Herd structure in Late Cretaceous polar dinosaurs: A remarkable new dinosaur tracksite, Denali National Park, Alaska, USA

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ABSTRACT

The discovery of a new tracksite of mostly hadrosaurid dinosaur footprints, made by a herd living in an ancient high-latitude continental ecosystem, provides insight into the herd structure and behavior of northern polar dinosaurs and perspective on populations of large-bodied herbivores in an Arctic greenhouse world. This tracksite occurs in the Upper Cretaceous Cantwell Formation in the Alaska Range (Denali National Park, Alaska, United States), and it is the largest tracksite known from this far north. Preservation of the tracksite is exceptional: most tracks, regardless of size, contain skin impressions and they co-occur with well-preserved plant fossils and invertebrate trace fossils of terrestrial and aquatic insects. Statistical analyses of the tracks show that individuals of four different age classes of hadrosaurids lived together in a large social group. Our research results independently corroborate the growth curve for hadrosaurids proposed by paleohistologists that suggests that these dinosaurs experienced a period of rapid growth early in their life history.

INTRODUCTION

Societal concerns abound regarding biotic responses to a warming Arctic. The Cretaceous of Alaska records a vast ancient Arctic continental ecosystem that can offer constructive insights into how biota might respond to a warm polar climate. Alaska contains the densest concentrations of reported Late Cretaceous dinosaur bones of any high-latitude location in the Northern or Southern Hemispheres (Rich et al., 2002). The region also served as a gateway that connected the Cretaceous faunas and floras of Asia to those in North America (Fiorillo, 2008). Alaskan bone beds (Fiorillo et al., 2010a, 2010b; Gangloff and Fiorillo, 2010) provide some insights into the terrestrial vertebrate fauna of the Late Cretaceous polar ecosystem; however, they offer limited data on dinosaur population structure and behavior. Here we report on a newly discovered tracksite containing thousands of exceptionally preserved footprints of hadrosaurids (Dinosauria) in central Alaska from the Upper Cretaceous Cantwell Formation in Denali National Park and Preserve. This tracksite formed at latitudes as high as or slightly higher than its current geographic position (Witte et al., 1987; Hillhouse and Coe, 1994; Lawver et al., 2002) during the Late Cretaceous and it provides unique insights into the population structure and behavior in a herd of large-bodied herbivores in a greenhouse Arctic setting.

Well-preserved hadrosaurid tracks, most of which contain skin impressions, demonstrate that the herd contained adults, subadults, juveniles, and very young individuals. This tracksite assemblage represents the first definitive evidence that hadrosaurids lived in multigenerational herds, a behavioral pattern not recognized previously from either bone beds or other track assemblages. Track length/width ratios independently support a hypothesized growth curve suggesting that young hadrosaurids had a brief period of rapid growth based on histological sectioning of bones (Horner et al., 2000; Erickson et al., 2001; Cooper et al., 2008). A growing data set supports a model that polar hadrosaurids were year-round residents of the high-latitude continental ecosystem (Fiorillo and Gangloff, 2001; Gangloff and Fiorillo, 2010; Chinsamy et al., 2012); thus this study provides insight for understanding a biological response to a modern warming Arctic.

BACKGROUND

The tracksite is in the lower part of the Upper Cretaceous Cantwell Formation in Denali National Park and Preserve, Alaska (Fig. 1). The Cantwell Formation comprises a lower, dominantly fluvial sedimentary unit and an upper, mostly volcanic unit (Ridgway et al., 1997). Sedimentation of the track-bearing lower unit was mainly in alluvial fan, braided to meandering stream, and lacustrine environments, at times with possible minor marine influence; floodplains showed poorly developed paleosols (Fiorillo et al., 2009). Pollen and megafloral data suggest that these sedimentary rocks are late Campanian or early Maastrichtian in age (Ridgway et al., 1997; Tomsich et al., 2010); thus, the Cantwell Formation is correlative with well-known dinosaur localities found elsewhere in Alaska (Fiorillo, 2008).

