

Spatial niche partitioning in dinosaurs from the latest Cretaceous (Maastrichtian) of North America

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We examine patterns of occurrence of associated dinosaur specimens ($n = 343$) from the North American Upper Cretaceous Hell Creek Formation and equivalent beds, by comparing their relative abundance in sandstone and mudstone. Ceratopsians preferentially occur in mudstone, whereas hadrosaurs and the small ornithopod *Thescelosaurus* show a strong association with sandstone. By contrast, the giant carnivore *Tyrannosaurus rex* shows no preferred association with either lithology. These lithologies are used as an indicator of environment of deposition, with sandstone generally representing river environments, and finer grained sediments typically representing floodplain environments. Given these patterns of occurrence, we argue that spatial niche partitioning helped reduce competition for resources between the herbivorous dinosaurs. Within coastal lowlands ceratopsians preferred habitats farther away from rivers, whereas hadrosaurs and *Thescelosaurus* preferred habitats in close proximity to rivers, and *T. rex*, the ecosystem's sole large carnivore, inhabited both palaeoenvironments. Spatial partitioning of the environment helps explain how several species of large herbivorous dinosaurs coexisted. This study emphasizes that different lithologies can preserve dramatically dissimilar vertebrate assemblages, even when deposited in close proximity and within a narrow window of time. The lithology in which fossils are preserved should be recorded as these data can provide unique insights into the palaeoecology of the animals they preserve.

Keywords: palaeoenvironment; lithology; *Triceratops*; *Edmontosaurus*; *Tyrannosaurus*; niche partitioning

1. INTRODUCTION

The coexistence (i.e. residing in the same biome) of large herbivorous vertebrates is seen in both extant and extinct ecosystems. For example, mule deer, white-tailed deer, elk, pronghorn, moose and bison compete for resources in the Northern Great Plains temperate grasslands biome, while giraffes, elephants, hippopotami, and numerous bovids compete in the African savanna biome [1,2]. Similarly, several species of both ceratopsian and hadrosaurian dinosaurs coexisted in the coastal lowland biome of the Late Cretaceous of North America [3]. Their coexistence could be explained by the competitive exclusion principle [4]; i.e. potentially competing species can only coexist if they occupy different realized niches. Niche differentiation, which reduces competition for limited resources between species and allows for their coexistence, can be broken down into three components: spatial separation (including use of different habitats), temporal avoidance (e.g. nocturnal versus diurnal) and dietary differences [5–7]. Determining the role played by each of these factors is difficult with extinct organisms, but dietary niche partitioning is frequently invoked [8–10].

Finding robust evidence for either spatial separation or temporal avoidance on a small geographical or temporal

scale (i.e. same basin or temporally restricted formation) is difficult with the vertebrate fossil record. Spatial separation is often used to explain the coexistence of extinct taxa simply by inferring palaeoenvironments (i.e. highlands versus lowlands), often without corroborating evidence [11]. Spatial and temporal separation is more commonly used on a broader scale (i.e. continental) to explain the distribution of extinct taxa through time [12,13] or space [14]. However the role of spatial separation is difficult to establish without understanding the palaeobiology and/or palaeoecology of the extinct taxa. For example, dietary niche partitioning in extinct herbivores can be used to infer spatial separation only when their food plants are known to occupy distinct habitats [15].

Alternatively, studies of association between fossils and the lithologies in which they are preserved could provide a better means of inferring a taxon's palaeoenvironment, which then can be used to determine the degree of spatial separation within a restricted geographical area. Although collectors have long noticed associations between taxa and particular sediments, (e.g. [16]) there have been few attempts to quantify these patterns for fossil vertebrates. Those studies that have attempted to quantify this pattern in the Morrison [17] and Hell Creek formations [18] did not find a statistically significant association between lithology and preservation of dinosaurs. However, a relatively small number of Morrison dinosaurs were studied. Furthermore, the localities studied were largely quarries excavated in the early days

