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LATE CRETACEOUS DINOSAUR BIOGEOGRAPHY AND ENDEMISM IN THE WESTERN INTERIOR BASIN, NORTH AMERICA: A CRITICAL RE-EVALUATION

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Abstract—North-south provinciality among Campanian and/or Maastrichtian vertebrates, especially dinosaurs, in the Western Interior basin of North America (specifically, between West Texas and southern Alberta, Canada) has been accepted by many vertebrate paleontologists for about 30 years. However, a critical review indicates that the case for provinciality based on non-dinosaurian vertebrates is weak to nonexistent, and that the case based on dinosaurs is problematic, resting solely on a few taxa of dinosaurs, most notably the chasmosaurine ceratopsids, which have also been used to identify extreme dinosaur endemism. Paleobiogeographic provinces can be rejected because of: (1) problems and biases in sampling; (2) the lack of topographic barriers in the Western Interior basin that would divide provinces; (3) the lack of significant climatic or vegetational differences and/or gradients to provincialize vertebrates; (4) how taxonomic (largely cladotaxonomic) decisions have been intimately involved in the perception of endemism and provinciality; (5) how the demonstrable diachroneity of most fossil assemblages undermines the ability to include them in biogeographic analyses; and (6) how the non-uniformitarian conclusions of those who argue for dinosaur provinciality and endemism undermine their own arguments. Not only do we demonstrate the biological and geological implausibility of dinosaur-based biogeographic provinces and high degrees of endemism in the Western Interior basin during the Late Cretaceous, but the arguments and analyses that have been marshalled to support such concepts are questionable. Consequently, there is no compelling evidence that there was any discrete biogeographic separation of the Campanian (or Maastrichtian) dinosaur-dominated vertebrate assemblages from north to south beteen Texas and Alberta in the Western Interior basin. Also, there is no compelling evidence of high degrees of dinosaur endemism in the Western Interior basin during the Campanian.

INTRODUCTION

During Late Cretaceous time, a seaway extended from the Gulf of Mexico to the Arctic Ocean across a broad swath of western North America, dividing it into western and eastern land areas (Fig. 1). To the west of the Western Interior seaway, a tectonically and volcanically active land called Laramidia (Archibald, 1996) sourced rivers that flowed eastward to the seaway's western shoreline. The sediments deposited by these rivers, and on their floodplains and deltas, and the sediments deposited in the Western Interior seaway, are the collective sedimentary fill of what has been called the Western Interior basin (e.g., Kauffman, 1984). These sediments contain one of the World's great fossil records of Late Cretaceous life.

Studies of the nonmarine biota of the Western Interior basin go back nearly to the beginnings of American paleontology, when, in the 1850s, Joseph Leidy described the first dinosaur fossils found in the American West. As these studies developed, it became clear by the early 1900s that the Western Interior Late Cretaceous was home to a broadly uniform biota of primitive flowering plants and conifers, turtles, crocodylians and dinosaurs. Thus, by 1919, Gilmore was able to identify vertebrate fossil assemblages dominated by hadrosaurid and ceratopsid dinosaurs extending from Alberta to New Mexico. And, today, such assemblages are now known to extend essentially the entire north-south length of Laramidia, from Alaska to northern Mexico.

By the late 1960s, some paleontologists began to recognize some differences among the Late Cretaceous dinosaur-dominated assemblages that they perceived to be coeval in the Western Interior basin, and attributed these differences to paleoenvironmental factors (Russell, 1967, 1969). From this grew the idea of north-south differences between the Campanian and/or Maastrichtian dinosaur assemblages, variously expressed as different communities, faunas, associations, biomes or provinces. First articulated by Sloan (1970, 1976), this idea was developed further by Lehman (1987, 1997, 2001), and finds its most recent expression in articles by Sampson and Loewen (2010), Sampson et al. (2010), Gates et al. (2010, 2012), Sampson (2012) and Loewen et al. (2013), among others. Most of these recent articles also identify high degrees of dinosaur endemism in the Western Interior basin.

Here, we critically review and question the identification of different dinosaur-based biogeographic provinces and of high degrees of dinosaur endemism in the Western Interior basin, specifically in the part of the basin between West Texas and southern Alberta, Canada. We conclude that there is no compelling evidence that there was any discrete biogeographic separation of the Campanian (or Maastrichtian) dinosaur-dominated vertebrate assemblages from north to south in the Western Interior basin nor was there an unusual amount of dinosaur endemism.

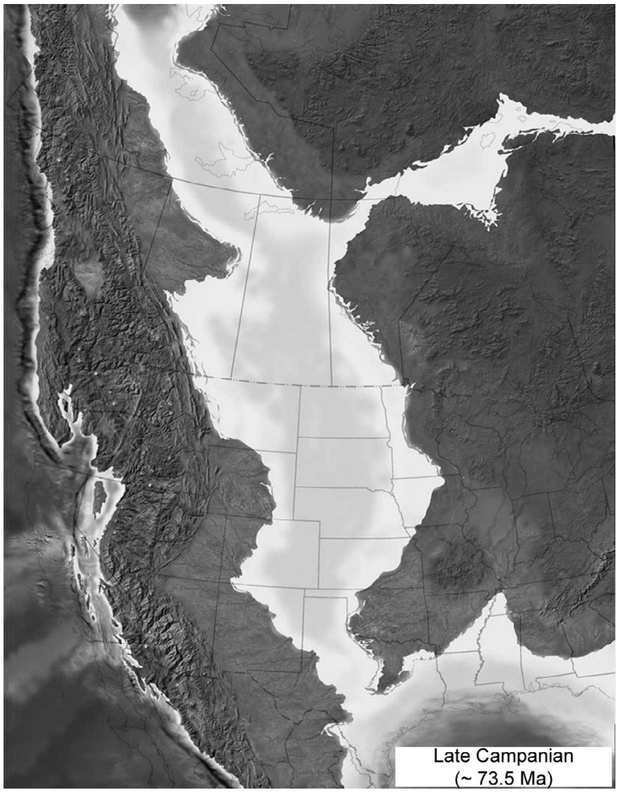

FIGURE 1. Paleogeographic map of the Western Interior seaway (©2014 Ron Blakey, Colorado Plateau Geosystems, Inc.).

CHRONOLOGY

The chronology of the nonmarine strata deposited during the Campanian-Maastrichtian interval in the Western Interior basin is constrained by the invertebrate (mostly ammonoid and inoceramid) biostratigraphy of intercalated marine units, palynostratigraphy, vertebrate biostratigraphy, radioisotopic ages and magnetostratigraphy. An extensive literature on this exists (see reviews by Lucas et al., 2012; Roberts et al., 2013, among others), and we present the vertebrate biochronology used here calibrated to the standard global chronostratigraphic scale and the numerical timescale (Fig. 2). This biochronology recognizes four Campanian-Maastrichtian land-vertebrate "ages" (LVAs), in ascending order, the Judithian, Kirtlandian, Edmontonian and Lancian, relevant to the discussion here.

HISTORY

Various ideas about the provinciality of the Late Cretaceous Western Interior biota, both in the marine and the terrestrial setting, have been proposed, and we review them here. Most of these revolve around the concept of a north-south divide in both the marine and nonmarine biotas.

The idea of provinciality in the Western Interior seaway began with Jeletzky (1968, 1971) and Sohl (1967, 1971), who identified north and south provinces based on the distribution of ammonoids and gastropods, respectively. More extensive analyses of the molluscan faunas identified a similar north-south division (e.g., Kauffman, 1973, 1977). These authors posited that the marine provinces were largely water-temperature determined—a northern province or sub-province represents a marine biota adapted to cool to temperate water, and a southern province or sub-province represents organisms adapted to warm to subtropical water. All of these analyses saw a broad area of overlap of the provinces/subprovinces, which graded into each other. Indeed, Kauffman (1984) argued that during the Late Cretaceous, major marine transgressions and regressions in the Western Interior seaway moved the boundaries of the sub-provinces he recognized to the north or south, sometimes more than 1000 km.

Nicholls and Russell (1990) provided a useful review of the published ideas about marine provinces in the Western Interior seaway. They also analyzed the distribution of marine Cretaceous vertebrates (primarily selachians and mosasaurs) to conclude that at least during one episode of the early Campanian, these animals also identified northern and southern subprovinces. Their subprovince boundary was vaguely located as somewhere south of Kansas.

Russell (1967, 1969) identified differences in the abundances of some dinosaur taxa in upper Maastrichtian (Lancian) sediments from Alberta, Saskatchewan and Montana to Wyoming that he attributed to a paleotopographic gradient from inland to coastal settings. Sloan (1970, 1976) first proposed the idea of north-south provinciality among the terrestrial vertebrates in the Western Interior basin, though he framed this as the difference among "terrestrial communities" (Table 1). Focusing on dinosaurs, which Sloan (1970) referred to as the "megaterrestrial community," he argued that there was considerable regional variation in "biofacies." Sloan thus recognized a northern "*Triceratops* community" (he also called it the "*Triceratops-Anatosaurus* community") distinct from a southern "*Alamosaurus* community" (he also called it the "*Alamosaurus-Pentaceratops-Parasaurolophus* community") divided from each other at approximately the southern border of Wyoming (Fig. 3). Nevertheless, Sloan (1970) recognized some overlap in the two "communities" based on *Alamosaurus* records from Wyoming, and some north-south variation within the "*Triceratops* community." Although Sloan stated that these communities are Maastrichtian, he clearly included some Campanian dinosaur assemblages (notably those with *Pentaceratops* and *Parasaurolophus*) in their composition. Sloan (1976) later argued that mountain ranges in southern Wyoming-central Colorado (~ 39°N latitude) separated the *Alamosaurus* and *Triceratops* "communities" (Table 1).

Lucas (1981; also see Lehman, 1981) argued for differences between "coastal" and more "inland" Late Cretaceous dinosaur communities. Thus, he identified Maastrichtian records of the sauropod *Alamosaurus* as coming from inland settings, different from the supposedly "coastal" settings with *Triceratops*. Lucas (1981) thus saw the difference between the "communities" identified by Sloan as not north-south, but as paleoenvironmentally controlled differences between dinosaurs that preferentially lived inland versus those that lived in "coastal" settings.

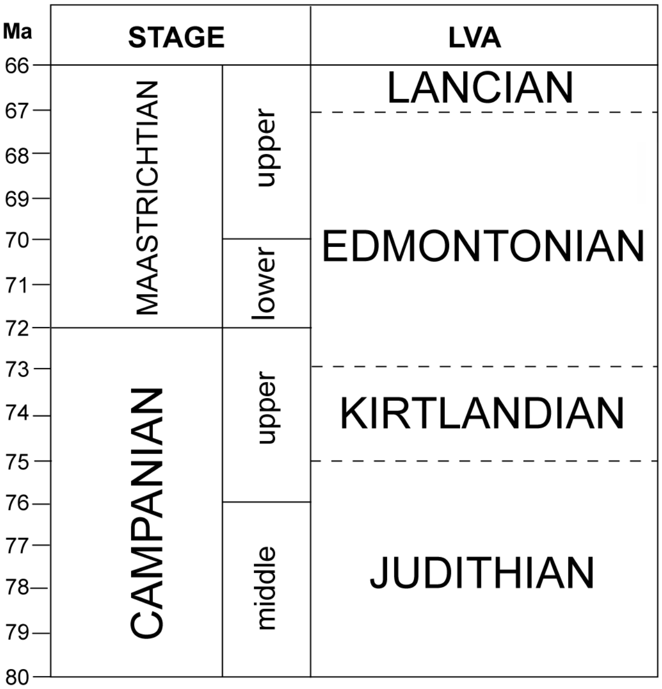

FIGURE 2. Correlation of Campanian-Maastrichtian land-vertebrate "ages" used in the Western Interior basin to the standard global chronostratigraphic scale and the numerical timescale.

Lehman (1987) analyzed late Maastrichtian (Lancian) paleoenvironments in the Western Interior to identify three dinosaur "faunas:" the *Leptoceratops*, *Triceratops* and *Alamosaurus* "faunas" (Table 1). He claimed that each of these "faunas" was "peculiar to a sedimentary/environmental province" (Lehman, 1987, p. 189). Thus, he identified the "*Alamosaurus* fauna" south of ~ 35°N latitude, in seasonal, semi-arid environments of intermontane basins; the "*Triceratops* fauna" north of 35°N latitude in humid coastal floodplains and swamps; and the *Leptoceratops* fauna north of 45°N latitude, in cool piedmont environments of Laramidian uplands. Lehman (1987) limited his analysis to dinosaur distribution, and claimed that changes

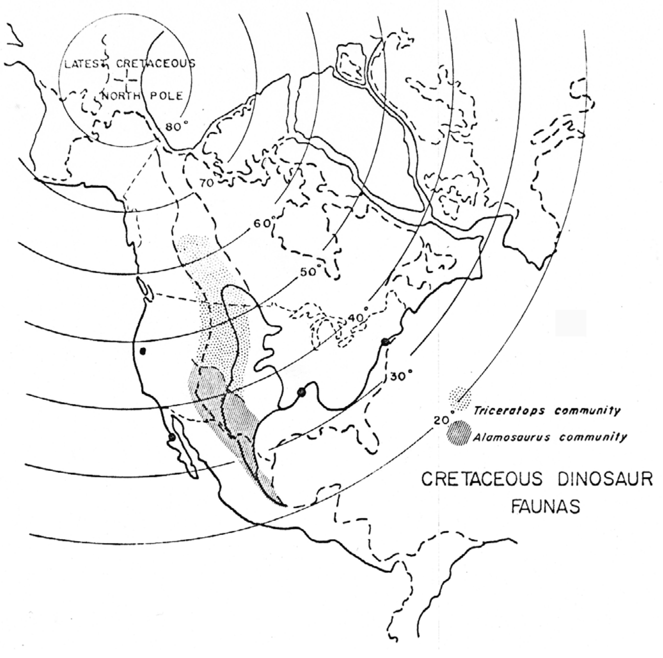

FIGURE 3. Sloan's (1970, fig 2) map of the distribution of the two dinosaur-based "communities" he recognized in the Western Interior basin.