Known thus far only from trace fossils, the vertebrate fauna from the Cantwell Formation includes records of fishes, avian and nonavian theropods, ceratopsians, pterosaurs, and hadrosaurids (Fiorillo et al., 2007, 2009, 2011; Fiorillo and Adams, 2012). Paleogeographic reconstructions place the depositional setting of the Cantwell Formation at or near its current latitude during the Cretaceous, making this an ancient high-latitude

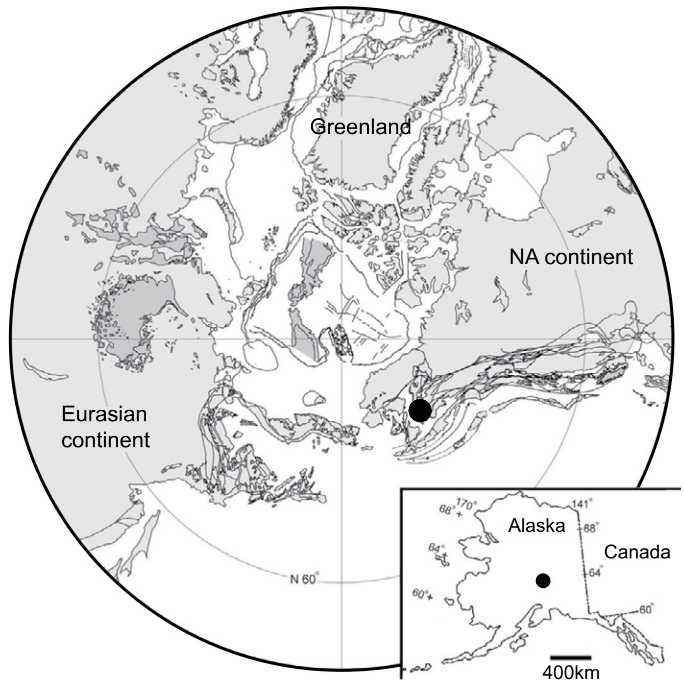

Figure 1. Polar projection of tectonic plates during the Late Cretaceous, with inset map of Alaska. NA—North America. Dots in both maps indicate location of Denali National Park.

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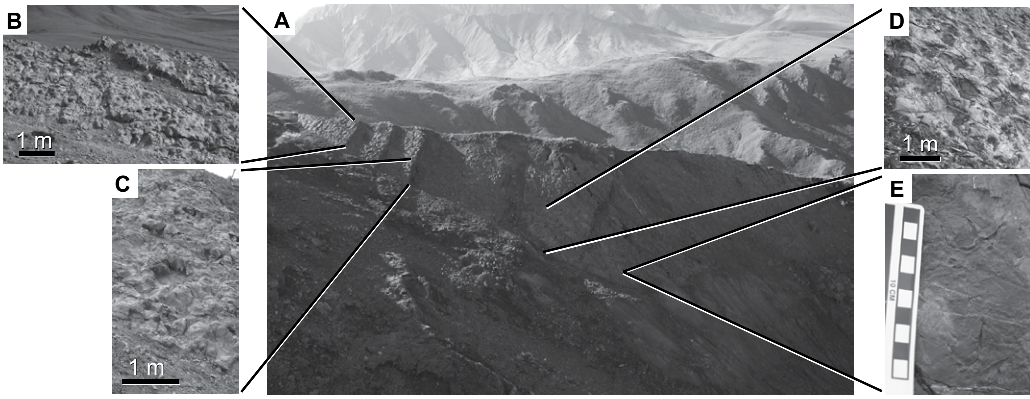

Figure 2. A: View of Denali National Park, Alaska, tracksite from the air. B: Left side of tracksite; each dimple in the bedding plane represents a dinosaur footprint. C: Hadrosaur trackway. D: Hadrosaur footprints from right side of tracksite. E: Two avian theropod tracks.

continental ecosystem (Fig. 1; Witte et al., 1987; Hillhouse and Coe, 1994; Lawver et al., 2002). Paleotemperature estimates for this interval of time, from rocks a few hundred kilometers to the north along the present Colville River, suggest that the mean temperature ranged from 2 to 4 °C for the coldest monthly mean, and 10 to 12 °C for the warmest monthly mean (Parrish and Spicer, 1988). The observed invertebrate trace fossil record from the Cantwell Formation (Fiorillo et al., 2009) corroborates a warmer paleotemperature for this region.