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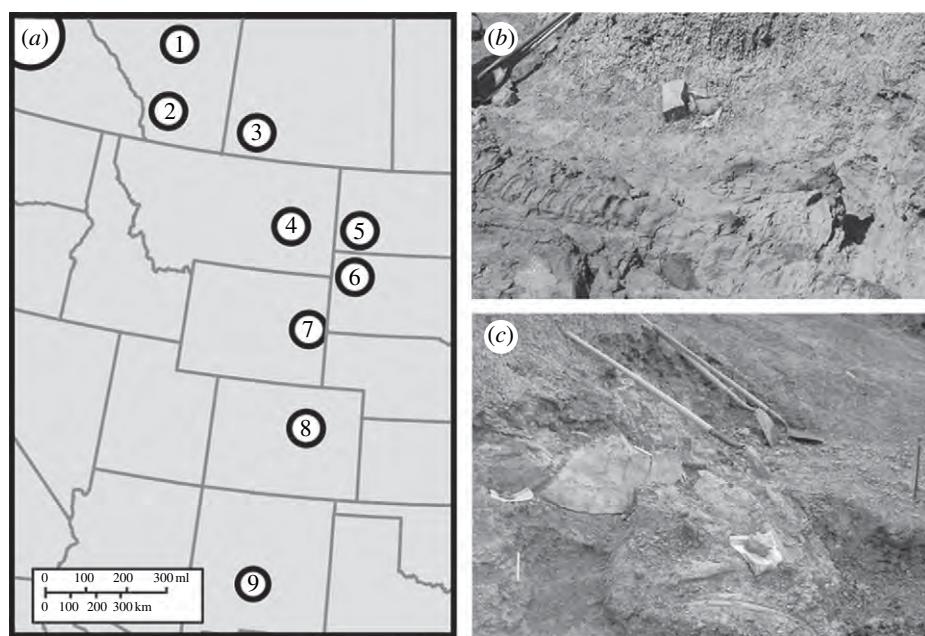


Figure 1. Map of localities and exemplar skeletons associated with lithology used in our analysis. (a) Localities where skeletons were collected ranged from southern Canada to the southern US: 1, Scollard Formation, Alberta, Canada; 2, Willow Creek Formation, Alberta, Canada; 3, Frenchman Formation, Saskatchewan, Canada; 4, Hell Creek Formation, MT, USA; 5, Hell Creek Formation, ND, USA; 6, Hell Creek Formation, SD, USA; 7, Lance Creek Formation, WY, USA; 8, Denver Formation, CO, USA; 9, McRae Formation, NM, USA. (b) Sandstone exemplar locality (MRF v08-AS) showing a partially articulated hadrosaur skeleton preserved in a poorly lithified sandstone. (c) Mudstone exemplar locality (NDGS 06-3.1) showing a disarticulated ceratopsian skull preserved in a mudstone.

of fossil collecting in the American West, and given the tendency for early collectors to focus collecting efforts on the best-preserved material, the sample may be biased (see below). White *et al.* [18] exhaustively prospected the Hell Creek Formation to examine the possibility of a relationship between dinosaur elements and fluvial architectural elements, but found no association between the two. Although this study rules out a collecting bias, the material examined consisted largely of isolated and dispersed bones and teeth. Isolated bones can easily be reworked, and the fact that a bone is isolated suggests that it has travelled from the skeleton and the site of death [19,20]. Finally, Lockley *et al.* [21] analysed the distribution of sauropod tracks and their palaeolatitude. They found an association between palaeolatitude and track sites and argued, based on the relationship between latitude and climatic environments, that this pattern reflects a lake margin habitat preference for sauropod dinosaurs.