TABLE 1. Tabular summary of proposals of dinosaur-based biogeographic provinces in the Western Interior basin during the Campanian and/or Maastrichtian. Land-vertebrate "ages" are abbreviated: E = Edmontonian, J = Judithian, L = Lancian.

Author	Age	Northern Province	Southern Province	Barrier/ Cause
Sloan (1970, 1976)	Maastrichtian	*Triceratops* community	*Alamosaurus* community	Southern border of Wyoming (mountain range) ~39˚ N
Lehman (1987)	Maastrichtian	*Triceratops* fauna; *Leptoceratops* fauna	*Alamosaurus* fauna	Topographic barrier due to regression of the Western Interior seaway; ~35˚ N for *Triceratops-Alamosaurus* separation; and ~ 45˚N for *Triceratops-Leptoceratops* separation
Lehman (1997)	Campanian	*Corythosaurus* fauna	*Kritosaurus* fauna	Latitudinal zonation in temperature and rainfall
Lehman (2001)	Campanian and Maastrichtian	*Maiasauria*/ *Einiosaurus* association; *Corythosaurus-Centrosaurus* association (J) *Anchiceratops-Saurolophus* association; *Pachyrhinosaurus-Edmontosaurus* association (E) *Triceratops-Edmontosaurus* association/ *Leptoceratops-Triceratops* association (L)	*Kritosaurus-Parasaurolophus* association (J-E) *Alamosaurus-Quetzalcoatlus* association (L)	Narrow climatic or other environmental tolerances and/or limited vegetational forage preferences of dinosaurs
Sampson and Loewen (2010); Gates et al. (2010); Sampson, (2012); Sampson et al. (2012); Loewen et al. (2013)	Campanian	Northern Province (Unnamed)	Southern Province (Unnamed)	Latitudinal temperature gradient?, topographic barrier (river system in N Utah-Colorado)? (uncertain)

in topography coincident with the retreat of the Western Interior seaway created the differences between the three "faunas."

Lehman (1997) proposed a late Campanian dinosaur biogeography of the Western Interior basin by comparing northern (Judith River and Two Medicine formations of Alberta-Montana) and southern (Fruitland/Kirtland formations of New Mexico, Aguja Formation of Texas) dinosaur assemblages. He thereby identified a northern "*Corythosaurus* fauna" dominated by crested lambeosaurine hadrosaurids, and a southern "*Kritosaurus* fauna" dominated by a single taxon of hadrosaurine (Table 1). He also identified diverse centrosaurine ceratopsids as characteristic of the northern "fauna," whereas the southern fauna had only a few chasmosaurine taxa. Notably, Lehman (1997, fig. 3) argued for the approximate contemporaneity of the dinosaur assemblages he was comparing, though by his own data the Fruitland/Kirtland formations are at least two million years younger than the Two Medicine and Judith River formations. He also discussed inherent biases based on sampling and outcrop area, and claimed north-south differences in some of the non-dinosaurian vertebrates, notably some fishes, turtles and crocodylians (see below).

Lehman (1997) attributed the division into northern and southern "faunas" to latitudinal zonation in temperature and rainfall. In so doing, he dismissed geographic barriers as too subtle to matter, oceanic circulation as also too small a possible factor and identified floral provinces as correlated with the dinosaur provinces. However, the floral provinces Lehman identified were based on old analyses (e.g., Batten, 1984) that have been substantially revised (see below). He drew the boundary between the dinosaur provinces at ~ 45°N latitude. Lehman (1997, p. 235) correctly noted that "recognition of provinciality suggests remarkably small geographic ranges for individual dinosaur species or genera," so he dismissed the idea of dinosaur migration (e.g., Hotton, 1980). This led Lehman (1997, p. 223) to conclude (in non-uniformitarian fashion) that "most dinosaur genera and species were endemic to areas much smaller than modern mammals of similar body size."

Lehman (2001) refined his previous study by identifying "associations" of hadrosaurids (hadrosaurs) and ceratopsids (ceratopsians) for three time slices (Judithian, Edmontonian [including the subsequently named Kirtlandian] and Lancian LVAs) in the Western Interior (Table 1). These associations were separated north-south during the Judithian and Edmontonian, but they were not so separated during the Lancian; instead, they were inland and coastal during the Lancian. Much of Lehman's (2001) paper focused on the diversity decline from Campanian to Maastrichtian dinosaur assemblages, because he regarded it as a given that "Late Cretaceous (Campanian-Maastrichtian) dinosaurs in the western interior of North America were remarkably provincial" (p. 310) and identified "distinct northern and southern biotic realms with a boundary in the vicinity of northern Colorado" (p. 313). Lehman (2001, p. 312) attributed the provinciality to the "limited vegetational foraging preferences, or narrow climatic or other environmental tolerances" of the dinosaurs. He thus reiterated his earlier conclusion that "many dinosaur genera and species had remarkably small geographic ranges" (Lehman, 2001, p. 311). Several workers (e.g., Sampson et al., 2004; Sampson and Loewen, 2005; Gates et al., 2005; Zanno et al., 2005) soon endorsed his conclusions.

Sullivan and Lucas (2006) re-evaluated the Judithian-Edmontonian dinosaur biogeography proposed by Lehman (2001). They did so by using the latest data to correlate the "dinosaur associations" Lehman had identified as provincial, showing them to be strikingly diachronous

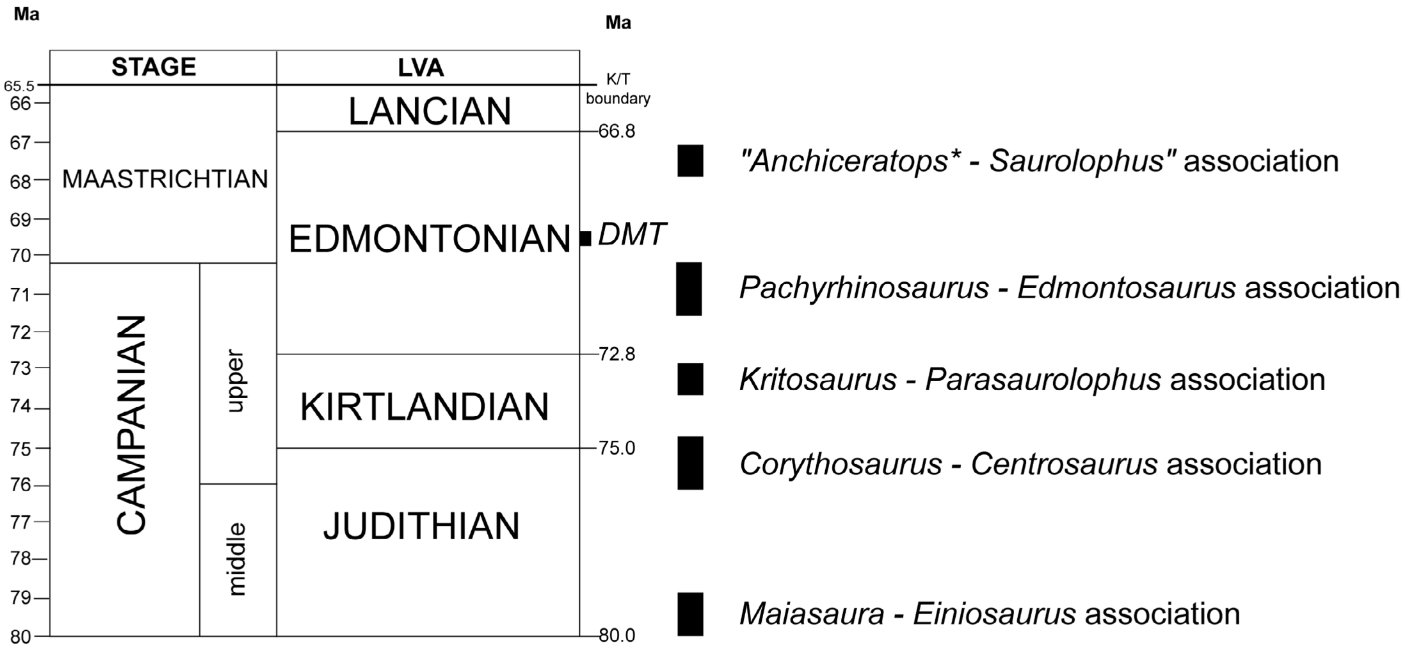

FIGURE 4. Correlation of Lehman's (2001) "dinosaur associations" of the Judithian, Kirtlandian and Edmontonian LVAs, demonstrating that they are not co-eval (from Sullivan and Lucas, 2006, fig. 6). DMT= Drumheller marine tongue.

(Fig. 4). They stated that "most of the taxonomic differences among these faunas have more to do with temporal position than with endemism or provinciality" (Sullivan and Lucas, 2006, p. 21). Thus, Sullivan and Lucas (2006) rejected the notion of north-south dinosaur provinces in the Western Interior basin during the Campanian-Maastrichtian.

Sampson et al. (2010) described two new chasmosaurine ceratopsids from the Campanian Kaiparowits Formation in Utah, and reassigned a species of *Chasmosaurus* from Alberta to a new genus, *Vagaceratops*. Thus, Sampson et al. (2010) argued that there were different chasmosaurines living to the north (Alberta) and south (Utah, New Mexico, Texas) (also see Sampson and Loewen, 2010). They concluded, based on their cladistic analysis of chasmosaurines, that the subfamily first evolved from forms in the southern Western Interior, where the most primitive taxa are found. Chasmosaurines then dispersed northward, but by 77 Ma a barrier prevented further north-south dispersal. Like Lehman before them, Sampson et al. (2010) were perplexed by the apparent endemism their taxonomy and correlations implied for such large animals, and were at a loss to identify the cause of such endemism. Sampson et al. (2010, p. 8) also claimed the contemporaneity of the ceratopsians they compared, stating that the "stratigraphic range of *Vagaceratops irvinensis* from Alberta overlaps with that of *Pentaceratops sternbergi* from New Mexico," even though their figure 7 of the stratigraphic ranges indicated (correctly, see below) otherwise.

Vavrek and Larson (2010) analyzed the overall (beta) diversity of the late Maastrichtian (Lancian) dinosaur assemblages of Laramidia. They found that diversity to be relatively low, largely due to sampling biases. Thus, no clear regional clustering exists among the dinosaur assemblages when compensating for differences in sample size. With these corrections, disparate sites, instead of neighboring sites, are most similar to each other, suggesting that the variation was not regional provincialism but more due to local variations or possibly the result of time averaging over the two or more million years of the late Maastrichtian. Vavrek and Larson (2010, p. 8265) concluded that the level of Maastrichtian beta diversity indicated a single dinosaur "community" during the Lancian in the Western Interior basin. They also stated that the Maastrichtian dinosaur provinciality advocated by Lehman (1987, 2001) was questionable because "such high levels of endemism would be unprecedented for any modern large-bodied terrestrial fauna."

Gates et al. (2010) reviewed the previous ideas about terrestrial provinciality in the Western Interior basin by analyzing six dinosaur-dominated vertebrate assemblages of Campanian age: Dinosaur Park Formation in Alberta; Judith River and Two Medicine formations in Montana; Kaiparowits Formation in Utah; Fruitland/Kirtland formations in New Mexico; and Aguja Formation in Texas. They admitted that there are biases in large vertebrate (dinosaur) sampling in the various Campanian units they examined, but claimed that adding microvertebrate data to their analysis has a "dampening effect on macrofaunal biases" (Gates et al., 2010, p. 374). However, due to "poor sample size" they eliminated the Two Medicine and/or Aguja vertebrate assemblages from some of their analyses. They also stated that including the median age of each fossiliferous formation in the analysis did not explain any of the variation, though the median ages they used and the results of that analysis were not presented. Their statistical analyses looked at the possibility of two or three "regions" (provinces), but provided no support for a three region result. Their two region analysis provided some support for two "biomes." However, according to Gates et al. (2010), latitudinal variation best explains the taxonomic differences between their datasets, and their analysis did not support recognition of two distinct biomes/provinces.

While Gates et al. (2010) employed multivariate statistics to add to their arguments, there are potential problems with the statistical methods used in their study. Thus, in using canonical correlation analysis (CCA), they failed to explain how the analysis meets the requirements for data quality inherent to this test. CCA, like all parametric statistical tests, assumes normality of the dataset being analyzed as well as random and independent samples. Fossil assemblages ("faunas") are inherently nonrandom because they go through multiple filters introducing bias, including taphonomic sorting, collection bias (e.g., what people decide to collect), exposure area and many other issues preventing a truly random sample. Therefore, the validity of the statistical analyses undertaken by Gates et al. (2010) is questionable.

Sampson (2012) emphasized the presence of different dinosaur taxa in the coeval Kaiparowits Formation of Utah and the Dinosaur Park Formation of Alberta. Thus, he claimed that almost all of the new species of dinosaurs to be named from the Kaiparowits Formation (14 of 15 species of hadrosaurids, ceratopsids and theropods) are different from those farther north. Sampson (2012, p. 44) concluded that "none of the more than 50 Campanian dinosaur species from numerous formations can yet be confidently placed in both the north and south" and thus that "at least two dinosaur communities existed on this landmass [Laramidia] for about a million years of Campanian time." Sampson drew attention to the fact that many of the coeval dinosaur taxa from the Kaiparowits and Dinosaur Park formations were large animals that weighed more than one ton. For their size, then, his conclusion is that their home ranges must have been very small. To explain that, he suggested several possibilities, namely that dinosaurs had low energy requirements, that there was unusually abundant food on the Late Cretaceous landscape and/or there were physical barriers the dinosaurs could not cross, perhaps a series of large rivers near the latitude of northern Utah/Colorado.

