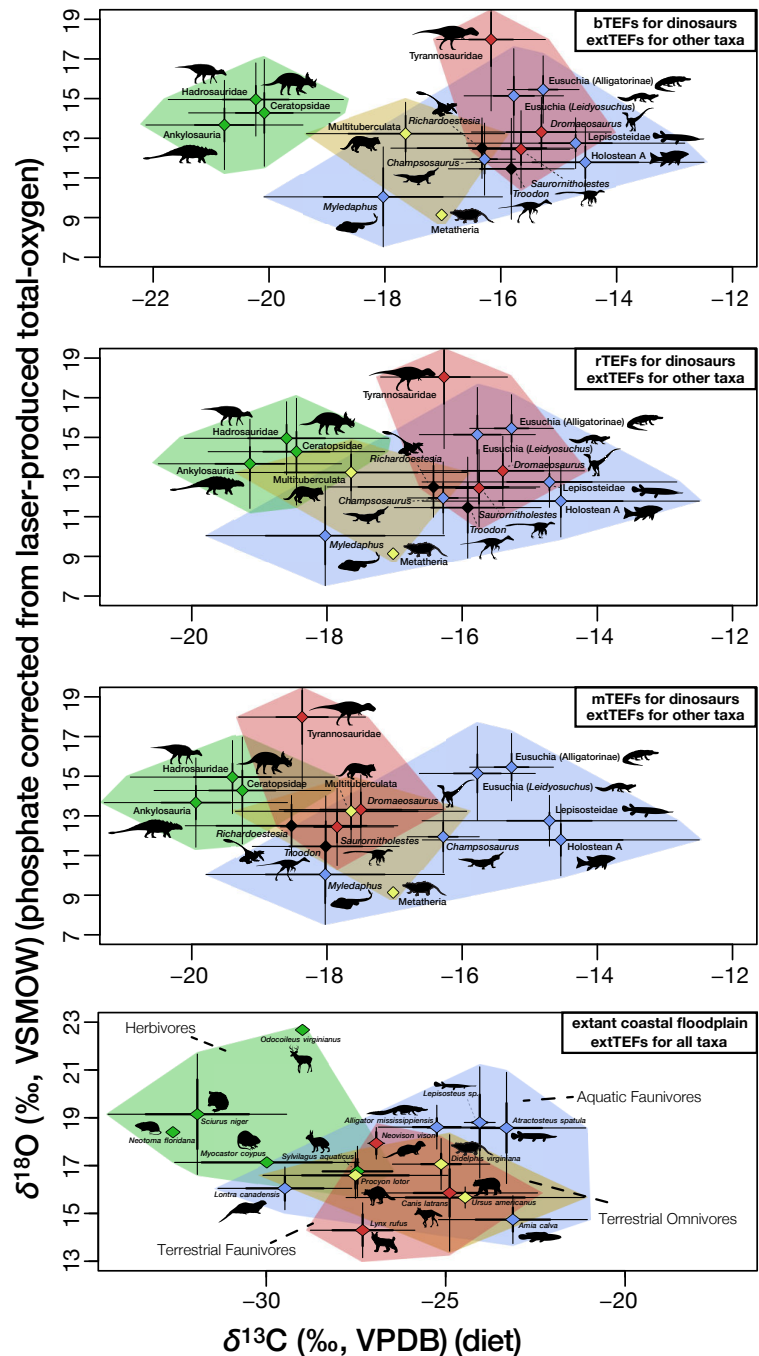


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359 Figure 2. Stable carbon isotope compositions of analyzed fossil taxa. Expected predator-prey
 360 isotopic offsets exist between tyrannosaurids and large ornithischians, and between aquatic
 361 reptiles and fish. No distinct separation present in the isotopic ranges of sampled ornithischians.