Our study instead tests for the spatial separation of extinct vertebrates by analysing the relationship between lithology and associated (i.e. two or more bones from the same individual within 1 m of each other) dinosaur specimens. This study includes associated specimens from the Hell Creek Formation and coeval formations in North America. We focused on the latest Maastrichtian of North America because it is one of the most exhaustively sampled time intervals, having produced hundreds of associated skeletons. The Hell Creek Formation and its coeval formations (Frenchman, Lance, lower Scollard, Denver, Willow Creek and McRae) are fossil-rich packages of terrestrial sedimentary rocks that were formed as part of a prograding clastic wedge of sediment associated with the retreat of the Western Interior Seaway. The formations are exposed in the northern Great Plains

of the United States and Western Canada (figure 1). These formations contain similar sediments including unconsolidated sands, crevasse-splay sandstones, rooted siltstones, grey to brown mudstones, and carbonaceous shales, which represent medium-sized meandering and laterally accreting fluvial channel systems and associated floodplains. Nine lithofacies have generally been recognized which can be pooled into two more inclusive palaeoenvironments: channel and floodplain [18,22–28] (table 1). Mudstone is the dominant lithology for the four floodplain lithofacies and sand is the dominant lithology for the five channel lithofacies (table 1) [18,22,23,25,27,28]. While exceptions to this pattern exist (e.g. mud-filled channels and sand draped floodplains), lithology can generally be used to distinguish between floodplain and channel environments (table 1).

These palaeoenvironments supported a rich megafauna [29], which, in turn, supported a variety of large to medium-sized herbivorous dinosaurs, including at least two ceratopsids, two hadrosaurs, *Thescelosaurus neglectus* [30], *Ankylosaurus* [31], *Edmontonia* [32], *Leptoceratops* [33], ornithomimids, caenagnathids, [34], and three pachycephalosaurs. With so many herbivores coexisting within the channel–floodplain coastal landscape it is probable that they exhibited some degree of spatial niche partitioning, similar to that seen in extant megaherbivores living together in the same region [7]. While large-scale palaeobiogeographic patterns for hadrosaurs and ceratopsians exist [12,13,35] and dietary partitioning was present between the two groups [8,10,36–40], the fine-scale spatial relationships of these megaherbivores are unknown. Were these megaherbivores partitioning vegetation within the same palaeoenvironment, or were they living in different palaeoenvironments altogether (e.g. floodplain further

Table 1. Summary of facies identified in the study area and interpreted fluvial architectural elements and the dominant lithology [18,22–28].

facies description	architectural element	dominant grain size	pooled architectural elements
medium-grained, cross-stratified sandstone (SS)	channel	sand	channel
inclined, heterolithic strata in medium- to fine-grained SS	point bar	sand	channel
inclined, heterolithic strata in medium-grained, cross-stratified SS	toe-of-point bar	sand	channel
fine-grained, cross-stratified SS interbedded with mudstones (MS)	distal levee	sand (some mud)	channel
purple- and green-banded rooted MS	Crevasse splay floodplain palaeosol	sand mud	channel floodplain
planar-laminated siltstones and MS	floodplain pond	mud	floodplain
non-coalified organic accumulations	floodplain swamp	mud	floodplain
coalified organic accumulations	peat swamp	mud	floodplain

away from the river channels versus in or near the channels)? Although diet can be used to infer an organism's palaeoenvironment when distinct plant communities are recognized [15], too little is known about either the spatial distribution of the plants [29] or the diets of dinosaurs to use this approach.

We compiled information on all associated dinosaur specimens for which lithologic data were available (see electronic supplementary material, table S1). We focused on associated specimens for two reasons. First, the association between skeletal elements suggests that the specimens are not reworked from one depositional environment to another, because reworking destroys the association between elements that are not sutured or fused [41]. Second, post-mortem transport will tend to be less for associated specimens than for isolated elements, because dissociation of elements requires transport of elements from the site of death. ([41,42]; See §4 for caveats).

Critically, our study includes information from both older collections where specimens were selectively collected and recent collecting efforts, which generally represent exhaustive collecting; i.e. fieldwork that attempts to collect all diagnostic material, regardless of completeness, preservation, or lithology, to provide a more accurate picture of the palaeocommunity. This dataset therefore allowed us to test whether or not collections accumulated during the early 1900s are biased towards a certain lithology. Therefore, our study can provide a precise picture of how dinosaurs are distributed across the landscape.