Gates et al. (2012) suggested that the onset of the Laramide orogeny triggered the diversification of dinosaurs in the Campanian of the Western Interior basin. In so doing, they ignored the likelihood that the apparent diversification is nothing other than an artifact of the far denser record of dinosaurs from the Campanian in the Western Interior basin when compared to either earlier or later time intervals of the Late Cretaceous. Further, Gates et al. (2012) suggested that a geologically-based estimate of the onset of the Laramide orogeny of 74.5 Ma should be revised to an older estimate of 78.5 Ma to better match their estimate of the timing of the dinosaur diversification.

Loewen et al. (2013) stated that during the Campanian there was dinosaur "high beta diversity and basin-scale endemism, with evidence for higher-order regional separation into northern and southern provinces." To explain the endemism, they endorsed previous suggestions of "latitudinal variation in floral diversity linked to latitudinal climate variability, sea-level fluctuation, and/or orogenic activity." They also argued that major marine transgressions of the Western Interior seaway isolated tyrannosaurids on Laramidia, leading to diversification within the clade.

Recently, Wick and Lehman (2013) discussed some of the disagreements over chasmosaurine alpha taxonomy, and argued that a progression from primitive to more advanced chasmosaurines is seen both north and south in the Western Interior basin. They thus stated that "this seems incompatible with the concept that northern and southern regions were home to highly provincial ceratopsid faunas" (Wick and Lehman, 2013, p. 14).

Most recently, Longrich (2014) identified *Kosmoceratops* (previously known only from Utah) and *Pentaceratops* (known previously from New Mexico and possibly Colorado) from the Dinosaur Park Formation in Alberta. These identifications, if substantiated (but see below), ran counter to the contention of Sampson et al. (2010) that there was north-south endemism of chasmosaurine ceratopsids. Longrich (2014) thus discussed at length and rejected the previous identifications of two dinosaur provinces and high degrees of dinosaur endemism in the Western Interior basin during the late Campanian.

TERMINOLOGY

The above review of the history of ideas of provinciality among Campanian and/or Maastrichtian dinosaur assemblages in the Western Interior makes it clear that the differing divisions have been referred to as communities, faunas, associations, biomes, sub-provinces or provinces (Table 1). We believe, nevertheless, that the various authors meant basically the same thing: a distinct dinosaur-dominated biota in a distinct region, whether the biota was characterized in ecological (biome, community, association, fauna) or biogeographic (sub-province, province) terms. To argue now about the proper meanings and correct application of these terms strikes us as a useless exercise in semantics.

Here, we use the term *assemblage* to refer to the collection of dinosaur and other vertebrate fossils from a given lithostratigraphic unit, such as in "dinosaur assemblage of the Kaiparowits Formation." We also use the term *province* to refer to the biogeographic divisions of the Western Interior terrestrial vertebrate biota proposed by other workers and reviewed above. The term province is classically treated as the lowest division in a hierarchy of global biogeographic subdivisions (Schmidt, 1954; Hallam, 1994). We believe that the diverse authors who have posited biogeographic divisions in the Western Interior basin were attempting to identify provinces, despite the varied terminology they applied to these divisions.

It is also important here to distinguish between what we would call *true endemism* and *apparent endemism*. What we call *true* endemism is the restriction of a taxon (usually a species) to a specific area that can be distinguished from the distributions of other taxa (cf. Platnick, 1991, 1992; Morrone, 1994). In contrast, what we would call *apparent* endemism is almost always what we perceive from the fossil record—an apparently restricted geographic distribution of a taxon based on sampling, outcrop distribution and/or taxonomic decisions. Clearly, what is being called endemism among dinosaur taxa in the Western Interior basin is *apparent* endemism, not *true* endemism. Or, at least, inadequate data exist to identify true endemism. Thus, we reject statements treating these fossil animals as exhibiting true endemism such as this: "despite large-to-giant body sizes, current evidence indicates that ceratopsids and hadrosaurids possessed relatively diminutive species ranges" (Sampson and Loewen, 2010, p. 417). Not only are such non-uniformitarian conclusions questionable (see below), but the data to support them are incomplete.

NON-DINOSAURIAN VERTEBRATES

A separate biogeographic province is not recognized by differences between one or a few taxa in different regions. Instead, it is recognized by an appraisal of the whole biota (e. g., Kauffman, 1984; Hallam, 1994). Indeed, Hallam (1994, p. 246) stressed that "most species are not abundant, and rare species should not be used in biogeographic studies, because their absence could be misleading." Nevertheless, as the above review makes clear, most of the terrestrial biogeographic divisions proposed for the Western Interior basin are based on just a handful of taxa, mostly a few genera of hadrosaurid, ceratopsid, theropod and/or titanosaurid dinosaurs. And, many of these are very rare taxa, particularly some chasmosaurine ceratopsid species.

Aware of this limitation, both Lehman (1997) and Gates et al. (2010) made some effort to analyze other, non-dinosaurian elements of the vertebrate fossil assemblages. Thus, Lehman (1997) claimed north-south differences in some of the Maastrichtian fishes, turtles and crocodilians. Gates et al. (2010, appendix) included all the vertebrate fossil taxa from the late Campanian assemblages in their analysis. Here, we discuss the major groups of non-dinosaurian vertebrates in terms of their Campanian-Maastrichtian paleogeographic distribution in the Western Interior basin.

Fishes

Lehman (1997) argued for differences in the abundance of some fish taxa—"*Lepisosteus*," "*Amia*" and *Myledaphus*—between different Campanian vertebrate assemblages in the Western Interior basin. However, given the uneven and incomplete study of Late Cretaceous fishes from the Western Interior basin, such differences, if they are real, are more likely due to differences in sampling or in the facies being sampled, than to biogeographic differences.

Brinkman et al. (2013) attempted to outline the biogeographic patterns of Osteichthyes in the Western Interior basin during the late Campanian. However, they compared only southern Utah and Alberta, and to evaluate a function (or pattern) properly, three or more points are needed. In other words, their study lacks the data to exclude other possible outcomes. Thus, they espouse a latitudinal gradient to explain differences in the osteichthyans between Utah and Alberta, and, to them, this implies climatic control. There is no attempt to exclude possibilities such as the likely existence of different drainage basins. Indeed, many extant South American fish faunas are sharply divided along the boundaries of watersheds (Hubert and Reno, 2006).

Brinkman et al. (2013) further suggested that a north-south provinciality could be based on differences in production related to day length, over the 14˚ of latitude between Alberta and southern Utah, creating greater seasonality. However, to our knowledge this has not been reported in estimates of Campanian climate, and the climate variation proposed does not fit recent estimates of a low thermal gradient of ~.4˚C/1˚ latitude in the Western Interior basin during the Late Cretaceous (Upchurch et al., 2015). In short, the conclusions of Brinkman et al. (2013) are questionable, as the necessary data to support their conclusions are absent.

Turtles

Late Cretaceous turtle paleobiogeography in the Western Interior basin presents a challenge to analysis, as many species and genera are known only from a single unit (e.g., *Gamerabaena* from the Maastrichtian of North Dakota). Further, many closely related species are known from different-aged localities, such as *Boremys grandis* (Kirtlandian) and *Boremys pulchra* (Judithian) (Sullivan et al., 2013), hindering direct comparisons of coeval taxa. In many such cases, where age control is good, a temporally sequential evolutionary species lineage (likely anagenetic) is plausible. Also, we note this pattern of *Boremys* species is argued against by Lively (2015), who considers several Judithian specimens from Utah to be *B. grandis*. However, the fragmentary nature of the specimens studied by Lively (2015) leads us to limit the assignment to *Boremys* sp., as the anterior portion of the shell in his material is poorly preserved. A further complicating factor is the prevalence of "trash can" taxa of Late Cretaceous turtles by which many similar specimens not diagnostic to a particular species are lumped into a given species or genus. A prime example of this is *Naomichelys speciosa*, which has little meaning in many of its uses beyond a solemydid turtle found in the Late Cretaceous of the Western Interior basin (Joyce et al., 2011; Lichtig and Lucas, 2015).

The taxonomy of fossil trionychid turtles from the Late Cretaceous of North America is poorly understood, which complicates comparisons

(Vitek and Joyce, 2015). Most of the trionychid genera are known from both northern and southern fossil assemblages.

Baenid turtles in the Western Interior basin are represented by many taxa endemic to their type locality. A few, such as *Denazinemys*, have been reported from a number of southern lithostratigraphic units and have been suggested to characterize a southern turtle "fauna" (e.g., Lively, 2015; Joyce and Lyson, 2015). This genus is known from the Kaiparowits (Utah), Fruitland, Kirtland, Menefee (New Mexico), and Aguja (Texas) formations and thus has a stratigraphic range encompassing most of the Campanian (Lichtig and Lucas, 2015).

Neurankylus is more challenging to assess, as most Late Cretaceous specimens were assigned to *N. eximius* at some point. In fact, the genus is more speciose, with *N. baueri* found in the south and *N. eximius* only known in the north. The largest question with regard to these is the specific identity of the *Neurankylus* of the Kaiparowits Formation. Lively (2015) named two additional species of *Neurankylus* in the Kaiparowits Formation, but we are unconvinced that these are meaningfully different from *N. baueri*. The minor differences in size and dorsal ridge morphology that Lively (2015) considered taxonomically significant appear to indicate sexual dimorphism. Further, the narrow extra scute discussed for *N.* "*hutchisoni*" (listed as marginal VI in Lively, 2015, fig. 2), is probably a supernumerary scute (or pathology), so it likely possesses only 12 marginal scutes. Finally, the suggestion of *N. baueri* having fused sutures and reaching maximum size at ~700 mm, in contrast to the Kaiparowits species *N. "hutchisoni"* and *N. "utahensis"* at 800-900 mm, overlooks that a well-preserved *N. baueri* from the Kirtland Formation of New Mexico has open sutures at 680 mm carapace length.

Cedrobaena and *Gamerabaena* are baenids apparently endemic to sites in the Maastrichtian of North Dakota that have no southern equivalents (Lyson and Joyce, 2009, 2010). This may be because of the lack of exploration of similar-aged units in the south, as well as facies differences, which present a complication to Maastrichtian turtle biogeography. Nevertheless, the Campanian baenids suggest a possible separation of *Denazinemys nodosa* and *Neurankylus baueri* in the south, and no *Denazinemys* and the presence of *N. eximius* in the north.

Fragmentary remains of chelydrid turtles have been reported from many formations in western North America. These range from the southernmost occurrence in Chihuahua, Mexico, to at least as far north as Montana. Most of this material is indeterminate and or undescribed, making a more detailed analysis impossible (Hutchison, 2008).

Lehman (1997) noted a southern distribution of the bothremydid *Bothremys*. Indeed, it is known in the Western Interior basin from New Mexico and Texas in different-aged Campanian deposits (see below).

Cifelli et al. (1999) claimed a southern distribution of the turtle *Compsemys* in the Western Interior basin, apparently overlooking that it was originally described from the Lancian Hell Creek Formation of North Dakota (Leidy, 1856). Other specimens have also been recovered from the Maastrichtian of Alberta and Montana (e.g., Lyson and Joyce, 2011).

The genus *Basilemys* is apparently endemic to North America, with four recognized species, *B. variolosa*, *B. sinuosa*, *B. gaffneyi*, and *B. praeclara* (Brinkman and Nichols, 1993; Sullivan et al., 2013). These are present in the Aquilan to Judithian, Judithian, Kirtlandian, and Lancian LVAs, respectively, which calls into question whether these are geographic variants or an evolutionary lineage. We suggest that, lacking contemporaneous northern and southern examples of each species, the latter is more plausible. This is consistent with the lack of sympatry among large species of extant tortoise. For example, *Centrochelys sulcata* and *Stigmochelys pardalis*, the third and fourth largest extant tortoises, are found close to each other in central and southern Africa, but their ranges do not overlap. Even smaller extant tortoises of the genera *Testudo* and *Agrionemys* are diverse, but also do not overlap geographically to any great degree (Bonin et al., 2006).

Hutchison et al. (2013) suggested latitudinal variation between Campanian turtle faunas based on the few species reportedly shared between the Dinosaur Park and Kaiparowits formations and their immediate neighbors. They further suggested that additional taxa (*Hoplochelys* and pleurodires) are limited to a more southern turtle assemblage in Texas and Mexico. The slightly younger Kirtland Formation does include these taxa, so timing of the units may be an issue, as the fossiliferous interval of the Aguja Formation of Texas is now considered to be at least two million years older than the Kirtland Formation (see below).

Holroyd and Hutchinson (2002) attempted to characterize the longitudinal variation of late Maastrichtian turtle faunas from North Dakota, Wyoming and Montana. They found a significant degree of variation between their sites that could not be directly linked to lithology. Holroyd and Hutchinson (2002) suggested that this is the result of the underlying heterogeneity of the aquatic environment. They also suggested that the more common occurrence of chelydrids and *Basilemys* in the southern part of their study area supports the latitudinal variation hypothesis of Sloan (1970) and Lehman (1987). Nevertheless, they pointed out problems with testing this and other proposed explanations of variation in Late Cretaceous turtle distributions.

In contrast, Holroyd et al. (2015) very recently suggested that the turtle faunas of the Western Interior basin do not identify a clear northern province. Conversely, they identified several southern turtles, including *Denazinemys,* that are only found from the Kaiparowits Formation of southern Utah and southward. They found no characteristic northern turtle fauna but suggested that chelydrids are only known from the Kaiparowits Formation and northward, possibly forming an overlapping northern fauna. However, Holroyd et al. (2015) apparently overlooked the reported presence of chelydrids in the Campanian of northern Mexico (Brinkman and Rodriguez, 2006), which would eliminate their only strictly northern taxon.

Brinkman (2003) suggested a north-south shift in the latitudinal gradient as an explanation of fluctuations in turtle diversity in the Late Cretaceous of the Western Interior basin. He explored the possibility of aridity controlling turtle diversity based on sedimentary clues (e.g. calcrete, coal, etc.) and found that the diversity runs counter to this hypothesis, with higher diversity in some of the "dry" units. Brinkman (2003) noted the unusually low turtle diversity of the Horseshoe Canyon Formation and argued that the abundance of other aquatic reptiles precludes a taphonomic reduction of turtle diversity as an explanation.

