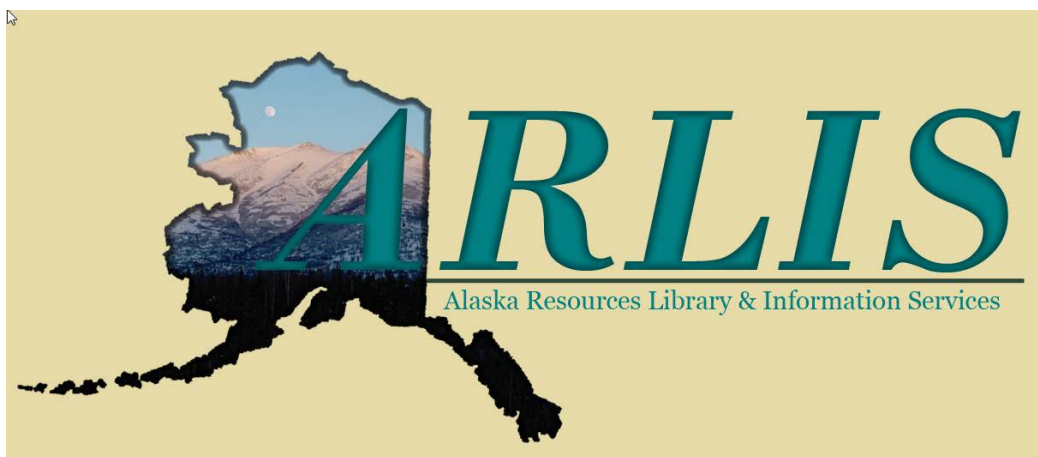


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SMALL HADROSAUR MANUS AND PES TRACKS FROM THE LOWER CANTWELL FORMATION (UPPER CRETACEOUS) DENALI NATIONAL PARK, ALASKA: IMPLICATIONS FOR LOCOMOTION IN JUVENILE HADROSAURS

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ABSTRACT: We report on a paired set of manus and pes tracks from the lower part of the Upper Cretaceous Cantwell Formation in Denali National Park, Alaska, USA. The tridactyl track is bi-lobed in the ‘heel’ and the morphology allows attribution to a hadrosaurid. While adult hadrosaurs typically reached body lengths of 1200 cm, the length of this Alaskan pes impression is approximately 11 cm, which provides a hip height estimate of approximately 44–45 cm for this trackmaker. The manus impression is approximately 3.6 cm wide and 2.75 cm long. While hypothesized through studies of skeletal anatomy, given the small body size of the hadrosaur that made these tracks, this paired set of impressions indicates that at least some juvenile hadrosaurs were facultative quadrupeds rather than obligatory bipeds.

INTRODUCTION

The posture of hadrosaurid dinosaurs has been a subject of significant discussion through the years (Osborn 1912; Galton 1970), but it is now generally accepted that adult hadrosaurs were facultative bipeds (Currie et al. 1991; Dilkes 2001; Senter 2012). However, in a detailed study of ontogenetic growth of forelimb and hindlimb elements in the hadrosaurid *Maiasaura peeblesorum* Dilkes (2001) hypothesized that juvenile forms were largely bipedal.

Here we report on a paired set of manus and pes tracks from the lower part of the Upper Cretaceous Cantwell Formation in Denali National Park, Alaska, USA (Fig. 1A). These tracks were discovered in negative relief on the surface of a large float block of lower Cantwell Formation coarse sandstone high on a remote mountain slope. Based on morphology of the pes and manus impressions, these tracks can be assigned to the ichnogenus *Hadrosauropodus*, and based on their small size, these tracks represent a very young hadrosaurid individual. Given the small size of the individual, the track pair described here provides evidence that juvenile hadrosaurs, like mature hadrosaurs, were likely facultative quadrupeds.

