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A multi-disciplinary perspective on habitat preferences among dinosaurs in a Cretaceous Arctic greenhouse world, North Slope, Alaska (Prince Creek Formation: lower Maastrichtian)

Anthony R. Fiorillo [a,*], Paul J. McCarthy [b], Peter P. Flaig [c]

[a] Perot Museum of Nature and Science, 2201 N. Field St., Dallas, TX, 75201, USA
[b] Department of Geosciences, and Geophysical Institute, University of Alaska, Fairbanks, AK, 99775, USA
[c] The University of Texas at Austin, Bureau of Economic Geology, Jackson School of Geosciences, Austin, TX, 78758, USA

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ABSTRACT

The Prince Creek Formation of northern Alaska is the most abundant source of polar dinosaur remains in the world, and now, corroborating data from this well-studied rock unit allow for making inferences about the paleoecological preferences for these extinct polar animals. The rock unit records high-latitude, alluvial sedimentation and soil formation on a low-gradient, muddy coastal plain. Compound and cumulative andic Entisols and Inceptisols formed on levees, point bars, crevasse splays, and along the margins of floodplain lakes, ponds, and swamps. Abundant organic matter, carbonaceous root traces, Fe-oxide depletion coatings, and zoned peds indicate periodic waterlogging, anoxia, and gleying, consistent with a high water table. In contrast, Fe-oxide mottles, ferruginous and manganiferous segregations, bioturbation, and less common illuvial clay coatings indicate recurring oxidation and periodic drying out of some soils. An integrated reconstruction of pedogenic processes and biota suggests that this ancient Arctic coastal plain was influenced by seasonally fluctuating water table levels and floods, and in distal areas, marine waters. Four of the five bonebeds in this study are from more distal areas, represented by lower delta plain facies, while the fifth bonebed is from a more proximal part of the basin, represented by a somewhat better drained coastal plain facies.

Bonebeds in the distal areas are dominated by *Edmontosaurus* sp. while the more proximal bonebed is dominated by the remains of the ceratopsian *Pachyrhinosaurus perotorum*. The distribution of these bonebeds, sedimentological facies, paleosols, and biota suggests that *Pachyrhinosaurus* may have preferred more upland environments while *Edmontosaurus* preferred lowland, deltaic environments. This distribution may be the result of physiological adaptation to the pronounced seasonality provided by polar terrestrial ecosystems. In contrast to a preferred habitat distribution of these large herbivores, the large predatory dinosaur *Nanuqsaurus hoglundi* seems to have had a more ubiquitous distribution across the landscape.

1. Introduction

Laramidia was the large narrow landmass in western North America during the latter Cretaceous that extended across a wide range of latitude (Archibald, 1996). This large landmass extended from close to the present northernmost and southernmost latitudes of North America, or in other words, modern-day Alaska to Mexico. The dinosaurian fauna of Laramidia includes various theropods such as tyrannosaurs, dromaeosaurs, and troodontids and various herbivores such as hadrosaurians, pachycephalosaurs, ceratopsians, ankylosaurs, and in the southern ranges of Laramidia, titanosaurs. Across this great latitudinal range, however, the common large-bodied herbivores within this continental ecosystem were hadrosaurian and ceratopsian dinosaurs.

A great deal of effort has been put forth to clarify the relationship between these dinosaurs and their environments across taxa and paleogeography (e.g., Brinkman et al, 1998; Eberth and Getty, 2005; Fricke and Pearson, 2008; Suarez et al., 2013; Eberth et al., 2013; Eberth and Bell, 2014). Habitat preferences for hadrosaurs and ceratopsians have been largely determined from the extensive work done in the Upper Cretaceous rocks of southern Alberta and Saskatchewan, North Dakota and Montana. For example, in the Campanian upper Belly River Group of western Canada, based on the distribution of fossil remains and facies, Brinkman et al. (1998) suggested that ceratopsians seemed to have preferred coastal habitats to the drier upland environments, particularly during the non-nesting time of year. It was pointed out by Eberth and Getty (2005) in their study of twenty ceratopsian bonebeds, however, that more than one ceratopsian taxon is represented within the Belly River Group and the Brinkman et al. (1998) scenario does not account for the potential for different behaviors within the group.