Extant turtle faunas vary greatly, but the exclusion of turtle taxa from an area can usually be traced to a geographic barrier. For example, different species of extant *Graptemys* inhabit different and distinct river systems in the southeastern United States (e.g., Ehret and Bourque, 2011). With no evidence for similar barriers and a lower temperature gradient in the Western Interior basin during the Late Cretaceous, we find it unlikely that well defined geographic provinces would develop among the turtles. Similarly, the southeastern corner of Missouri has a vastly different extant turtle fauna than the rest of the state, which transitions across a divide over just a few kilometers. The upland habitat represented on the northern side of this divide likely represents a lower preservation potential than the southern area. The southern area, continuing into Arkansas, is characterized by broad flood plains and swamps, matching the inferred depositional environments of much of the Upper Cretaceous in the Western Interior basin.

Turtles thus provide a few Campanian-Maastrichtian taxa that may have northern versus southern distributions in the Western Interior basin. However, identifying northern and southern turtle-based provinces in the Campanian or Maastrichtian of the Western Interior basin is largely confounded by taxonomy, uneven sampling, facies biases and diachroneity.

Squamates

Gao and Fox (1996) summarized the stratigraphic distribution of Late Cretaceous (Aquilan-Lancian) lizards of western Canada. However, they made no attempt to compare them to the Late Cretaceous lizard assemblages to the south.

Cifelli et al. (1999) suggested that the presence of the teiid lizard *Polyglyphanodon* in the Maastrichtian North Horn Formation of Utah and at localities in California may suggest a southern lizard "fauna." This is based on the apparent absence of this genus in more northern assemblages. However, although rare, teiids are known from the Milk River, Oldman, Fruitland, Lance, Hell Creek, Frenchman and Scollard formations (Sullivan, 1981; Gao and Fox, 1996). Clearly, teiids were well established throughout much of Laramidia during the middle Campanian-late Maastrichtian, with their apparent diversity severely diminished by the late Maastrichtian (Gao and Fox, 1996).

In a broader based analysis, Nydam et al. (2013) discussed sampling-based problems in the use of Late Cretaceous lizards to form a biogeographic hypothesis. The potentially most significant of these is that lizards seem to either be rare at a given site and thus "endemic," or they are common at a site and widespread. This suggests that at least some of the apparent endemism is driven by the rarity of the specimens, rather than the actual distribution of the lizard taxa.

Snakes are very poorly known in the Upper Cretaceous strata of the Western Interior basin, represented by only one taxon, *Coniophis* sp., from a handful of localities spanning Albian to Campanian time.

Nydam et al. (2013) argued that the occurrences of *Coniophis* sp. in the Cedar Mountain, Dakota, Straight Cliffs, Wahweap and Kaiparowits formations of Utah, and the single report of "*Coniophis cosgriffi*" (a species considered a nomen dubium, see Sullivan and Lucas, 2015) from the Fruitland Formation of northwestern New Mexico (Armstrong-Ziegler, 1978), suggest a possible southern province with snakes absent in the north. However, *Coniophis precedens*, which was based on an isolated vertebra from the "*Ceratops* beds" of Wyoming (Marsh, 1892), has also been reported in more northern regions, from the middle Campanian Milk River Formation of Alberta (Fox, 1975; Holman, 2000) and the upper Maastrichtian Lance and Hell Creek formations of Wyoming and Montana (Gilmore, 1938; Estes, 1964; Estes et al., 1969). Thus *Coniophis,* as currently understood, not only spans an unusually long period of time, but it was widespread in Laramidia. We also note that the record of this taxon in India is questionable due to the fact that the taxon is based on plesiomorphic features and in need of revision (Rage et al., 2004).

Parenthetically, Longrich et al. (2012) assigned new skull material to *Coniophis* and suggested that this snake is more basal than previously thought, sharing features of both lizards and snakes. However, as Nydam (2013) correctly pointed out, this new skull material is of lizard affinities and therefore not attributable to *Coniophis*. Moreover, there is no direct association of trunk vertebrae to skull material, so the collection of fossil material published by Longrich et al. (2012) is a chimera, a fact supported by the unusually long ghost lineage posited in the phylogenetic analysis of this composite snake.

Based on the rarity of fossil lizards and snakes, we conclude that the Campanian and Maastrichtian records of squamates in the Western Interior basin is too incomplete and/or too subject to sampling biases to be used in biogeographic analysis.

Crocodylians

Irmis et al. (2013) reviewed the crocodile assemblage of the Kaiparowits Formation of Utah and compared it to other Western Interior basin crocodile assemblages. They found that *Deinosuchus* has a broad geographic range from Montana to Texas (and it extends to the Gulf Coast and the Atlantic Coastal Plain: Lucas et al., 2006a). In contrast, *Brachychampsa* is known from the Kaiparowits, Menefee, Fruitland and Kirtland formations in the Campanian, suggesting a small geographic range for this taxon, though this genus has been reported from the late Maastrichtian Lance Formation (Estes, 1964) and the Hell Creek Formation of Montana and the Dakotas (Gilmore, 1911; Estes et al., 1969; Brochu, 1999).

Brochu (1999) concluded that *Leidyosuchus* is the basalmost North American alligatoroid. Wu et al. (2001) considered *Leidyosuchus* to be endemic to North America but restricted it to the northern portion of the continent. Irmis et al. (2013) further suggested that *Leidyosuchus* is not present in units south of the Kaiparowits Formation, though Lucas et al. (2006b) identified cf. *Leidyosuchus* in the Fruitland Formation of New Mexico. Nevertheless, as re-emphasized by Farke et al. (2014), *Leidyosuchus* is also known from Alberta, so its distribution crosses any proposed province boundary based on dinosaurs.

At present, we conclude that the record of diagnostic crocodile fossils is not extensive enough to identify biogeographic patterns in the Western Interior basin during the Campanian-Maastrichtian.

Pterosaurs

In their description of *Navajodactylus boerei* from the lower Kirtland Formation (Hunter Wash Member) of northwestern New Mexico, Sullivan and Fowler (2011) provided a useful review of the distribution of pterosaurs in the Campanian-Maastrichtian strata of the Western Interior basin (also see Barrett et al., 2008). Although Sullivan and Fowler (2011) referred two specimens from the Dinosaur Park Formation to *Navajodactylus boerei* (an incomplete proximal end of a left 1st wing phalanx and fused extensor tendon process, and an incomplete left 1st wing phalanx and fused extensor tendon process), the geographic and stratigraphic distribution of this taxon needs unequivocal support through documentation of more complete material.

The giant *Quetzalcoatlus northropi*, which was originally described from the Javelina Formation (Maastrichtian) of Texas, has questionable occurrences (?*Quetzalcoatlus*) in both the Oldman Formation of Alberta and the Hell Creek Formation (cf. *Quetzalcoatlus*) of Montana (Witton and Naish, 2008). A specimen of "*Quetzalcoatlus*" has also been reported from the Aguja Formation of Texas (Kellner and Langston, 1996; Sullivan and Fowler, 2011). In light of the uncertainty of these taxonomic assignments, pre-Maastrichtian occurrences of *Quetzalcoatlus* may be viewed with skepticism.

Lehman (2001) identified an "*Alamosaurus*-*Quetzalcoatlus* association" during the late Maastrichtian in the southern Western Interior basin, but the probable record of this giant pterosaur in Montana undermines that concept. Suffice it to say, most Campanian-Maastrichtian pterosaur records in the Western Interior basin are based on fragmentary material, and/or on unique specimens, that identify apparent endemic taxa, so this is not a record that lends itself to biogeographic analysis.

Birds

The Upper Cretaceous birds of the Western Interior basin represent various taxa, which are known primarily from isolated skeletal elements (e.g., Chiappe and Wittmer, 2002). Most of the named taxa are found in the upper Maastrichtian Lance Formation in Wyoming. However, some other taxa, such as the three species of *Cimolopteryx* (*C. maximus*, *C. petra*, and *C. rara*), are known from the upper Maastrichtian Frenchman and Hell Creek formations. Both species of *Avisaurus*, *A. archibaldi* and *A. gloriae,* are known from the Hell Creek Formation (upper Maastrichtian) in Montana, whereas *Hesperornis* and *Ichthyornis* are the two oldest Upper Cretaceous birds from the Western Interior basin. The fossil remains of *Hesperornis* are found in lower Campanian deposits, whereas those of *Ichthyornis* are from Turonian-Campanian deposits (Everhart, 2005).

The fossil bird record from the Western Interior basin during the Campanian-Maastrichtian thus resembles that of pterosaurs in being based largely on fragmentary material with a few apparent endemic taxa known from little more than their type specimens. Furthermore, as volant animals, one might not expect any biogeographic separation of pterosaurs and birds across an area the size of the Western Interior basin, though there are some birds endemic to smaller regions today. However, much better fossil records of both groups will have to be discovered and analyzed to evaluate that assertion.

Mammals

Cifelli (2000) suggested the possibility of provinciality in the Cretaceous mammal faunas of North America, but noted that there are insufficient data to draw this conclusion. We agree with that conclusion, which was followed by Sullivan and Lucas (2006) and Lucas et al. (2012), who argued against using mammals to define Late Cretaceous biochronological units (LVAs) in the Western Interior basin because of the relatively poor, uneven and incomplete record of fossil mammals and their relatively young and unstable taxonomy.

For example, because of the rarity and questionable taxonomic identity of many of the New Mexican Late Cretaceous mammals, these fossil mammals need to be re-assessed in a comprehensive way before they can be deemed useful for any biostratigraphic correlation and/or paleogeographic assessment (see Sullivan and Lucas, 2015). The fact is that vast screenwashing operations need to be undertaken throughout the Western Interior basin to develop the record of mammals (and other microvertebrates) to the point where meaningful comparisons can be made between assemblages. A few units have received such sampling, but even within them only a few sites and a limited range of facies have been sampled.

Furthermore, we note that Late Cretaceous mammals were mostly very small animals, so we would expect them to show fair degrees of true endemism based on small home range size, though current data are insufficient to evaluate even this uniformitarian hypothesis. Therefore, we conclude that our understanding of the Campanian-Maastrichtian record of fossil mammals in the Western Interior basin is inadequate to evaluate biogeographic hypotheses.

DINOSAURS

The case for provinciality in the Western Interior basin during the Campanian and/or Maastrichtian thus rests on dinosaur distribution, as advocates of that provinciality have long made clear. The strata that yield the Campanian-Maastrichtian dinosaur fossils extend from Alaska to Mexico, though analysis of biogeographic patterns has only focused on the area from southern Alberta to either New Mexico or West Texas (Fig. 1). In this region, numerous dinosaur genera and species represent 13 family-level clades of ornithischians and saurischians. The Campanian ornithischian dinosaurs belong to the following families: Ankylosauridae, Ceratopsidae, Hadrosauridae, Pachycephalosauridae, and Thescelosauridae. The saurischian theropods include the following families: Alvarezsauridae, Caenagnathidae, Therizinosauridae, Dromaeosauridae, Ornithomimidae, Troodontidae, and Tyrannosauridae. Members of these families were also present in the Maastrichtian, with the addition of the giant titanosaurid sauropod *Alamosaurus sanjuanensis*.

The family Ceratopsidae is a diverse group that is divisible into two subfamilies commonly (and incorrectly) called Centrosaurinae and Chasmosaurinae. By International Commission of Zoological Nomenclature rules (especially Article 61), the correct names are Pachyrhinosaurinae and Ceratopsinae (respectively), but we use Centrosaurinae and Chasmosaurinae here to maintain continuity with the published literature. Both the centrosaurines and chasmosaurines were present in the Campanian and Maastrichtian and had a wide paleogeographic distribution throughout Laramidia (e.g., Chinnery-Allgeier and Kirkland, 2010; Sampson and Loewen, 2010). Ideas about their provinciality and the endemism of chasmosaurines are confounded by taxonomic disagreements, discussed at greater length below.

The case for dinosaur provinciality, nevertheless, has only been based on a few dinosaur groups, primarily ceratopsids, hadrosaurids and tyrannosaurid theropods. This is because many other groups are known from very limited records (e.g., Alvarezsauridae, Therizinosauridae, Thescelosauridae). Other dinosaur groups (such as Ankylosauridae and Pachycephalosauridae) are known from a range of taxa, mostly restricted to individual lithostratigraphic units, or only known from their type material, and/or mostly diachronous. Titanosaurids, which had a widespread distribution (Africa, Europe, South America and Asia) in the Early to Late Cretaceous (Wilson, 2005; Dal Sasso et al., 2016) may be the only geographically restricted dinosaur group in the Late Cretaceous with only one taxon (*Alamosaurus sanjuanensis*) in the southern Western Interior basin (Texas, New Mexico and Utah) during Maastrichtian time (Jasinski et al., 2011).

Ceratopsids (chasmosaurines and centrosaurines) have already been discussed above and have played a pivotal role in supporting the recognition of paleogeographic provinces. Suffice it to say, disagreements over chasmosaurine alpha taxonomy and their evolutionary (phylogenetic) development from primitive to more advanced chasmosaurines have been documented in both northern and southern dinosaur faunas in the Western Interior basin (Wick and Lehman, 2013). However, there is little in the way of temporally or geographically overlapping strata in which these dinosaurs occur, so claims of endemic species are, in reality, apparent, certainly not true endemism.

Prieto-Márquez (2010) posited that the Hadrosauridae originated in North America and dispersed into Asia by late Santonian time. Saurolophines seemed to have originated in North America, while lambeosaurines originated in Asia by the late Santonian. Four saurolophine dispersal events occurred from North America to Asia during the Campanian and early Maastrichtian, with a fifth southward dispersal to South America by late Campanian time (Prieto-Márquez, 2010). Lambeosaurines dispersed from Asia to Europe by early Campanian time and arrived in North America no later than the onset of the late Campanian. Although Prieto-Márquez (2010) did not address any specific endemism within North America (Laramidia), he demonstrated the rather rapid and widespread dispersals of various hadrosaurid clades.