DENALI NATIONAL PARK TRACKSITE

This new tracksite is exposed on a steeply dipping (38°) wedge-shaped bedding plane that extends for ~180 m, is as much as 60 m wide, and contains thousands of vertebrate tracks (Fig. 2; Fig. DR1 in the GSA Data Repository[1]). The exact location of this tracksite is on file with Denali National Park and Preserve. In addition to these tracks, surface trails and shallow burrows of a variety of invertebrates are common. The seasonal distribution of modern equivalents of these invertebrate trace fossils suggests that the tracksite formed in the warmest months of the year during the Late Cretaceous (Ward, 1992; Thorp and Covich, 2001). The preservation of the dinosaur tracks across the bedding surface is consistent, suggesting that time averaging during tracksite formation was minimal.

The most abundant tracks are attributable to hadrosaurids, based on morphology, and range from adults, subadults, and juveniles to very young individuals (Fig. 3). No spatial association of different sized tracks was found. Key characters that identify the tracks as hadrosaurid are that they are wider than long, tridactyl with digits that terminate bluntly, and have a wide, bi-lobed heel (Currie et al., 2003; Lockley et al., 2004). In addition, the tracks at this site, regardless of size, often preserve (~50%) skin impressions (Fig. 3) that match patterns previously identified for hadrosaurids (Lockley et al., 2004), and support our interpretation that these are true surface tracks rather than undertracks. Given the morphological similarity between tracks with skin impressions and those without, we attribute the lack of skin impressions to taphonomic or erosional processes. Tracks attributable to hadrosaurs are referred to as *Hadrosauropodus* (Lockley et al., 2004), and thus far the only described hadrosaurian body fossil material from Alaska has been attributed to *Edmontosaurus* (Gangloff and Fiorillo, 2010). Discrimination of original tracks from undertracks is crucial in that surface tracks can be used for estimates of body sizes of track makers. The tubercles on these tracks decrease in size distally, and tubercle size increases as foot size increases.

The largest tracks at this site correspond with the large sizes of other reported adult hadrosaurid tracks of comparable age from Mongolia (Currie et al., 2003) and western North America (Lockley et al., 2004). Previous reports of adult hadrosaurid material from the Cretaceous of Alaska have referenced fragmentary bones (Fiorillo and Gangloff, 2001); complete remains of full-sized adult hadrosaurids have yet to be found. The discovery of tracks of these proportions is significant in that clearly adult-sized tracks (Fig. 3) indicate that adult polar dinosaurs were approximately the same size as their southern counterparts.

Elephants are a commonly used modern analog for dinosaurs. A simple technique for estimating population age structure in elephant herds is to examine size differences in hind foot impressions left in the substrate (Western et al., 1983), a technique successfully applied to the fossil record of elephants (Bibi et al., 2012). A scatterplot of length-width measurements of complete tracks at the Denali National Park and Preserve tracksite (Fig. 4) reveals a significant trend, even though not all tracks were amenable to measuring due to overprinting by successive tracks. Euclidean, Bray-Curtis, and Manhattan cluster analyses of maximum lengths and widths of tracks show four statistically significant data clouds within the large cloud of points on the scatter plot. Cophenetic correlation coefficient values are Euclidean, 0.8456; Bray-Curtis, 0.9229; and Manhattan, 0.847. These four data clouds are interpreted as