GEOLOGICAL SETTING

The Cantwell Formation is exposed throughout much of the central Alaska Range. It is the prominent rock unit exposed within sight of much of the eastern stretch of the park road within Denali National Park. The Cantwell Formation varies in thickness but is up to 4000 meters thick and comprises a lower, dominantly fluvial sedimentary unit and an upper, dominantly volcanic unit. These informal subunits are referred to as the lower and the upper Cantwell Formation, respectively (Ridgway et al. 1997). Rocks of the lower Cantwell Formation consist of conglomerates, organic-rich and fossiliferous sandstones, mudstones, and to a much lesser extent, coals. The lower Cantwell Formation has been interpreted as an alluvial fan system on the basis of frequent changes in facies and current directions, and evidence for debris flows and syndepositional deformation (Ridgway et al. 1997). Deposition of the lower Cantwell Formation occurred within an asymmetrically aligned thrust-top basin formed

between Wrangellia and the margin of North America during the accretion of the former (Ridgway et al. 1997; Lawver et al. 2002). The rocks were subsequently uplifted and exposed during the rise of the modern Alaska Range.

The geologic age of the upper Cantwell Formation is Paleocene to Eocene with dates of 60–55.5 Ma (Cole et al. 1999). Gilbert et al. (1976) named this upper unit the Teklanika Formation, but the unit name was not accepted by subsequent workers. In the most recent basin-wide study of the stratigraphy of the Cantwell Formation, Ridgway et al. (1997) refer to the subdivisions as the lower and the upper Cantwell Formation and like several other workers (Fiorillo et al. 2009, 2011; Tomsich et al. 2010, 2014) we follow their nomenclature.

Pollen analysis for the lower Cantwell suggests that these sedimentary rocks were deposited during the late Campanian or Maastrichtian (Ridgway et al. 1997), while a more recent paleofloristic study restricted the age to the Maastrichtian (Tomsich et al. 2010). Recent zircon U-Pb dates from bentonites within the lower Cantwell Formation have provided ages of 69.5 ± 0.7 Ma, 71.5 ± 0.9 Ma, and 71.0 ± 1.1 Ma (Salazar Jaramillo 2014; Tomsich et al. 2014).

Tomsich et al. (2010) provided a mean annual temperature estimate based on a composite flora for the unit as 7.42 ± 1.2° C, and a growing season precipitation estimate of 229.4 ± 334.5 mm. Given that the southern margin of Alaska was near its current latitude during the Cretaceous (Hillhouse and Coe 1994), it can be assumed that the basin in which the Cantwell was deposited was also near its present latitude at that time, implying that these environmental conditions applied to this high latitude setting.

The hadrosaur tracks described here were discovered very near previously described pterosaur and therizinosaur track sites (Fiorillo et al. 2009; Fiorillo and Adams 2012) for which the geologic sections were described in great detail. Those works provide a reasonable proxy for the depositional setting of the new hadrosaur track site. The new tracks were discovered as negative relief impressions on the surface of a large float block of coarse sandstone. The locality is high on a remote mountain slope (Fig. 1B). Because the lower Cantwell Formation is the only rock unit