Initially, hadrosaurids were seen as part of the provinciality of dinosaurs in the Western Interior basin (Lehman, 1997). However, only a few years later, Willamson (2000) questioned a north-south dichotomy in hadrosaurids. More recent work, too, has not sustained any obvious north-south division among the hadrosaurids. Thus, for example, Gates et al. (2012, fig. 2) presented a phylogeny of saurolophine hadrosaurs that shows no clear separation of north and south groups. More importantly, the ages they assign the saurolophine taxa indicate few are strictly coeval—most are separated in time by a million or more years.

The family Tyrannosauridae is divided into two subfamilies: Albertosaurinae and Tyrannosaurinae (Currie, 2003; Brusatte and Carr, 2016). The Albertosaurinae is the less inclusive subfamily, and most of its records are northerly in the Western Interior basin, whereas the Tyrannosaurinae is more widely distributed. There is a high degree of apparent endemism, as virtually every good skull of a tyrannosaurid is the type specimen of a taxon known from little more than that type specimen. Loewen et al. (2013) suggested that within Laramidia each depositional basin contained endemic tyrannosaurid species, but we see this largely as an artifact of sampling and oversplit cladistic taxonomy. Moreover, these depositional basins are only remnants of a more widespread depositional environment and biome. The existing outcrop areas capture only a small portion of the plants and animals that no doubt lived far beyond the current boundaries of outcrop belts.

The phylogenetic relationships of various tyrannosaurid taxa have been invoked to indicate higher-level biogeographic divisions between Alberta, Montana and Wyoming versus Utah and New Mexico. However, only a few of the taxa are contemporaneous (e.g., *Nanotyrannus* and *Tyrannosaurus*) and others are not contemporaneous (e.g., *Bistahieversor*, *Lythronax*, and *Teratophoneus*). Brusatte and Carr (2016) discussed the migration of tyrannosaurids to and from Asia and North America and indicated that there is no tyrannosaurid record before the Campanian in North America. However, isolated diagnostic teeth from the Milk River Formation (Santonian) were referred by Larson (2008) to Tyrannosaurinae, indicating the pre-Campanian occurrence of tyrannosaurines in North America.

Thomson et al. (2013) suggested that Campanian tyrannosaurids can be separated into northern and southern groups, thus identifying provinciality in Laramidia. However, as noted by Thomson et al. (2013), it is difficult to support such a conclusion, given that phylogenetic analyses (e.g., Brusatte et al., 2009, 2010; Carr and Williamson, 2010; Fiorillo and Tykoski, 2014; Lü et al., 2014; Brusatte and Carr, 2016) do not recover northern and southern groups of tyrannosaurids. Thus, there is no compelling evidence of north-south provinciality of Campanian-Maastrichtian tyrannosaurids in the Western Interior basin.

The Campanian-Maastrichtian dinosaurs invoked as provincialized in the Western Interior basin are either large dinosaur taxa and/or taxa interpreted as employing herding behavior. Smaller or rarer dinosaur taxa provide numerous problems and difficulties for attempting to assess their distribution (e.g., Jasinski et al., 2015). Indeed, even the taxa discussed above are often known from rare and/or fragmentary material. As numerous taxa are known from a single specimen, this gives the false impression of endemic taxa and distinct faunas and provinces (see quote from Hallam, 1994 above).

The titanosaurid *Alamosaurus sanjuanensis* is generally considered the only large sauropod from the Maastrichtian of North America (Lehman, 1981; Lucas et al., 1987; Lucas and Hunt, 1989; Lucas and Sullivan, 2000; Fowler and Sullivan, 2011; Jasinski et al., 2011). *Alamosaurus* fossils found outside of the San Juan Basin of northwestern New Mexico have been reported in Texas, Utah and Wyoming (Lucas and Sullivan, 2000), though recent efforts by the authors cannot confirm the Wyoming (Evanston Formation) occurrence. Apparently absent from North America during most of the Cenomanian-Campanian (the "sauropod hiatus" of Lucas and Hunt, 1989), various workers have suggested two possible routes by which these dinosaurs immigrated to North America during the Maastrichtian, from Asia or from South America (e.g., Lucas and Hunt, 1989; Upchurch, 1998; Wilson and Sereno, 1998; D'Emic et al., 2010; Fowler and Sullivan, 2011). Clearly, *Alamosaurus* was a mobile animal and shows no high degree of endemism, though its distribution in the Western Interior basin is apparently confined to inland, not coastal depositional systems, as first argued by Lucas (1981).

Other dinosaur groups need to be briefly considered. Ankylosaurids and pachycephalosaurids are well known from both Asia and North America. Both groups have strong intercontinental ties and similar Asian and North American taxa (Asian *Prenocephale* compared to North American *Sphaerotholus* [=*Prenocephale* (in part)]; North American *Nodocephalosaurus* compared to Asian *Saichania* and *Tarchia*) are well established (Sullivan, 1999, 2000; Arbour et al., 2014). But, because of the diachroneity of the strata in which these taxa occur, their distributions are not, or cannot be considered, truly endemic.

NONMARINE INVERTEBRATES (BIVALVES AND GASTROPODS)

The nonmarine invertebrate record in the Campanian-Maastrichtian of the Western Interior basin is very relevant to any identification of nonmarine provinces and endemism. These nonmarine invertebrates, primarily unionoidan bivalves and gastropods (prosobranchs and pulmonates), are present in many of the Campanian-Maastrichtian freshwater fossil assemblages in the Western Interior basin, with a published record that extends from southern Canada to northern Mexico (e.g., White, 1883a, b, 1905; Stanton, 1916; Russell, 1935, 1964, 1976; Yen, 1945, 1954; Tozer, 1956; Hartman, 1984, 1987; Lucas et al., 1995; Tapinala and Roberts, 2013). Based on the biology of extant representatives, these invertebrates can only disperse through connected riverine and lacustrine systems (cf. Good, 2004). Significantly, they show no obvious north-south division in the Western Interior basin. For example, most of the taxa described from the Campanian of northern

Sonora, Mexico, by Lucas et al. (1995) are also known from southern Alberta, Canada.

Clearly, as the literature cited above indicates, there are apparently endemic species of some of these Late Cretaceous nonmarine bivalves and gastropods in the Western Interior basin stratigraphic units. But, overall, no clear gradient or geographic pattern in diversity is apparent from their distribution. Furthermore, the widespread distribution of many Late Cretaceous nonmarine invertebrate taxa in the Western Interior basin implies interconnected fresh waterways in Laramidia from Canada to Mexico.

Ironically, nonmarine invertebrates are just the animals for which we would expect to see endemism and biogeographic separation, given their limited dispersal abilities, especially compared to most vertebrates. Instead, and certainly at the generic level, there is no clear pattern of separation into provinces of Late Cretaceous nonmarine bivalves and gastropods across the Western Interior basin, though there are some apparently endemic species known from different rock formations. A more detailed analysis of their distribution should be undertaken.

DISCUSSION

The case for north-south provinciality among Campanian-Maastrichtian vertebrates, especially dinosaurs, has been accepted by many vertebrate paleontologists for at least 30 years. However, as reviewed above, the case based on non-dinosaurian vertebrates is weak to nonexistent. Instead, identification of Campanian (and/or Maastrichtian) vertebrate provinciality in the Western Interior basin rests entirely on a few groups of dinosaurs, notably the chasmosaurine ceratopsids. Proposed high degrees of dinosaur endemism have also been linked primarily to chasmosaurine distribution.

Here, we present an analysis of the arguments for dinosaur provinciality reviewed above in the light of problems and biases in sampling; the lack of topographic barriers in the Western Interior basin to divide provinces; the lack of climatic or vegetational differences and/or gradients to provincialize vertebrates; how taxonomic decisions (particularly with regard to chasmosaurines) have been intimately involved in the perception of endemism and provinciality; how the demonstrable diachroneity of some fossil assemblages obviates including them in biogeographic analyses; and how the non-uniformitarian conclusions of those who argue for dinosaur provinciality and endemism undermine their own arguments.

Sampling

Uneven and incomplete sampling is a large problem in comparing Late Cretaceous vertebrate assemblages in the Western Interior basin. Lehman (1997) and Gates et al. (2010) discussed this issue, and both concluded that uneven sampling of the dinosaurs existed. However, according to Gates et al. (2010), it could be obviated by eliminating "under sampled" assemblages from their analyses. Thus, Gates et al. (2010) variously eliminated or discounted the Two Medicine Formation and/or Aguja Formation assemblages in their analyses because they were less sampled than the other vertebrate assemblages being analyzed. Furthermore, Gates et al. (2010, p. 374) stated, as quoted above, that adding microvertebrate taxa to the samples they analyzed has a "dampening effect on macrofaunal biases." That may be true in terms of the statistical analysis of an entire faunal list, but it in no way obviates the biases inherent in under sampling of the macrofauna.

We view the sampling problems differently than did Lehman (1997) and Gates et al. (2010). Thus, we contend that the available data suggest that all of the Campanian-Maastrichtian vertebrate-bearing stratigraphic units in the Western Interior basin are under sampled. As an example, consider a plot of dinosaur species recognized from the Kaiparowits and the Fruitland/Kirtland formations over time (Fig. 5). These plots show a dramatic upturn in the number of dinosaur taxa during the last two decades, and no indication that the taxonomic diversity is approaching an asymptote. Any consideration of the history of dinosaur collecting in the Kaiparowits and Fruitland/Kirtland formations (Sullivan and Lucas, 2006; Titus and Loewen, 2013) indicates that this diversity has been driven by sampling and study effort, and it is likely that as we discover more species our knowledge of past diversity will increase. This may be even more true of the microvertebrate diversity than of the dinosaurs, because most vertebrate diversity in any ecosystem, past and present, is in the small vertebrates.

Indeed, if we look at vertebrate diversity in today's tropical environments, such as Peru and Angola, we find diversity on the order of 3000 vertebrate species (e.g., Leaché et al., 2006; Rodriguez and Young, 2016). The lists of taxa from six formations in the Campanian of the Western Interior basin compiled by Gates et al. (2010, appendix 1) identify 150-160 species of vertebrates from all of the units combined. The individual stratigraphic units have much less diversity documented by their fossil assemblages. Of course, it could be argued that the modern vertebrate diversity is not directly comparable to the Late Cretaceous vertebrate diversity. For example, about half the modern diversity is in bird species, and perhaps birds were less diverse during the Late Cretaceous. Nevertheless, the Western Interior vertebrate assemblages are at least 10 times less diverse than Modern vertebrate faunas from comparable environments. Clearly, vertebrate diversity in late Campanian units in the Western Interior basin is greatly under sampled.

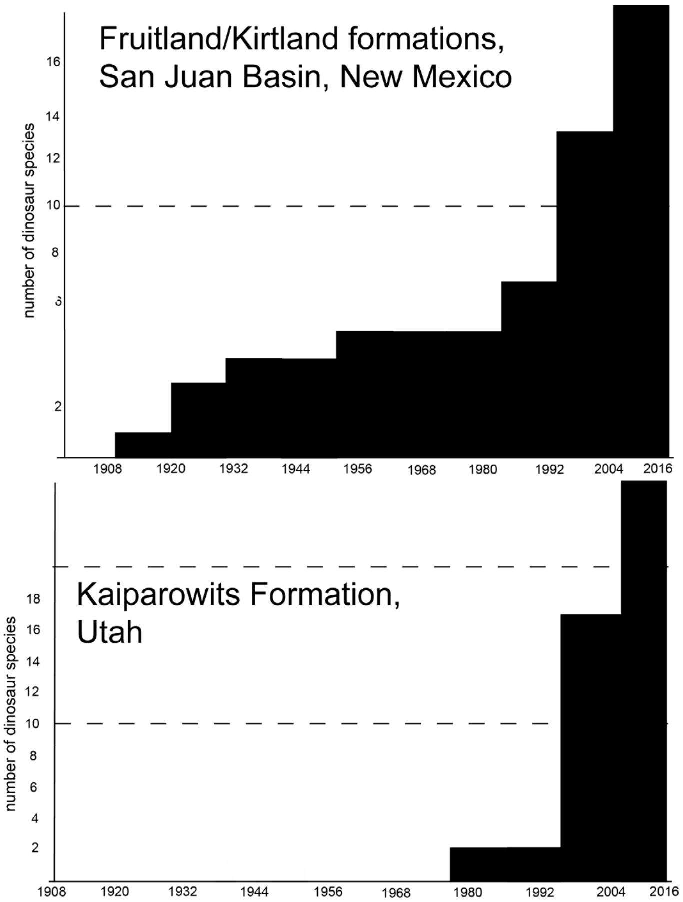

FIGURE 5. Histograms showing the number of dinosaur taxa recognized from the Kaiparowits and the Fruitland/Kirtland formations as a function of the dates of paleontological studies/publications.

Topographic Barriers

Topographic barriers, including mountain ranges, river systems and drainage divides, do impact the distributions of animals. However, not all taxa may experience similar effects on their distribution by a given topographic barrier. For example, fishes are often limited to a given drainage basin or set of drainage basins, but many dinosaurs could likely traverse such drainage basins with little difficulty. Alternatively, Cretaceous-Paleocene turtles suggested to have inhabited major river channels such as *Neurankylus* (Knell, 2012), may have had their distribution limited by the proximity of habitable channels.

Paleogeographic reconstructions of the Western Interior basin during Cenomanian-Maastrichtian time all agree in showing an essentially continuous north-south coastal plain from West Texas to Alberta lacking mountainous barriers to north-south dispersal (Fig. 6). With the onset of the Laramide orogeny, and the beginning of the last withdrawal of the Western Interior seaway, in Maastrichtian time there were small uplifts and localized depositional centers well west of the seaway, as well as a broader coastal plain, but still no evident topographic barriers to north-south dispersal (Fig. 6). Indeed, the Maastrichtian landscape of Laramidia is larger and more topographically diverse than the Campanian landscape.