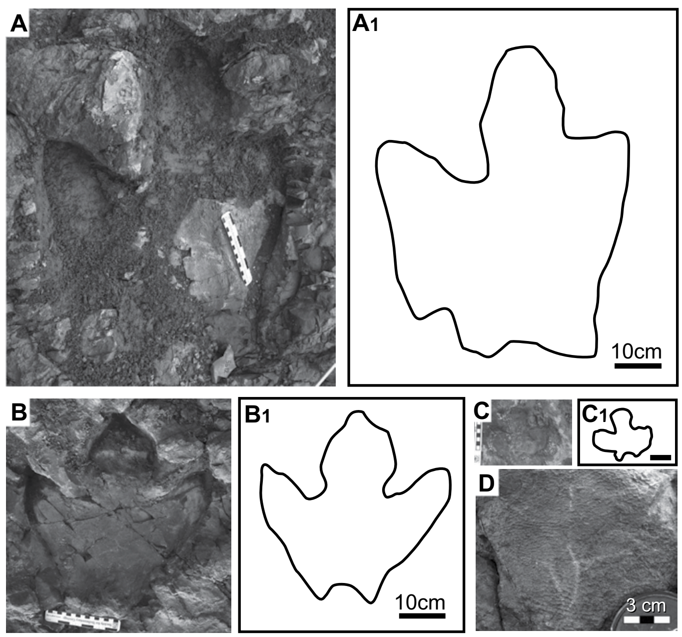

Figure 3. A–C: Size ranges of tracks found at Denali National Park, Alaska, tracksite. D: Adult hadrosaurid track with skin impressions. Scale bar for C1 is 5 cm.

[1]GSA Data Repository item 2014267, summary of the history of the site discovery, and photographs showing associated invertebrate trace fossils that determine the time of season of track formation, is available online at www.geosociety.org/pubs/ft2014.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

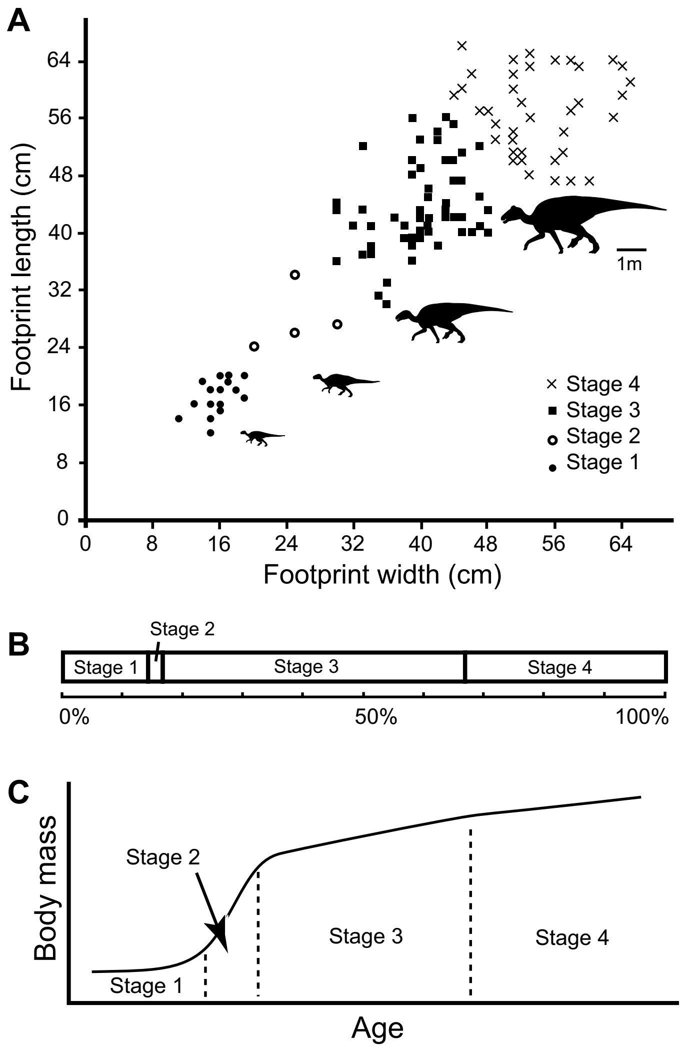

Figure 4. A: Bivariate plot of footprint length-width measurements (N = 127) with results of cluster analysis superimposed, showing growth stages 1–4. Different size classes are consistent with populations of animals that breed seasonally (Ricklefs and Miller, 2000). B: Relative frequencies of each growth stage. C: Relative frequencies of each growth stage as function of body mass. This curve independently corroborates hypothesized growth curve for hadrosaurid dinosaurs proposed by others (Erickson et al., 2001; Cooper et al., 2008).

four distinct ontogenetic age groups of individuals. Figure 4 shows the frequency of each age of individuals. The most common tracks belong to stages 3 and 4 animals (84% combined), followed by the smallest tracks of stage 1 (13%). Stage 2 individuals are uncommon (3%). Figure 4 also shows a projected growth curve for polar hadrosaurids based on these frequencies. The curve suggests that growth in young hadrosaurids (stage 2) had a brief period where it was very rapid. These tracks therefore independently support a growth curve hypothesized for hadrosaurids based on histological sectioning of bones (Horner, 2000; Erickson et al., 2001; Cooper et al., 2008).