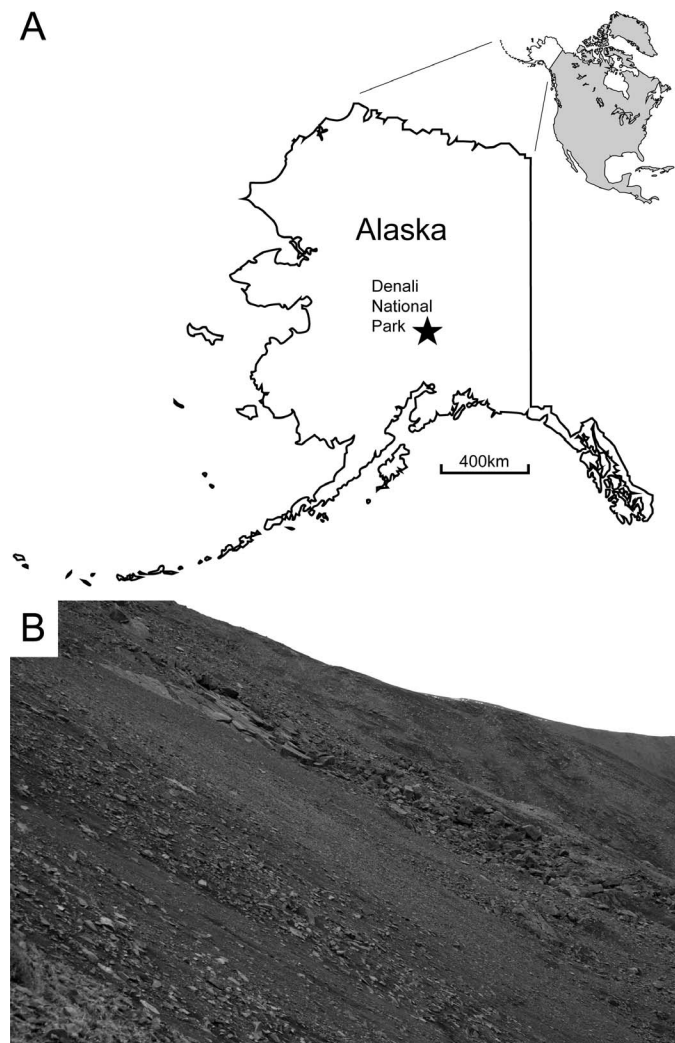


FIG. 1.—A) Location of Denali National Park, Alaska, United States of America, shown by black star in outline of the state of Alaska. B) Photo of steep slope in vicinity of track location, illustrating the nature of weathering, block displacement, and in situ bedding exposure in the area.

comprising the mountain, the float block is confidently attributed to this formation.

Taken together, the geological, floral, and paleoecological evidence suggests a depositional environment for the lower Cantwell Formation as having been formed in a low-lying floodplain. Contained on the floodplain were small lakes and ponds that were dissected by small channels fed by a larger tributary stream on an active fan lobe. Conifers dominated the forest, which had an understory of ferns and horsetails. Flowering trees and other angiosperm shrubs probably lined stream and lake margins. The many lithofacies successions and the different floral compositions (Tomsich et al. 2010) testify to the natural changes that occurred on an ancient landscape.

METHODS

Precise locality data are on file with the Perot Museum of Nature and Science in Dallas, Texas, the Resource Office of Denali National Park, and the Natural Resources Team within the Regional Office of the National Park Service, Anchorage, Alaska. A mold of the tracks described here was made in the field using Smooth-On Equinox™ 50 silicone rubber. In the laboratory at the Perot Museum of Nature and Science, a polyester resin

and fiberglass cast was made from the mold. A total divarication measurement between the innermost and outermost digits was made and compared to other reported hadrosaur tracks. The cast of the specimen described here (DMNH 2010-07-09) is curated and housed at the Perot Museum of Nature and Science, Dallas, Texas, United States.

To create Figure 2B, a polyester resin cast of the specimen was scanned using a NextEngine HD Scanner. The specimen was scanned at a resolution of 2000 points per square inch. ScanStudio software (ShapeTools 2015; proprietary to the NextEngine hardware) was used to create a final model composed of 1,921,165 points. The model was exported as a binary STL file, which was then manipulated in the software CloudCompare (Girardeau-Montaut 2016) to render a color elevation map of the specimen surface.

DESCRIPTION

The tridactyl pes track is bi-lobed, while the manus track is weakly lunate to ovoid (Fig. 2A–2C). The pes impression is approximately 11 cm in length, and 14.6 cm in width (Fig. 2D). The divarication angle between digits II and IV of the pes is approximately 63°, an angle consistent with other purported hadrosaur tracks (Currie et al. 2003; Fiorillo et al. 2014a). The manus impression is approximately 3.6 cm wide and 2.75 cm long. The distance between the heel of the pes to the middle of the manus track is approximately 23 cm. Key characters that identify the tracks as hadrosaurid are: the pes impression is wider than long; the pes impression is tridactyl with wide digits that terminate bluntly; and it has a wide, bi-lobed ‘heel’ (Currie et al. 2003; Lockley et al. 2004; Diaz-Martinez et al. 2015). Similarly the weakly lunate to ovoid shape of the manus track is also characteristic of hadrosaurids (Currie et al. 1991; Vila et al. 2013). Tracks attributable to hadrosaurs are referred to as *Hadrosauropodus* (Lockley et al. 2004; Diaz-Martinez et al. 2015), an ichnogenus that has been documented elsewhere in the lower Cantwell Formation of Denali National Park (Fiorillo et al. 2014b).