* Corresponding author.
E-mail address: Anthony.fiorillo@perotmuseum.org (A.R. Fiorillo).

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In their examination of carbon and oxygen stable isotopic signatures in the enamel of teeth of both hadrosaurs and ceratopsians from the Maastrichtian Hell Creek Formation of North Dakota, Fricke and Pearson (2008) also concluded that the preferred ceratopsian habitat was coastal. Furthermore, Fricke and Pearson (2008) concluded that hadrosaurs preferred more forested inland areas. Together, these studies suggest that, though broadly defined, habitat preferences were exhibited during the Late Cretaceous by these two large-bodied herbivorous dinosaurs.

Recently, Suarez et al. (2013) examined stable oxygen isotopes in the enamel of a variety of dinosaurs from the Prince Creek Formation and suggested a different distribution of dinosaurs within this ancient Arctic greenhouse ecosystem. From their isotopic results, they inferred that *Pachyrhinosaurus perotorum* ingested water that was more enriched in ^{18}O than that for other herbivorous dinosaurs, including *Edmontosaurus*, and suggested that *Pachyrhinosaurus* foraged away from riparian areas, preferring instead the conifer forests located up-dip and away from major fluvial channels on more stable landscapes (Suarez et al., 2013). Here we offer integrated taphonomic and sedimentologic data that corroborate the model put forth by this geochemical study. The five bonebeds that form the basis of this work are tightly constrained stratigraphically and thus are near coeval (Flaig et al., 2011, 2013).

Further, in this report, we expand the understanding of the paleoecology of dinosaurs and their respective habitat preferences because our study area that includes Early Maastrichtian strata of the Prince Creek Formation of northern Alaska was located at a higher latitude, some twenty to twenty-five degrees paleo-poleward of these other study areas in southern Canada and the continental United States (Brinkman et al., 1988; Eberth and Getty, 2005; Fricke and Pearson, 2008; Fig. 1). Thus the Prince Creek Formation provides the opportunity for paleoecological insight into dinosaur ecology from a Paleo-Arctic perspective.

These dinosaur skeletal remains are found in bonebeds in a variety of alluvial environments in the Prince Creek Formation (Fiorillo et al., 2010a, 2010b; Flaig et al., 2011, 2013; Flaig et al., 2014). Bonebeds are notable occurrences in the fossil record as they potentially record a wealth of paleobiological information (see Rogers et al., 2007 for overview) and are one of the most important sources of information in understanding ancient ecosystems. Many aspects of the Prince Creek Formation bonebeds have been discussed in detail elsewhere (Fiorillo et al., 2010a, 2010b; Gangloff and Fiorillo, 2010; Flaig et al., 2014). The individual bonebeds contain the macrofossil skeletal remains of many individuals of herbivorous dinosaurs, have extraordinary concentrations of associated skeletal bones and large percentages of juvenile remains, and tend to have limited biodiversity (Fiorillo et al., 2010a, 2010b; Gangloff and Fiorillo, 2010). As such, these bonebeds indicate that at least for part of the year, the Prince Creek Formation ceratopsians and hadrosaurs were gregarious (Fiorillo et al., 2010a, 2010b; Gangloff and Fiorillo, 2010). Histological data suggest that the time of death of the hadrosaurs from some of these bonebeds was during the early spring (Chinsamy et al., 2012), which may reflect that they were gregarious at least at this point in the year.