The size range of very small to very large hadrosaurid tracks from the surface of this tracksite also demonstrates that polar hadrosaurids lived in multigenerational social herds. Animals congregate for a variety of reasons, from independent gatherings such as vultures on a carcass (Ricklefs and Miller, 2000) to interdependent family groups (Wilson, 1980). Given previous behavioral interpretations of hadrosaurids (Horner and Gorman, 1988; Horner, 2000), this tracksite records an aggregation of extended families exhibiting some aspect of postnatal parental care extending beyond the nest, and incorporating the very young into the herd. Similar social structures are observed today in such megaherbivores as elephants, which can occur as extended clans that include 100 or more animals of immature progeny to mature adults (Western et al., 1983; Owen-Smith, 1992) Previous reports of small hadrosaurid tracks have been taken to indicate that some age segregation occurred within hadrosaurid herds, as these tracks occurred separate from occurrences of juvenile or adult tracks (Carpenter, 1992). Other studies characterized hadrosaurid herds as being composed of two age classes (Horner, 2000). The Denali National Park and Preserve tracksite instead indicates that polar hadrosaurids lived in multigenerational herds and that these hadrosaurids engaged in extended parental care. The intimate association of track sizes in the tracksite also suggests that, for at least some part of the year, hadrosaurids lived in herds composed of four age classes.

NONMIGRATORY INFERENCE

The profound seasonality of high-latitude ecosystems was the basis for early workers to invoke long-distance migration models for dinosaurs in the high latitudes, where animals would have had to travel several thousands of kilometers to warmer climes. These animals, however, did not migrate significant distances to lower latitudes during the winter, based on (1) a biomechanical argument from hadrosaurid bones found in northern Alaska (Fiorillo and Gangloff, 2001) and a histological argument from hadrosaurid bones found in northern Alaska (Chinsamy et al., 2012), and (2) evidence from this new tracksite for very young juvenile hadrosaurids in the herd that would have been incapable of making such a long journey.

Many skeletal elements of immature hadrosaurids have been recovered from the Liscomb Bone Bed along the Colville River (Fiorillo and Gangloff, 2001; Gangloff and Fiorillo, 2010). Femora range from 45 to 39 cm long, suggesting that these individuals had body sizes similar to the upper limit of stage 1 individuals from the Denali tracksite. The smallest femur, with a circumference of 186 mm, represents an individual that could have migrated 6400 km/yr, at maximum, for a total migration distance, or 3200 km one way (Alexander, 1985; Hedenström, 2003). Caribou migration distances are often mentioned as possible analogs for distances that hadrosaurids might have been capable of achieving as they traveled from high latitudes to the temperate latitudes for warmer climes (Brouwers et al., 1987; Parrish et al., 1987; Currie, 1989). These numbers, however, represent total distances walked by caribou, measured through telemetry, and no caribou walk these distances in a straight line. If we assume similar behaviors in movement for hadrosaurids, then these hypothesized migration distances are inadequate to have taken the hadrosaurids out of the northern polar region. The Denali National Park and Preserve hadrosaurids, therefore, lived in high latitudes year round, and this new tracksite records a multigenerational a herd during the warmest months of the year.

CONCLUSIONS

In summary, available data strongly suggest that polar hadrosaurids were year-round residents of the high latitudes. Furthermore, the Denali National Park and Preserve tracksite assemblage represents the first definitive evidence that Arctic hadrosaurids lived in multigenerational herds, a behavioral pattern not previously recognized from either bone beds or other track assemblages. The demographic profile of this dinosaurian herd also shows that a warm greenhouse polar world was capable of supporting a thriving large-bodied herbivore population.

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