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 megafossil 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 Late Cretaceous, making this an ancient high-latitude...
DENALI NATIONAL PARK TRACKSITE

This new tracksite is exposed on a steeply dipping (38°) wedge-shaped bedding plane that extends for ~180 m, as much as 60 m wide, and contains thousands of vertebrate tracks (Fig. 2; Fig. DR1 in the GSA Data Repository1). 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 Hadrosauripods (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 estimating 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 hadrosaurs 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 successsive 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. Cophe netic correlation coefficient values are Euclidean, 0.8456; Bray-Curtis, 0.9229; and Manhattan, 0.847. These four data clouds are interpreted as...
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.

**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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