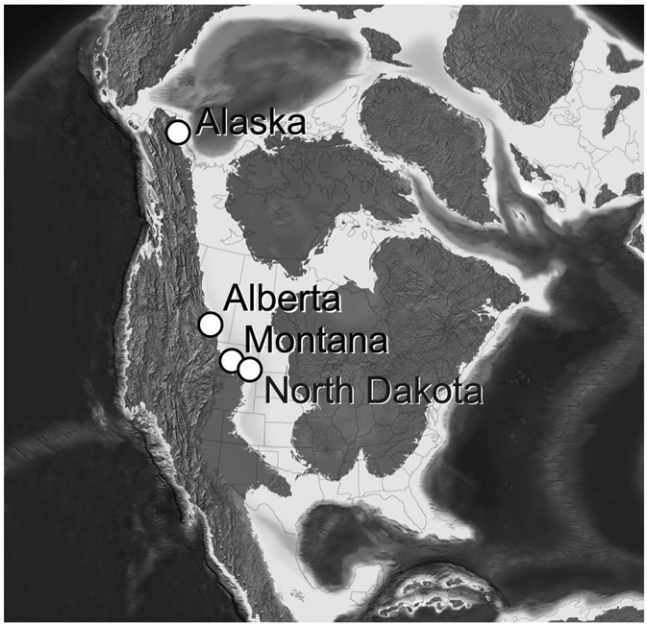

Fig. 1. Paleogeographic map of North America showing the relative position of the dinosaur sites in Alaska, Alberta, Montana, and North Dakota. The base map is for the Late Cretaceous (75 Ma) from Ron Blakey (Northern Arizona University, URL: http://jan.ucc.nau.edu/~rcb7/namK75.jpg).

Despite the known lateral topographic complexity of floodplain sub-environments and the corresponding effects on water table levels and drainage conditions (Wright, 1992; McCarthy and Plint, 2003), a general up-dip improvement in drainage conditions can still be documented for the Prince Creek Formation (Brandlen, 2008; Flaig et al., 2011, 2013). By integrating data on the distribution of bonebeds with paleopedological and biotic data and sedimentary facies from both more proximal and distal settings, we provide insights into Arctic dinosaur habitat preferences for the predatory dinosaur guild and corroborate a previous model proposed for preferred habitat selection among the large herbivore guild.

First, and not surprisingly, the predatory dinosaur guild does not show similar evidence of habitat partitioning. Previous work on the microwear patterns on the teeth of multiple taxa of small theropods from the Prince Creek Formation showed that these animals were eating similar food items (Fiorillo, 2008). The occurrence of theropods across the range of sedimentary facies within the Prince Creek Formation is presumably the result of theropod dinosaurs following food resources (i.e., prey) wherever they are found in the ecosystem.

And secondly, the preferred habitat selection for hadrosaurs and ceratopsians in this more northern region, based on the relationship of the faunal composition within bonebeds to sedimentary environments supports the ecological model put forth based on stable isotopes (Suarez et al., 2013). This pattern is the reverse of the pattern found to the south. In the Prince Creek Formation, it seems that hadrosaurs preferred the more distal, wetter, lower delta plain environment while the ceratopsians' preferred habitat was the more proximal upper coastal plain. Given the high-latitude setting of the Prince Creek Formation during deposition, this difference in habitat preference may relate to the limited resources available in the highly seasonal physical environment of the ancient Arctic.

2. Geological setting

Mull et al. (2003) revised the Cretaceous and Tertiary stratigraphic nomenclature for the Colville basin of the North Slope of Alaska. Following their nomenclature, the vast majority of the known Cretaceous vertebrate fossil localities, and all the bonebeds in northern Alaska, are contained within the Prince Creek Formation (Fig. 2).

The complex stratigraphy of the Prince Creek Formation crops out semi-continuously for approximately 72 km (Fig. 3) along the Colville River in northern Alaska (Fig. 4). Most of the published detailed stratigraphic and fossil data relevant to the Upper Cretaceous strata of northern Alaska are from penecontemporaneous marine equivalents of the Prince Creek Formation (e.g., Schrader Bluff Formation) due to the more readily collectible and identifiable invertebrate fossils (Brouwers et al., 1987; Waller and Marincovich, 1992). Phillips (1990; 2003). Conrad et al. (1990) were the first to attempt to construct a detailed stratigraphic and chronometric framework that included the highly fossiliferous terrestrial interval assigned unequivocally to the Prince Creek Formation. These studies were confined to a very restricted segment of