2. MATERIAL AND METHODS

Data were obtained from 43 public institutions (see electronic supplementary material). For each associated specimen, the lithology, elements preserved, formation, and date when the specimen was collected were recorded (see electronic supplementary material, table S1). The lithology of the matrix was broken into two classes: mudstone (grain size = 0.00006–0.0624 mm in diameter) and sandstone (grain size = 0.0625–2 mm in diameter; [43]; table 1). In many cases the lithology was directly observed from matrix still adhering to the bones. In other cases, lithologic data

were obtained from the literature, or from the institutions' preparators, collections managers, or curators (see electronic supplementary material, table S1). Our dataset included 343 associated specimens, including 149 specimens from mudstone and 194 specimens from sandstone (see electronic supplementary material, table S1). Overall, more specimens have been collected from sandstone, with a 1.3 to 1 sandstone to mudstone ratio.

Only specimens where two or more bones from the same individual were found in close association (less than 1 m) were included in the analysis. The majority of specimens analysed (approx. 290; see electronic supplementary material, table S2) were much more complete with at least 10 bones present. We included (i) articulated specimens, (ii) disarticulated but associated skeletons, and (iii) associated but dispersed remains. Isolated elements showing no evidence of association were excluded [19]. A total of 343 associated specimens were analysed (see electronic supplementary material, table S1).

When possible, specimens were identified to species, but we analysed more inclusive clades (e.g. Ceratopsia, Hadrosauria, etc.) to include those specimens where species identification could not be determined, and to avoid taxonomic debate surrounding some of these dinosaurs (e.g. *Dracorex* versus *Stygimoloch* versus *Pachycephalosaurus*; [44]; see electronic supplementary material, table S1). However, with regard to the *Nanotyrannus* versus *Tyrannosaurus* debate, we follow Carr & Williamson [45] and assign all tyrannosaurids to *Tyrannosaurus rex*.

One-way χ^2 -tests were used to determine whether there is a statistically significant difference between the expected frequencies of occurrence for each taxon and lithology (i.e. each taxon is randomly distributed with respect to lithology) versus the observed frequencies of occurrence.

The first analysis compared the distribution with respect to lithology (sandstone versus mudstone) for each group of dinosaurs. A second analysis compared the lithology of those dinosaurs collected in 1940 or earlier to exhaustively collected specimens to determine whether specimens from each lithology were randomly distributed with respect to collecting practices. The third analysis included only data from those institutions that collected exhaustively (MRF, PTRM, UCMP, TMP and RSM).

Personal observations of older collections (collected in 1940 or earlier), as well as 15 years of fieldwork in the Hell Creek Formation of North Dakota by one of us (T.R.L.), suggest that they are biased towards a sandy lithology because this is generally where the highest quality specimens are found (T. R. Lyson & N. R. Longrich, personal observation; [16,17,42,46]). Brown [16], who collected many of these skeletons, says: ‘In the Lance and Hell Creek beds... fossils preserved in clay are invariably distorted to such a degree that they are rarely presentable as exhibition material or reliable for determining specific characters. In consequence *such specimens are rarely collected* [emphasis ours].’ We attempted to eliminate this bias by comparing the lithology of each group of dinosaur using only collections that collected exhaustively. A total of 124 such specimens were analysed (see electronic supplementary material, table S1).

3. RESULTS

The first χ^2 -test, including all specimens, found a non-random distribution of dinosaurs with respect to lithology (figure 2). Hadrosaurs ($n = 80$) show a strong association with sandstone ($\chi^2 = 182.55$, d.f. = 1, $p < 0.001$), by a 15 : 1 ratio. Likewise, *Thescelosaurus* ($n = 19$) occurs preferentially in sandstone ($\chi^2 = 18.50$, d.f. = 1, $p < 0.001$) by an 8 : 1 ratio (figure 2a). By contrast, ceratopsids ($n = 161$) are associated with mudstone ($\chi^2 = 30.60$, d.f. = 1, $p < 0.001$) by a ratio of almost 2 : 1 (figure 2a). Ornithomimids ($n = 10$) are more common in mudstone but the sample is too small to be statistically meaningful. *Tyrannosaurus rex* ($n = 45$) shows no significant association with either lithology.