DISCUSSION AND CONCLUSIONS

Tracks attributable to juvenile hadrosaurs have been documented previously from the lower Cantwell Formation of Denali National Park (Fiorillo et al. 2014b). The smallest of these previously reported tracks range in overall length from 12.5–15 cm, and as part of a growth series, the juvenile trackmakers were attributed to growth stage 1 (Fiorillo et al. 2014b). Given the small size of the pes impression in this report, we also attribute the trackmaker responsible for it to an individual in growth stage 1.

The standard equation to determine hip height from footprints of dinosaurs is approximately four times the track length (*sensu* Alexander 1976; Henderson 2003). Based on that relationship, this pes track provides a hip height estimate of approximately 44 cm for this trackmaker. Adults of many Campanian and Maastrichtian North American hadrosaurs typically reached body lengths of 1200 cm, with a hip height for the Maastrichtian hadrosaurid *Edmontosaurus* of approximately 250–265 cm based on the flexion angles of the hindlimb derived from skeletal reconstructions (Henderson 2003).

Subsequent field investigation in the immediate area revealed that the tracks described here are preserved in part of a larger bedding plane that contains numerous hadrosaur tracks of various sizes that record the actions of a multi-generational herd of these dinosaurs. Adult-sized tracks within this entire assemblage are approximately 64 cm long (personal observation), a length that provides a hip height for adult hadrosaurs of 256 cm (Fig. 3A).

Additional insight into the size of this particular juvenile hadrosaurid can be obtained from the estimate for hip height, and the relationship between hip height and body length. Henderson (2003) estimated hip height for adult forms of *Edmontosaurus regalis* as 2.66 m and provided