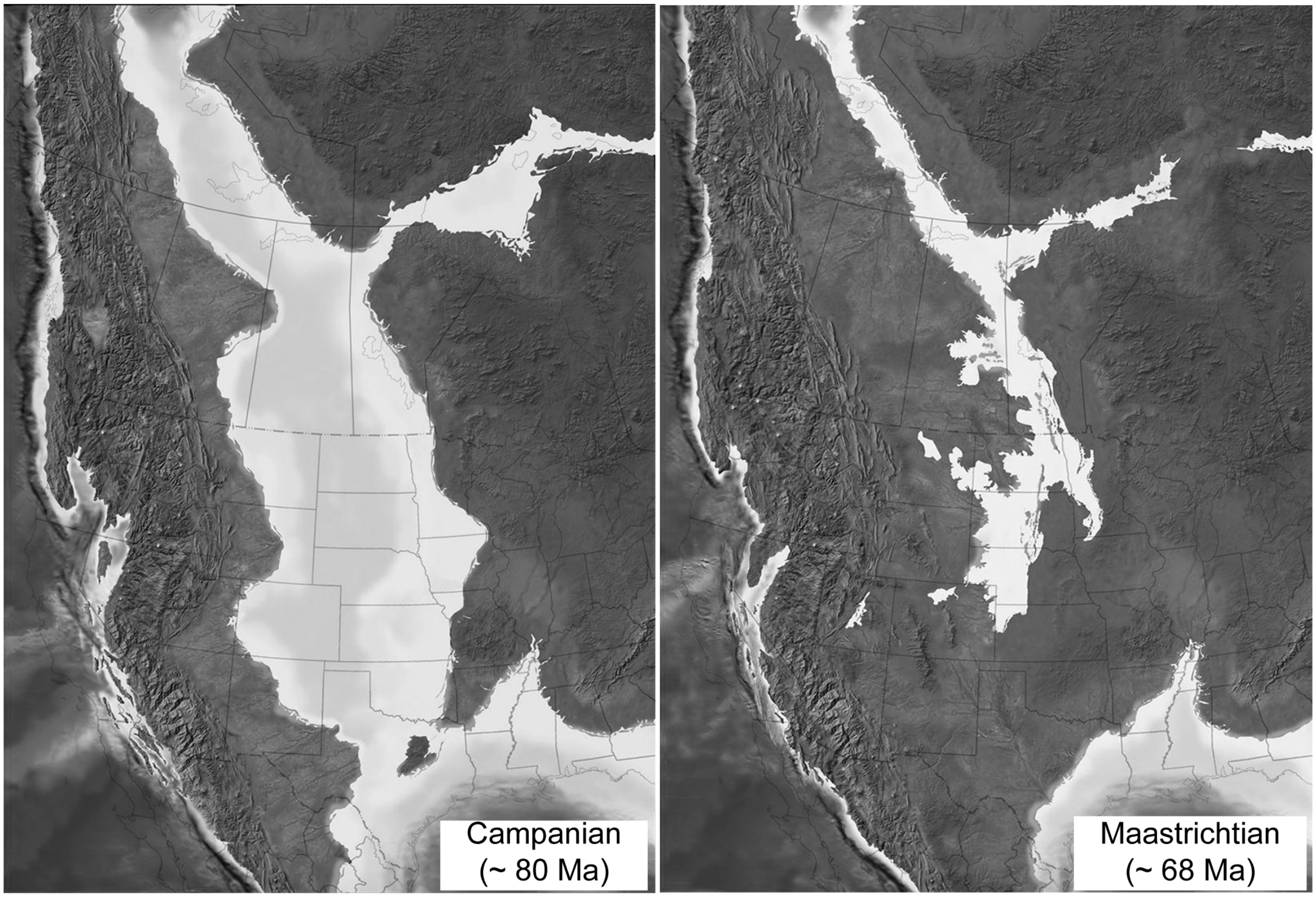

FIGURE 6. Paleogeographic maps of the Western Interior basin during the Campanian and the Maastrichtian (©2014 Ron Blakey, Colorado Plateau Geosystems Inc.).

Large river systems traversed parts of the Laramidian coastal plain, but there is no evidence that any of these rivers was large enough to provide a barrier to north-south dispersal, if that is even possible. For example, today's Amazon River is much larger than any Late Cretaceous river on Laramidia, yet the Amazon presents no substantial barrier to vertebrate dispersal (e.g., Cracraft, 1985; Costa et al., 2000; Souza, 2005; Pramuk, 2006; Hubert and Renno, 2006; Arzamendia and Giraudo, 2009). We conclude that there were no topographic barriers to north-south vertebrate dispersal in Laramidia during the Campanian-Maastrichtian that would have provincialized the vertebrate biota, particularly the large dinosaurs. Repeated claims of topographic barriers creating dinosaur provincialism in the Western Interior basin (e.g., Sampson, 2012; Loewen et al., 2013) are simply unsubstantiated.

It is also important to point out that the Laramide orogeny began during the Campanian, with various estimates of its onset, ranging from 75 to 80 Ma based on the age of synorogenic sediments (e.g., Lawton, 1994; Cather, 2004). The Western Interior basin had been created by the earlier Sevier orogeny. The first effect of the Laramide orogeny was to create broad, gently downwarped Campanian depositional basins (Lawton, 1994). Only during the Maastrichtian is there evidence of the beginning of localized deformation of the Laramide foreland to form small uplifts and smaller depocenters (Fig. 6). However, even into Paleocene time, the Laramide depositional basins remained relatively large until a surge in the orogeny during the Eocene wrench faulted the foreland (e. g., Chapin and Cather, 1981; Dickinson et al., 1988; Cather, 2004).

Despite this, Laramide mountain building has been invoked as a factor that affected the diversification and provinciality of dinosaurs during the Campanian in the Western Interior basin. Thus, Gates et al. (2012) suggested that the onset of the Laramide orogeny triggered the diversification of dinosaurs in the Campanian of the Western Interior basin, which they refer to as "the Campanian biodiversity surge." Instead, the apparent diversification is little more than an artifact of the far denser record of vertebrates from the Campanian when compared to earlier intervals of the Late Cretaceous. Furthermore, Gates et al. (2012) embrace what we believe is a fundamental misunderstanding of the topographic effects of the Laramide orogeny as outlined above. Thus, there is no geological evidence for a substantial increase in topographic diversity during the Campanian in Laramidia due to the Laramide orogeny. This increase in topographic diversity took place during the Maastrichtian, yet in the Western Interior basin dinosaur diversity drops from the Campanian to the Maastrichtian.

Indeed, because the inferred timing of the orogeny does not exactly match the timing of the proposed "diversity surge," Gates et al. (2010) even argued that the estimate of the onset of Laramide deformation should be revised downward from 74.5 (the age they chose based on geological evidence) to 78.5 Ma (based on the inferred diversification). However, as Longrich (2014) noted, this is questionable reasoning—hypothesize that the orogeny drove diversification, then change the duration of the orogeny to match the duration of the diversification.

Some recent arguments for dinosaur provinciality on Laramidia have been tied to the supposition of a relatively small Laramidian land area that was periodically isolated (e.g., Sampson and Loewen, 2010; Loewen et al., 2013). However, for example, in positing the isolation of Laramidia ("long interval of Laramidian isolation"), Loewen et al. (2013, p. 1) ignore the fact that dinosaur distributions indicate a relatively long term connection of Laramidia to Asia, and intermittent Campanian-Maastrichtian connections to South America. Thus, as Longrich (2014) among many others have noted, dinosaurs (including a long list of theropods, ceratopsids, pachycephalosaurids, ankylosaurids and hadrosaurids) were clearly migrating back and forth from Asia to Laramidia during the Campanian-Maastrichtian.

Climate

The climate of the Late Cretaceous of the Western Interior basin has long been identified as equable with a much more limited latitudinal gradient than the climate of the same region today (e.g., Wolfe and Upchurch, 1987; Amiot et al., 2004; Upchurch et al., 2015). Thus, it has been estimated that the latitudinal gradient during the Late Cretaceous was ~0.4˚C/ 1˚ latitude rather than the 0.8-1.0˚C/ 1˚ latitude of central North America today (Upchurch et al., 2015). This agrees with estimates based on oxygen isotopes from terrestrial vertebrate fossils in the Western Interior basin (Amiot et al., 2004). A climate-based divide between provinces is also argued against by the climate inferences of Wolfe and Upchurch (1987) based on analysis of the megaflora, which indicate a Late Cretaceous megathermal (tropical) climate extending to a paleolatitude of 45-50˚N or 55-60˚N, present-day latitude. This is well north of any of the dinosaur assemblages invoked in ideas about provinciality, which are all within this megathermal zone.

This Late Cretaceous climate gradient is also similar to the climate gradient that has been estimated for the Eocene of North America, and is further suggested to resemble the climate of present-day Southern Hemisphere mid-latitudes (Greenwood and Wing, 1995). The Eocene of western North America shows no evidence of north-south provinciality of the mammal-dominated faunas. This raises the question, why would a greater provinciality prevail during the Late Cretaceous with similar latitudinal temperature gradients? Furthermore, the Cretaceous and Eocene gradients are substantially lower than today's temperature gradients in the same region, where, again, a north-south provinciality is lacking.

Climate is often the *deus ex machina* of paleontological studies aimed at explaining fossil distribution. Thus, when no other factor can be identified to explain a fossil distribution, some vague idea of climate variation is often invoked. We believe that this is exactly what some authors (Lehman, 1987, 1997; Sampson et al., 2010; Gates et al., 2010) have done—i.e., speculated on an unknown Late Cretaceous temperature gradient in the Western Interior basin as a cause of north-south dinosaur provinciality. Actual data on the climate, as stated above, do not support their speculations. Indeed, it would seem that the low Late Cretaceous temperature gradient would have the opposite effect of what various authors have claimed, and not cause latitudinal zonation of the terrestrial biota based on temperature.

Vegetation

Plants track climate, and floral provinces or other floral heterogeneity have been suggested as a possible driving mechanism for dinosaur provinciality in the Western Interior basin. Indeed, Lehman (1997) suggested that Late Cretaceous palynological provinces (southern *Normapolles* and northern *Aquillapollenites* provinces) closely align with his proposed zonation of dinosaur faunas. However, Batten (1984), cited by Lehman (1997) as the primary source of these palynological provinces, placed the geographic boundary between the *Aquilapollinites* and *Normapolles* pollen provinces in the vicinity of the U.S.-Canadian border rather than at the latitude of northern Colorado, where Lehman drew the boundary between his proposed dinosaur provinces. Furthermore, Batten's (1984) ideas on Late Cretaceous palynofloral provinciality in the Western Interior basin have been greatly revised.

Thus, more recent work has indicated that all of the Campanian palynofloras in the Western Interior basin, from Alberta to New Mexico, belong to the *Aquillapollenites* province. As Braman and Koppelhus (2005, p. 117) observed, the *Aquillapollenites* province "stretched from at least northern New Mexico northward to the Arctic islands and includes Alaska…." They go on to state that among the pollen assemblages of the *Aquillapollenites* province "similarities are numerous" (p. 121). This is why a geographically far-reaching biostratigraphic zonation of palynomorphs of the Western Interior Basin by Nichols (1994; also see Nichols and Sweet, 1993) works.

Campanian-Maastrichtian megafossil plants are not provincialized in the Western Interior basin over the transect West Texas-Alberta (e.g., Upchurch and Wolfe, 1993; Wolfe and Upchurch, 1997; Miller et al., 2013). Therefore, no case for plant provinciality, based on the megaflora or the palynomorphs can be made in that portion of the Western Interior basin. No doubt there were local differences in vegetation on the Campanian-Maastrichtian landscape of the Western Interior basin. However, these differences do not define floristic provinces or identify a significant latitudinal gradient in the Late Cretaceous floras from Texas to Alberta. Speculation on local variation in the floras (Sampson, 2012) lacks any basis in data.

Nevertheless, as G. Upchurch (written commun., 2016) points out, in the Late Cretaceous Western Interior basin, the plant fossils, climatically sensitive sediments and climate modeling do indicate some habitat heterogeneity that undoubtedly would have influenced the distribution of vertebrates, perhaps including dinosaurs. This is best understood for the Maastrichtian, during which three climate zones have been identified in western North America: (1) a southern evaporite zone, outside of the Western Interior basin, (2) a mid-latitude warm and humid belt, and (3) a high latitude temperate and humid belt (e. g., Nichols et al., 1990; Upchurch and Wolfe, 1993; Chumakov et al., 1995; Upchurch et al., 1999; Hay and Floegel, 2012). The boundary between the mid-latitude humid belt and high latitude temperate belt is in southern Canada. Within the zone of subtropical to paratropical vegetation, which is the mid-latitude warm and humid belt, and encompasses the area from West Texas to southern Alberta, some Campanian and Maastrichtian latitudinal differentiation of plants based on macrofossils is apparent (Upchurch and Wolfe, 1993).

Ideas about dinosaur biogeography have been confined to this vegetational zone, so whatever gradient there may have been in plant diversity could have affected vertebrate distribution within that zone. Nevertheless, the lack of distinct biogeographic separation among the vertebrates suggests that the plant gradient was not a factor significant enough to provincialize vertebrate distribution in that zone.

G. Upchurch (written commun., 2016) also notes that there is evidence of a late Campanian to Maastrichtian coastal-to-interior gradient among the plants. This is documented by the distribution of coals, calcretes and other "dry" paleosols, and a coastal-to-interior gradient in wood floras that has been attributed to aridity and water table depth (e. g., Upchurch et al. 1999; Wheeler and Lehman 2005; Estrada-Ruiz et al., 2012). For the Campanian, modelling of climate and vegetation indicates a coastal-to-interior gradient of vegetation in the northern Western Interior, with coastal shrublands and interior forests (DeConto et al., 1999). However, a clear correlation between such coast-to-interior gradients and vertebrate distribution remains to be demonstrated.

So, we predict that there may be a biogeographic separation of the Campanian Alaskan dinosaurs and other vertebrates from those found in the Alberta-West Texas portion of the Western Interior basin, though the vertebrate record from Alaska is not yet extensive enough to evaluate this possibility. However, not surprisingly, we cannot recognize a distinctive biogeographic separation of vertebrates between West Texas and southern Alberta, which is within one major temperature zone and one fairly uniform paleoflora.