Of the 113 specimens collected in 1940 or earlier, 85 are from sandstone and only 28 are from mudstone. Compared with more recent, exhaustive collecting (124 specimens: 60 sandstone, 64 mudstone), associated specimens collected in 1940 or earlier are biased towards sandstone ($\chi^2 = 417.92$, d.f. = 1, $p > 0.001$).

In a separate test, we compared the lithology using only specimens from institutions that collected exhaustively. Again, hadrosaurs ($n = 28$) show a strong and significant association with sandstone ($\chi^2 = 44.78$, d.f. = 1, $p < 0.001$), while ceratopsids ($n = 55$) show a similar association with mudstone ($\chi^2 = 11.32$, d.f. = 1, $p < 0.001$). Again, *T. rex* ($n = 14$) shows no significant association with either lithology (figure 2b).

4. DISCUSSION

This study reveals a strong pattern of association between dinosaurs and the rock in which they are buried: ceratopians preferentially occur in mudstone, *Thescelosaurus* and hadrosaurs preferentially occur in sandstone, and *T. rex* shows no association with either (figure 2). These patterns are difficult to explain using known taphonomic processes. River channels can cut down through muddy overbank deposits and rework overbank-hosted specimens into channel deposits and flooding river channels can transport relatively intact carcasses long distances from their point of death [47,48]. Such processes could obscure associations between species and lithology, but it is unclear how this would produce the observed patterns. Additionally, reworked specimens typically lose

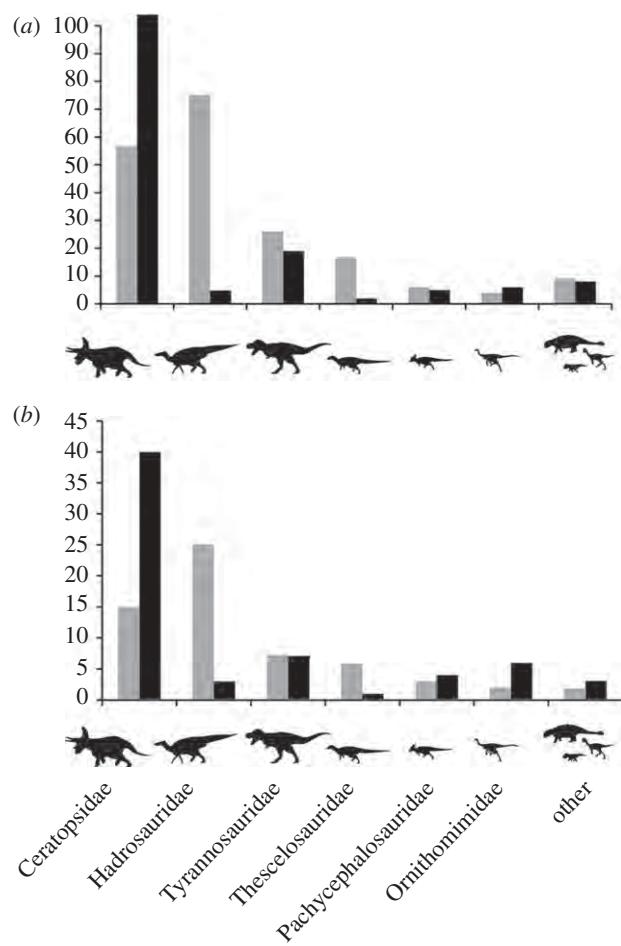


Figure 2. Bar graphs showing the relative proportion of each dinosaur group found in mudstone (black bars) and sandstone (grey bars). When the entire dataset ($n = 343$) was analysed (a) ceratopians have a significant association with mudstone, hadrosaurs and *Thescelosaurus* have a significant association with sandstone, and *Tyrannosaurus rex* has no preferred association with either lithology. The exhaustive dataset ($n = 124$; b) shows the same patterns, although more pronounced.

their skeletal association and reworked specimens are often redeposited as isolated elements or part of a larger bonebed, both of which were excluded from this analysis. In addition, fossils found in floodplain deposits are generally interpreted as representing the site of death because the energy needed to remove elements from the channel and deposit them on the floodplain rarely exists [18,49,50]. Finally, numerous actualistic taphonomic studies on vertebrate skeletal hard parts indicate that out-of-life-habitat transport generally affects relatively few individuals in a given fossil assemblage ([47] and references therein). In sum, we are unaware of a taphonomic process that would associate only some species with a specific lithology and, more importantly, actualistic taphonomic studies indicate a high spatial fidelity for associated specimens and their habitat.