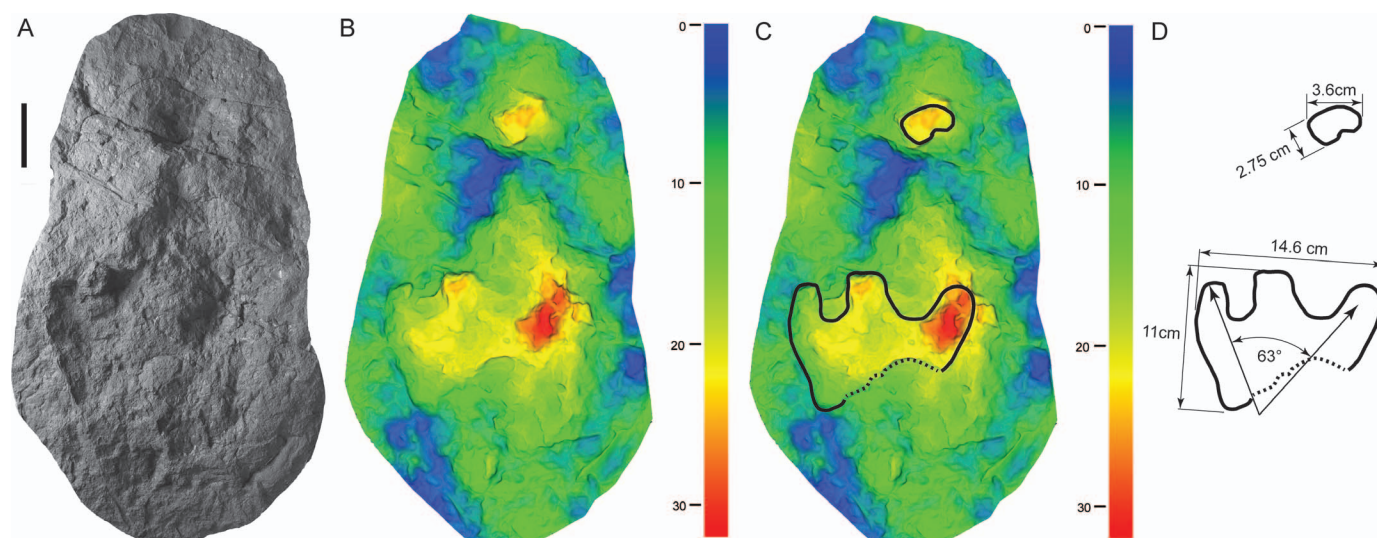


FIG. 2.—**A)** Cast of DMNH 2010-07-09, juvenile hadrosaurid pes and manus impressions. **B)** Surface elevation map of DMNH 2010-07-09 cast. Color scale indicates relative elevation, with numbers indicating distance in millimeters below upper surface. **C)** Drawing that outlines the pes and manus impressions in A and B. Dashed line marks margin of pes track covered with overlying rock that partially fills the impression. **D)** Outlines of pes and manus impressions showing dimensions and divarication angle between pedal digits II and IV. Scale bar (A, C) = 5 cm.

an axial body length measurement of 10 m. Taking these estimates provides a relationship of body length as approximately $3.76 \times$ hip height. Using the estimate of 44 cm obtained from the length of the pes impression described here, the body length of this trackmaker was approximately 165 cm (Fig. 3B).

Alternatively, the distance between the pes and manus track can provide an estimate of the distance between the shoulder and hip joints. Thulborn (1990) suggested that for quadrupedal animals this distance can be estimated by measuring from the mid-point between a pair of pes impressions to the midpoint between a pair of manus impressions. Such paired impressions are not available with this set of tracks but the co-occurrence of these tracks still provide an approximate, albeit not ideal, estimate for the gleno-acetabular length. While within mammalian taxa there are numerous examples of pes impressions nearly or entirely overstepping the manus impressions, in ornithopod trackways that contain manus tracks, the manus impressions are located well ahead of the pes tracks. Given these ambiguities, with only one set of impressions to base

the estimation of body length, it is recognized that this estimate may be smaller than actual body size. Reconstructions of hadrosaur skeletons suggest that their snout-to-tail length is approximately 3.5 times the gleno-acetabular distance (Fig. 3). The distance between the manus and pes impressions of the small hadrosaurid track pair is approximately 23 cm, which provides an approximation of 80 cm for the total body length for this individual from the lower Cantwell Formation. Given the assumptions of this latter method, it seems more likely the body length was closer to the first estimate rather than the second. Regardless of which method is accepted, the tracks described here were made by a very small hadrosaur individual.

Although previously hypothesized based on studies of skeletal anatomy of juvenile hadrosaurs (Dilkes 2001), this paired set of impressions suggests that, like their much larger parents, at least some juvenile hadrosaurs were facultative quadrupeds rather than obligatory bipeds, regardless of their small body size. This suggests large size and by implication body mass was not the driving factor behind the adoption of quadrupedality in hadrosaurs.

Lastly, it is commonly appreciated that tracks, either fossil or modern, are all about the relationship between animals and their world. The science of tracking animals provides opportunities to understand how animals lived, moved, and interacted with aspects of their environment. As such, the fossil track occurrence discussed here is one more example of the contributions provided by traces in understanding aspects of dinosaur paleobiology.

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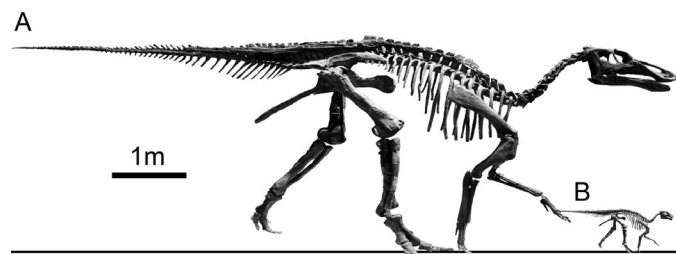


FIG. 3.—Size comparison between adult or near-adult sized hadrosaurid and a juvenile track maker. **A)** Adult skeleton based on a 64 cm foot length, matching largest hadrosaurid pes tracks in the lower Cantwell Formation in the immediate vicinity. **B)** Skeletal reconstruction of a young juvenile hadrosaurid with pes length matching the 11 cm long pes track described here. Both skeletons to scale, and based on reconstructed skeleton exhibited at the Perot Museum of Nature and Science, comprised in part by juvenile hadrosaurid bones in the Perot Museum collections from the correlative Prince Creek Formation, North Slope, Alaska, United States of America.

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