Taxonomy

Taxonomic decisions are primary in the discussion of biogeographic provinces and endemism, because it is geographic differences at the taxonomic level that identify biogeographic regions. This is most simply revealed by considering the dramatic changes in the alpha (genus- and species-level) taxonomy of chasmosaurine ceratopsids during the last decade (Table 2).

A decade ago, *Chasmosaurus* was recognized from Alberta to Texas. However, since that time, various species of *Chasmosaurus* have been removed from the genus and assigned to new genera: *Agujaceratops* of Lucas et al. (2006c) and *Vagaceratops* of Sampson et al. (2010). New genera of chasmosaurines have been named: *Kosmoceratops* and *Utahceratops* of Sampson et al. (2010), *Mojoceratops* of Longrich (2010a) and *Titanoceratops* of Longrich (2010b). Furthermore, Longrich (2014) recently reported *Kosmoceratops* and *Pentaceratops* from Alberta, though Campbell et al. (2016) argue that *Kosmoceratops* is not present in Alberta, and also conclude that *Mojoceratops* is a synonym of *Chasmosaurus*. In contrast, Longrich (2015) synonymizes *Vagaceratops* with *Chasmosaurus*. Wick and Lehman (2013) and Sullivan and Lucas (2015) do not regard *Titanoceratops* as distinct from *Pentaceratops*. Longrich (2010b) also stated that Maastrichtian *Ojoceratops* of Sullivan and Lucas (2010) is a synonym of *Triceratops*, which would place that genus as far south as New Mexico. However, Jasinski et al. (2011) argued that *Ojoceratops* is distinct, a position we reiterate here.

Our purpose here is not to resolve disagreements over chasmosaurine taxonomy or identifications. However, it is important to realize that the taxonomy of chasmosaurines has evolved rapidly during the last decade, recognizing many new taxa, most of which are only known at present from one lithostratigraphic unit (Table 2). This gives the appearance of great endemism among chasmosaurines according

TABLE 2. Recent, differing alpha taxonomies of chasmosaurine ceratopsids. CMN= Canadian Museum of Nature.

Original Taxon	**other referrals**	**Longrich (2015)**	**Campbell et al. (2015)**	**this paper**
Monoclonius belli Lambe 1902	*Ceratops belli* Hatcher, 1907	*Chasmosaurus belli*	*Chasmosaurus belli*	*Chasmosaurus belli*
	Protorosaurus belli Lambe, 1914		*Chasmosaurus belli*	
	Chasmosaurus belli Lambe, 1914		*Chasmosaurus belli*	
Monoclonius canadensis Lambe 1902	*Ceratops canadensis* (Hatcher et al., 1907)		*Chasmosaurus* sp.	
	Eoceratops canadensis (Lambe, 1915)		*Chasmosaurus* sp.	
	Chasmosaurus canadensis (Lehman, 1990)	cf. *Mojoceratops*	*Chasmosaurus sp.*	*Chasmosaurus* sp.
Chasmosaurus brevirostris Lull, 1933			*Chasmosaurus* sp.	
Chasmosaurus kaiseni Brown, 1933	*Chasmosaurus canadensis* (Lehman, 1989)	cf. *Mojoceratops*	*Chasmosaurus* sp.	*Chasmosaurus* sp.
	cf. *Mojoceratops* (Longrich, 2010)		*Chasmosaurus* sp.	
Chasmosaurus russelli Sternberg, 1940		*Chasmosaurus belli*	*Chasmosaurus russelli*	*Utahceratops russelli* Fowler (in press)
Chasmosaurus irvinensis Holmes et al., 2001	*Vagaceratops invinensis* Sampson et al. 2010	*Chasmosaurus irvinensis*	*Vagaceratops irvinensis*	
Chasmosaurus mariscalensis Lehman, 1989	*Agujaceratops mariscalensis* Lucas et al. 2006	*Agujaceratops mariscalensis*	*Agujaceratops mariscalensis*	*Agujaceratops mariscalensis*
Kosmoceratops richardsoni Sampson et al. 2010				
Mojoceratops perifania Longrich 2010	*Chasmosaurus russelli* (Maidment and Barrett, 2011)		*Chasmosaurus russelli*	*Chasmosaurus russelli*
CMN 2280	*Chasmosaurus russelli* (Godfrey and Holmes, 1995)		*Chasmosaurus russelli*	
CNM 8801	*Kosmoceratops* sp. (Longrich, 2014)		*Chasmosaurus* sp.	*Chasmosaurus* sp.
Pentaceratops aquilonius Longrich 2014				Chasmosaurine indet.

to Sampson et al. (2010), though Longrich (2014), with different taxonomy and identifications, sees a broader distribution of some chasmosaurine taxa, one that certainly does not support recognition of two biogeographic provinces in the Western Interior basin.

As an example of how important this unresolved taxonomic discussion is, consider Longrich's (2014) identification of *Pentaceratops* in Canada, a tremendous range extension of the genus. This is of "*P. aquilonius*" from the Dinosaur Park Formation, which would not only be the northernmost record of the genus, but also its oldest record. In contrast to Longrich (2014), we conclude that "*P. aquilonius*" is not referable to *Pentaceratops*. The holotype is a fragmentary corner of the right side of the frill consisting of the distal portion of the right squamosal with four episquamosals (1-4) and the right lateral portion of the parietal bearing two epiparietals (2- 3). The parietal bar is much broader distally than that of *P. sternbergi* based on comparison to the holotype. The paratype of "*P. aquilonius*" consists of three parietal fragments, one consisting of two epiparietals, putatively the right (conjoined) epiparietals 1 and 2, and the isolated left epiparietals 1 and 2. This paratype is less informative than the holotype and undiagnostic. "*P. aquilonius*" thus is a *nomen dubium,* and we assign its type material to Chasmosaurinae indeterminate. This viewpoint echoes that of Mallon et al. (2016) who also consider it to be a *nomen dubium*.

The current alpha taxonomy of chasmosaurines (and of many dinosaurs) is cladotaxonomy, in which virtually all morophological variation is deemed to be of phylogenetic significance and therefore is used to create taxa. Concepts of epigenetic variation are ignored. Those creating such chasmosaurine cladotaxonomy would do well to recall Ostrom and Wellnhofer (1986), who drew attention to the range of cranial variation in a single extant African bovid species, arguing that it is comparable to all of the variation seen in the skulls of the many named species of *Triceratops* (though note that subsequent work has identified more than one species of *Triceratops*, e.g., Scannella et al., 2014). We redraw this comparison (Fig. 7) by illustrating the variable skull morphology of what Grubb (1972) regarded as a single species (divided into subspecies) of the African Buffalo. These animals live in sub-Saharan Africa over an area of about 7 million square miles, which is two to three times the size of Laramidia. If this much variation over so large an area resolves into one species, why should comparable variation in chasmosaurines over a much smaller area resolve into several genera?

We note that the chasmosaurines in question represent a two-million-year-long time interval, so they are not a single, contemporaneous population, as are the African Buffalo. Nevertheless, morphological variation is not entirely of phylogenetic/taxonomic significance, and variation in extant species often provides a way to gauge the amount of variation that may have been present in extinct populations. Indeed, we would ask whether chasmosaurine cladotaxa have a sound basis in Neo-Darwinian concepts of population variation, and, if not, how can they be used to analyze provinciality and endemism?

Regardless of how chasmosaurine taxonomy is done, and regardless of how disagreements over chasmosaurine taxonomy are resolved, only a few taxa are being discussed, and some of the apparent endemics are not coeval (see below). Therefore, to posit dinosaur provinces and high degrees of endemism on the shifting sands of the cladotaxonomy of a few chasmosaurines, some of which are demonstrably diachronous, is unjustified.

Diachroneity

The issue of the comparison of diachronous dinosaur assemblages in the biogeography of the Western Interior Late Cretaceous has been discussed before (Sullivan and Lucas, 2006; Jasinski et al., 2015). In short, comparing dinosaur taxa from assemblages of different ages to then claim that the differences between them are biogeographic in nature cannot be supported.

To address this issue, Gates et al. (2010) suggested that a two-million-year-long time bin is adequate temporal resolution, claiming

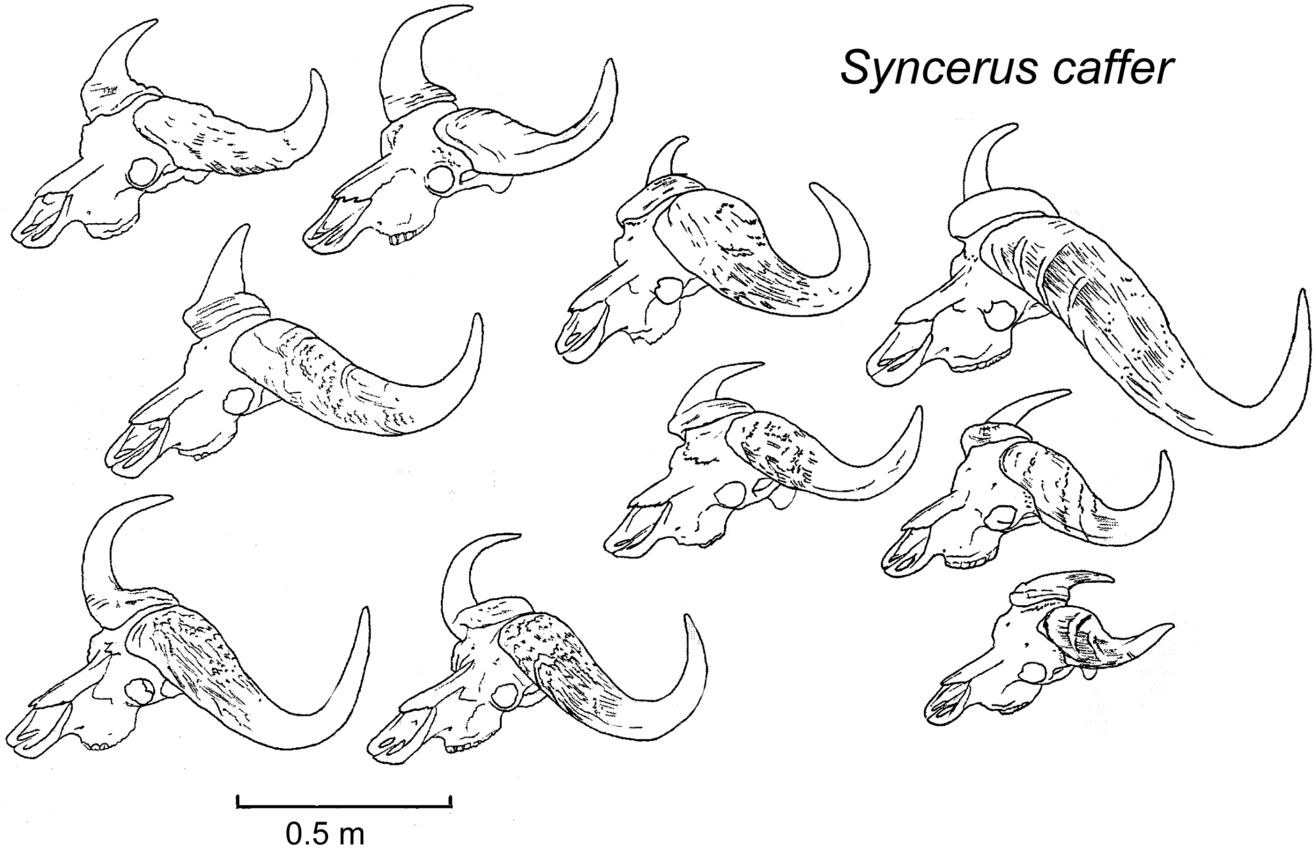

FIGURE 7. Skulls of the African Buffalo *Syncerus caffer* from sub-Sharan Africa showing some of the range of cranial variation in this species (modified from Grubb, 1972).

that in their analysis the differences due to time were statistically insignificant. However, as Kauffman (1984) noted, many shifts in biotic distribution occur on very short timescales geologically speaking, most within the Milankovitch spectrum of 100 kyr or less. Furthermore, two million years is a tremendous amount of both ecological and evolutionary time, during which many species would normally arise and become extinct. Therefore, if we compare Campanian dinosaur taxa from different assemblages in the Western Interior basin with only two-million-year resolution, how can we say the differences between taxa are not underlain by evolutionary changes in the assemblages and or ecological shifts over much shorter time intervals? Indeed, Mallon et al. (2012) well demonstrate how much evolutionary change took place among some dinosaur lineages during two million years or less of Late Cretaceous time. Two million years is thus not sufficient temporal resolution to argue that there were contemporaneous provinces.

As another way of looking at this issue, let us consider the approximately two-million- year-long timespan of the Plio-Pleistocene Blancan land-mammal "age" and its extensive vertebrate fossil assemblages in New Mexico (Morgan and Harris, 2015). In this two-million-year interval, numerous changes took place due to evolution, particularly at the species level. For this reason, early and late Blancan, mammal-dominated assemblages in New Mexico differ substantially in taxonomic composition. Indeed, if the early and late Blancan assemblages in New Mexico were found in Alberta and New Mexico, rather than both in New Mexico, one could easily hypothesize that they are so different that they represent two biogeographic provinces.

As an example at the taxonomic level of the largest mammal in these assemblages, the early Blancan proboscidean *Stegomastodon primitivus* and the late Blancan *S. mirificus* are temporally successive species, likely ancestor and descendant in an anagenetic lineage (Lucas et al., 2011). Again, if found in Alberta and New Mexico using only two-million-year temporal resolution, they could be viewed as endemic species in different provinces, much as Sampson et al. (2010) would have us view some of the "endemic" Campanian chasmosaurines. This again confirms that two million years provides too coarse of temporal resolution to resolve whether differences between taxa in different areas are evolutionary or biogeographic in origin.