Alternatively, this pattern could be explained by ecology—that is, some dinosaurs died more frequently in particular environments because they lived more frequently in those environments (figure 3). This hypothesis largely depends on the ability of using lithology to distinguish between channel and floodplain palaeoenvironments. Nine lithofacies are generally

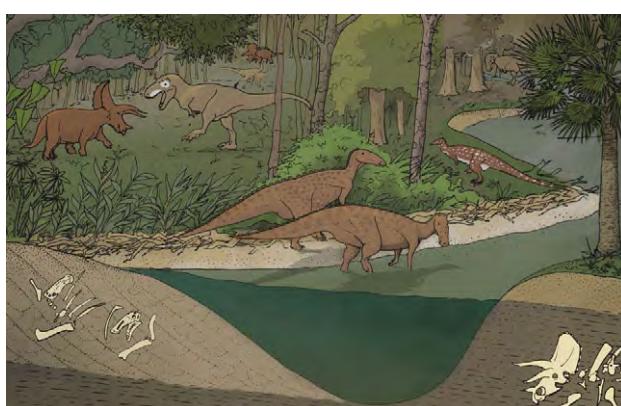


Figure 3. Hypothetical illustration of the latest Maastrichtian landscape that shows dinosaurs occupying different palaeoenvironments (floodplain versus channel margins). Hadrosaurs and *Thescelosaurus* largely occupy environments near river channels, ceratopsians occupy environments distal to the river channels, and *Tyrannosaurus rex* occupies both environments.

recognized in the study area [18,22,23,25,27,28]. As summarized in table 1, channel lithofacies are generally composed of sandstone, and floodplain lithofacies are generally composed of mudstone. Despite rare exceptions, such as mud-filled channels and sand-draped floodplains, the dominant floodplain and channel lithofacies in the study area are partly characterized by their lithology, indicating that there is a sound basis for using lithology to distinguish between floodplain and channel palaeoenvironments ([51–53]; table 1). However, it is not possible to distinguish between lithofacies *within* either floodplain or channel palaeoenvironments without associated sedimentological data. Given that the dominant floodplain and channel lithofacies are largely composed of mudstone and sandstone, respectively, and the large number of associated specimens analysed, it seems reasonable to conclude that the observed pattern between lithology and associated specimens is the result of ecology.

This ecological interpretation suggests a degree of spatial niche partitioning, with ceratopsians primarily occupying floodplains, and hadrosaurs and *Thescelosaurus* primarily occupying channel margins. This could help explain how the environments of the late Maastrichtian were able to support numerous large-bodied herbivores including the ceratopsids *Triceratops* and *Torosaurus*, and the hadrosaurids *Edmontosaurus* and *Anatotitan*. Therefore these data strongly support the hypothesis that different herbivores populated different parts of the coastal Western Interior Seaway during the latest Maastrichtian. Unsurprisingly, *Tyrannosaurus rex* shows no association with either environment. As the sole large carnivore in the terrestrial ecosystem, it must have been something of a generalist. Regardless of whether it was a predator, a scavenger, or both, *T. rex* would probably have followed the megaherbivores, and megaherbivores inhabited both the floodplain and the river margins.