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



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

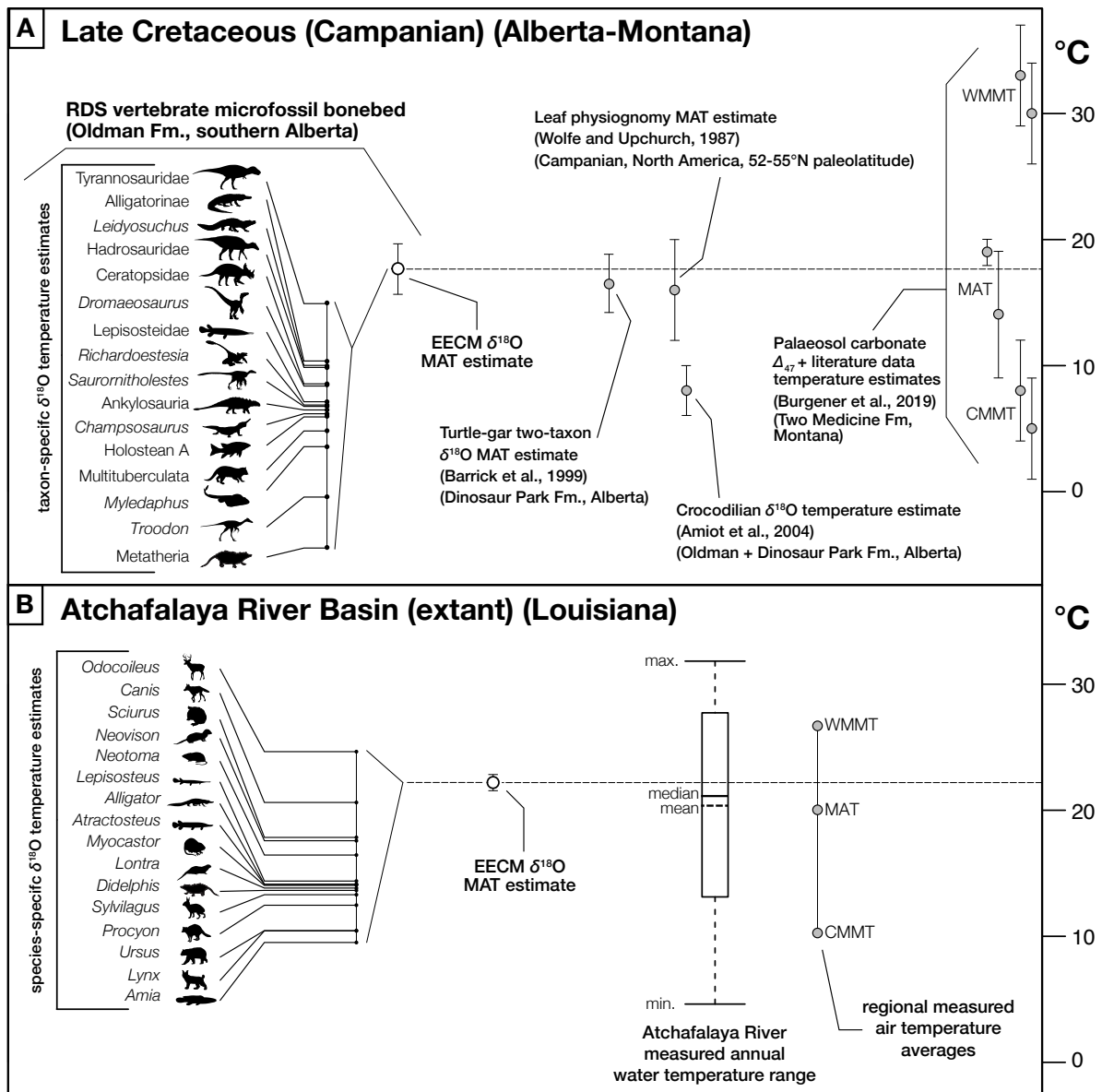


Figure 4: Oxygen isotope-based temperature estimates. A, individual taxon isotope-temperature estimates from Cretaceous paleoecosystem compared to endotherm-ectotherm-combined-mean (EECM) estimate from same data, alongside temperature estimates from other proxies (MAT= mean annual temperature, WMMT=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

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