The current discussion of Campanian dinosaur provinciality has focused on six dinosaur-dominated vertebrate fossil assemblages: Dinosaur Park Formation in southern Alberta, Judith River Formation in central Montana, Two Medicine Formation in northwestern Montana, Kaiparowits Formation in southern Utah, Fruitland/Kirtland formations in northwestern New Mexico and Aguja Formation in West Texas (Fig. 8). Roberts et al. (2005, 2013) provided a compilation of the radioisotopic ages (Ar/Ar ages of airfall ash beds, except in Texas, where the ages are U/Pb ages of magmatic crystals) in these units, though their most recent compilation inconsistently corrects these ages based on a new age of the standard, Fish Canyon sanidine (D. Fowler, personal commun., 2016). Inconsistencies aside, the late Judithian ages of dinosaurs from the Dinosaur Park, Judith River, Two Medicine and Kaiparowits formations has long been clear—all are older than about 75 Ma, and encompass assemblages at least as old as 76 Ma (Fig. 8). The Fruitland/Kirtland assemblage is younger, Kirtlandian, definitely younger than 75 Ma, and probably closer to 74 Ma. Thus, claiming synchroneity of the Fruitland/Kirtland dinosaurs and the Judithian assemblages from Utah, Montana and Alberta is to equate assemblages that are separated in time by one to two million years. As discussed above, this cannot produce meaningful comparisons for biogeographic analysis.

Eberth (2015), in his review of the dinosaur bonebeds in the Cretaceous of Alberta, placed the top of the Dinosaur Park Formation at 75.0-75.2 Ma and the bottom at 76.4-75.9 Ma. Gates et al. (2010) incorrectly placed the top of the Dinosaur Park Formation at 74.2 Ma (see also Sullivan and Lucas, 2006, 2014). In New Mexico, the DEP ash, near the base of the Fruitland Formation (Neh-nah-ne-zad Member), has been dated at 75.56 ± 0.41 Ma (Fassett and Steiner, 1997), which is well below, and thus older than the fossiliferous Fossil Forest Member of the Fruitland Formation, which yields the older part of the characteristic Kirtlandian LVA vertebrate fossil assemblage. The "principal fossil bearing intervals" indicated for the Kaiparowits Formation (see Roberts et al., 2013, fig. 6.3) are no younger than 75 Ma, thus they are older than, and not coeval with, the fossil assemblages that define the Kirtlandian LVA of Sullivan and Lucas (2003, 2006). Moreover, the Judithian ends at 75 Ma, and there was long a hiatus of 2.3-3 Ma between the Judithian and “Edmontonian,” which is largely occupied by Kirtlandian time and largely coincides with the marine transgression of the Bearpaw Formation in south-central Alberta (Sullivan and Lucas, 2003, 2006). The Kirtlandian is not a “sub-age” of either the Judithian or Edmontonian, as these two LVAs have long been known not to be temporally successive (Russell, 1964, 1975).

Furthermore, a very precise point can be made about the correlation of the chasmosaurines named from Utah and Alberta by Sampson et al. (2010). The type material of *Kosmoceratops richardsoni* and *Utahceratops gettyi* from Utah are from the lower middle unit and upper lower unit of the Kaiparowits Formation, very close to 76 Ma based on the isotopic ages (Roberts et al., 2013, fig. 6.3). The holotype of *Vagaceratops irvinensis*, in contrast, is near the very top of the Dinosaur Park Formation, very close to a radioisotopic age of 75 Ma. Thus, *Vagaceratops* is not contemporaneous with *Kosmoceratops* and *Utahceratops*, and all are older than *Pentaceratops* from New Mexico, despite the statements to the contrary by Sampson et al. (2010).

Sullivan and Lucas (2006) considered the fossil vertebrates of the upper shale member of the Aguja Formation to be of Kirtlandian age. The bulk of the Aguja Formation vertebrate fossil assemblage comes from this unit. In contrast, Sankey and Gose (2001) considered the upper shale mammals to be Judithian, although they correlated their magnetostratigraphy to chron 32, which implies a Kirtlandian to Edmontonian age. Most recently, Lehman and Wick (2012) endorse an early Judithian age of the vertebrate assemblage of the upper shale member, attaching it to a radioisotopic age of ~ 76 Ma (Befus et al., 2008). If we accept that age assignment (Fig. 7), the Aguja vertebrate fossil assemblage either barely temporally overlaps and/or is older than any of the assemblages to which Gates et al. (2010) compared it, so diachroneity may explain any differences between it and those assemblages (Fig. 8).

The point is that the diachroneity of some of the Campanian dinosaur assemblages (and taxa) being compared to identify provinces and endemism undermines attributing any differences to biogeography. Further work refining the ages of Upper Cretaceous fossil-bearing strata in the Western Interior basin is important, but the higher degrees of resolution often lead to the recognition of more diachroneity and temporal distinction between important strata. Nevertheless, while this makes direct comparisons between these strata difficult, it allows for more accurate interpretations. Any possible comparisons and interpretations made between Upper Cretaceous fossil-bearing strata in the Western Interior basin must take potential diachroneity under consideration.

TABLE 3. Estimates of home range sizes (in square miles) of a two ton dinosaur using different methods (see text for discussion).

method	2 ton dinosaur home range	2 ton carrying capacity*
Harestad and Bunnel (1979)	21	142,857
Turner et al. (1969)	64	46,875
Theoretical metabolic scaling	10	300,000

*Based on a 3 million square mile Laramidia.

Non-uniformitarian Outcomes

The proposals of Campanian and/or Maastrichtian dinosaur provinciality in the Western Interior basin produce a remarkably non-uniformitarian result, namely that large dinosaurs (animals weighing well over a ton, such as the chasmosaurines) must have had small home ranges and a level of endemism much less than that of living large mammals. Lehman (1997) discussed this at length, even quantifying the projected differences in home ranges and advocated dinosaur endemism on this scale as a unique aspect of their biology (but see Wick and Lehman, 2013, for what amounts to a retraction of this idea). Vavrek and Larsson (2010), as quoted above, rejected this non-uniformitarian result out of hand. However, more recent advocates of dinosaur provinciality (e.g., Sampson, 2012) accept this non-uniformitarian result, though they are clearly perplexed by the underlying cause(s).

It has long been known that the home range of a terrestrial vertebrate is closely correlated to body size (e.g., Turner et al., 1969; Harested and Bunnel, 1979). We estimated the home range of a two-ton dinosaur using the equations of Harestad and Bunnel (1979) and Turner et al. (1969), which are based on extant mammals and lizards, respectively (Table 3). This suggests that, based on scaling from modern mammals, a home range of approximately 21 square miles would be expected for a two-ton ceratopsian. This is similar to estimates of extant elephant home ranges from Shannon et al. (2006), which are 20-30 square miles for lone individuals (orphans or bull elephants). Alternatively, scaling off of extant lizards, a home range of 64 square miles would be expected for a two-ton ceratopsian. In addition, a theoretical metabolic scaling of home range size mentioned in both of these papers was calculated for the two-ton dinosaur, resulting in a home range of 10 square miles. From these home ranges, carrying capacity (number of animals that can be supported in a given area) was calculated for an approximately three million square mile Laramidia by the method of Ryan and Jamieson

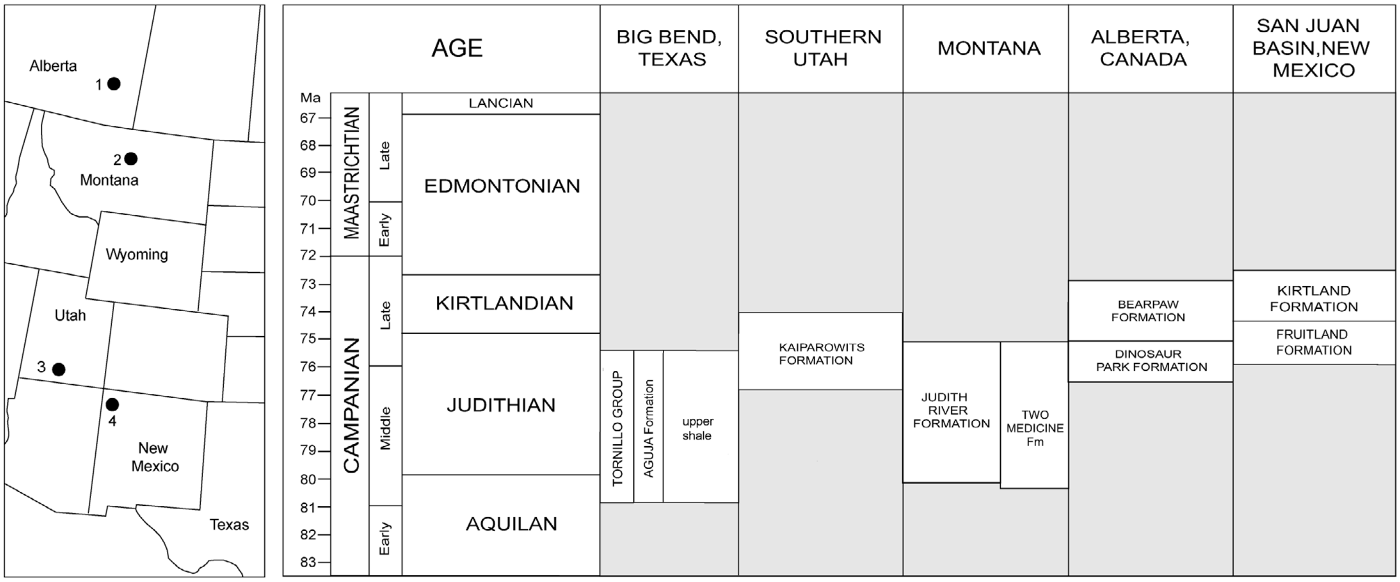

FIGURE 8. Map and correlation chart. Map shows location of main vertebrate-fossil assemblages discussed in the text and correlated in the chart. Assemblages are: 1 = Dinosaur Park Formation, Alberta; 2 = Two Medicine and Judith River Formations, Montana; 3 = Kaiparowits Formation, Utah; 4 = Fruitland and Kirtland formations, New Mexico; and 5 = Aguja Formation, Texas. Chart correlates the Campanian dinosaur assemblages being considered in recent analyses of dinosaur biogeography in the Western Interior basin.

(1998) (Table 3).

These inferences suggest that even the most conservative estimates (those based on metabolic scaling) limit the carrying capacity of the Western Interior basin to just a few hundred thousand individual, two-ton dinosaurs. This is a small population relative to pre-industrial populations of modern large animals such as elephants, which numbered 3-5 million in sub-Saharan Africa (an area of about 7 million square miles) at the beginning of the 20th century. This is problematic for ideas of endemism of large bodied dinosaurs, because it is an estimate of too few dinosaurs living on Laramidia. For example, the 7500 square mile San Juan Basin would only support ~350 two ton dinosaurs with the home range suggested by the method of Harested and Bunnel (1979). If the ceratopsians were endemic to the San Juan Basin, this is too few individuals to maintain a viable species population by modern population biology standards. Alternatively, scaling by extant lizards (Turner et al., 1969) would suggest only ~120 two-ton dinosaurs in the San Juan Basin. An animal the size of a chasmosaurine would necessarily need to inhabit a large geographic range, as do today's African elephants inhabiting most of Africa.

Uniformitarian outcomes should be the null hypotheses of paleobiogeographic analyses. The non-uniformitarian outcomes embraced by those who posit Late Cretaceous dinosaur provinciality and endemism in the Western Interior basin thus undermine their conclusions.

WHY POSIT PROVINCIALITY AND ENDEMISM?

Given the issues just discussed, the logical conclusion is that there should be no evidence of provinciality or unusual endemism among the dinosaur assemblages in the Western Interior basin or that the fossil record of these assemblages is inadequate to identify such provinciality, if it existed. That is our conclusion based both on the principles/factors discussed above and a review of the Western Interior basin record, as analyzed by various authors.

Indeed, why would animals as large as most of the Campanian-Maastrichtian dinosaurs be provincialized over as small an area as the coastal plain of eastern Laramidia between West Texas and southern Alberta in a megathermal climate with no known physical barriers to separate provinces? The proposed Late Cretaceous terrestrial vertebrate provinciality and endemism in the Western Interior basin also creates some non-uniformitarian problems, particularly indicating that the large dinosaurs had smaller geographic ranges than living tetrapods of comparable (and even much smaller) sizes. Furthermore, the inability to identify a barrier—topographic, climatic or otherwise—makes it impossible to understand what created the hypothesized provinces.

Without doubt there was some true endemism among Western Interior Late Cretaceous dinosaurs that cannot be accounted for by sampling biases, taxonomy or diachroneity. True endemism exists today within biogeographic provinces, driven by local barriers or biological interactions, such as competition or dietary specialization. Indeed, Longrich (2014, p. 306) discussed such dinosaur endemism, concluding that it, at least in part, may have been due to competition: "competitive interactions may be a driver of dinosaur endemism."

CONCLUSIONS

This critical review demonstrates not only the biological and geological implausibility of faunal provinces and true endemism of dinosaurs in the Western Interior basin from Texas to Alberta during the Campanian-Maastricthian, but the questionable nature of the arguments and analyses that have been marshalled to recognize such concepts. We find no compelling evidence of provinciality or unusual endemism in the non-dinosaurian vertebrates or even in the dinosaurs, themselves. Nonmarine invertebrates (unionoidans and gastropods) also show no provinciality or unusual endemism. An accurate understanding of the topography, climate and vegetation of the Campanian-Maastrichtian Western Interior basin does not identify barriers or gradients between West Texas and Alberta that would have provincialized the dinosaurs or created unusual levels of dinosaur endemism. Indeed, many of the data used to support provinciality and endemism are confounded by sampling biases, taxonomy and diachroneity of the fossils being compared. Finding evidence to support the presence of Campanian-Maastrichtian faunal provinces and true endemic taxa in the Western Interior basin, if they exist, will require more fieldwork, coupled with conceptually and methodologically sound analyses of that evidence.

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