Our study shows that the association between particular taxa and lithology provides important palaeobiological information. Given this result, and given that out of habitat transport for associated vertebrates is unlikely [47], the relative occurrence of species in various lithologies is likely to contain a great deal of information

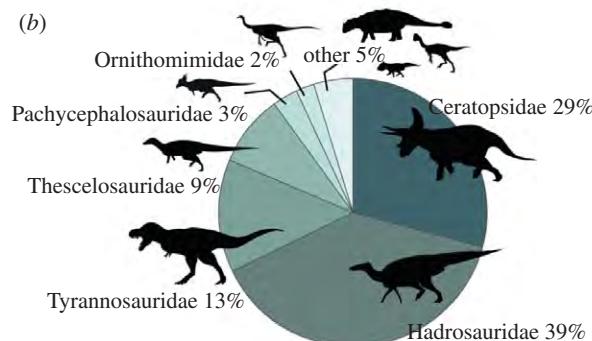
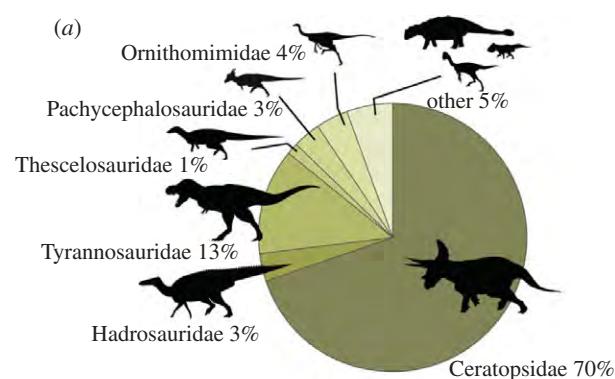


Figure 4. Pie graphs of the lithology using the entire dataset showing the different proportions of each dinosaur group found in sandstone and mudstone. (a) Mudstone ($n = 149$) contains a highly uneven fauna dominated by ceratopsids, while the other taxa are only rarely found. (b) Sandstone ($n = 194$) contains a more even fauna with hadrosaurs most abundant, followed closely by ceratopsids and tyrannosaurids.

about the habitats that the animal favoured in life. This implication suggests that vertebrate palaeontologists need to pay more attention to studying and recording the lithology of finds.

Despite the fact that the sediments of the Upper Cretaceous of North America were deposited in close proximity and within a narrow window of time, the different lithologies preserve dissimilar vertebrate assemblages. Differences in dinosaur assemblages between formations have long been appreciated [14]. Some of these differences are thought to represent biogeographic differences, with different dinosaurs having different geographical ranges. Other variations are thought to result from long-term changes in community structure, or evolution and extinction of dinosaur lineages. However, given the observed patterns between lithology and dinosaur species, which is observed over an extensive geographical area (figure 1) and a narrow window of time, the patterns shown here suggest that a third factor, the preserved lithology that is sampled, could potentially influence our reconstruction of dinosaur and other vertebrate communities in terms of which taxa dominate. The reconstruction of Western Interior palaeocommunities based on occurrences from sandstone versus occurrences from mudstone would produce very different results (figure 3). Mudstone contains a highly uneven assemblage that is dominated by ceratopsids, which form approximately 70 per cent of the sample. In sandstone,

the assemblage is more even, and hadrosaurids are the most common dinosaur (figure 4). Thus, it appears that the community structure can be highly dependent upon which lithology is being sampled.

Our study also shows that earlier collections from the Upper Cretaceous of North America were heavily biased towards sandstone, with the result that an uncritical examination of museum collections would provide a highly biased picture of the fossil record. This emphasizes the importance of collecting fossils in a systematic fashion and preserving information contained in the association between fossils and sediments, and raises the issue of how sampling biases affect our understanding of dinosaurian communities. If different habitats preserve different dinosaur communities, then one would expect that sampling a wider range of habitats would recover a larger number of distinct communities. However, most of what we know about the dinosaurs from the Western Interior comes from lowland floodplain environments. It seems unlikely that such a limited sample can provide a complete picture of the palaeoecology of North America in the Late Cretaceous. This suggests that one must be cautious when attempting to extrapolate from such limited geographical areas. For instance, the supposed Late Cretaceous decline in dinosaur diversity [54] is largely based on collections from the Hell Creek and Lance Creek assemblages. If these assemblages differ so dramatically between floodplain and overbank deposits, to what extent can the patterns seen in the Hell Creek and Lance formations be generalized to the rest of North America, or to the rest of the world? Thus, the implications of lithology must be taken into account when comparing vertebrate assemblages in order to understand palaeobiogeography or long-term changes in community structure and diversity.

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