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ON THE SIGNIFICANCE OF A LATE CRETACEOUS TYRANNOSAUR TRACK FROM ANIAKCHAK NATIONAL MONUMENT (CHIGNIK FORMATION, CAMPANIAN – MAASTRICHTIAN), SOUTHWESTERN ALASKA

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ABSTRACT Here we report on the new discovery of a large track, attributed to a tyrannosaur, from Aniakchak National Monument in southwestern Alaska. The track is from the Late Cretaceous (Campanian: Maastrichtian) Chignik Formation, a cyclic sequence of rocks, approximately 500-600 m thick, representing shallow marine to nearshore marine environments in the lower part and continental alluvial and coastal plain environments in the upper part of the section. The track is from within rocks representing estuarine settings. The Chignik Formation is part of the Peninsular Terrane and paleomagnetic reconstructions based on the volcanic rocks of this terrane suggest that the rock unit was deposited near its current latitude of almost 57° N. This track adds to the biodiversity of the ichnofauna known from this rock unit, and the size of the track adds to our understanding of adaptation by high-latitude tyrannosaurs throughout the region.

KEYWORDS Footprint, Theropoda, High-latitude, Biogeography, Dinosauria, *Nanuqsaurus*

INTRODUCTION

In 2001, an inventory and monitoring program initiated by the United States National Park Service, Alaska Region, resulted in the first discovery of Cretaceous dinosaurs in southwestern Alaska, in Aniakchak National Monument (Fiorillo and Parrish, 2004). Further, this discovery was the first documentation of any dinosaur record in any Alaska National Park (Fiorillo and Parrish, 2004). Subsequent work at Aniakchak has shown that the Cretaceous Chignik Formation has an abundant and diverse record of dinosaur footprints (Fiorillo et al., 2018a, 2019).

These fossil vertebrate occurrences are approximately correlative with the famous fossil bone deposits of the Prince Creek Formation of the North Slope of Alaska (e.g., Parrish et al., 1987; Gangloff and Fiorillo, 2010; Fiorillo, 2018), which are located approximately 1500 kilometers north of this study area on the Alaska Peninsula. Together these discoveries demonstrate that terrestrial ecosystems could support dinosaurs across a vast geographic region in ancient high-latitude Alaska.

This study documents the occurrence of a previously unrecognized large theropod track, attributable to a tyrannosaur larger than any previously encountered in the Upper Cretaceous Chignik Formation of southwestern Alaska. The track was discovered during the 2022 field season. This report serves two purposes. First, it expands the known vertebrate ichnotaxonomic biodiversity within this rock unit, by adding a large, 55 cm long tyrannosaur track to the previously documented dinosaur fauna. Secondly, the discovery of a large tyrannosaur track, approximately 60% larger than previously recorded from theropod tracks from the study area in southwestern Alaska adds to our understanding of the adaptative pressures faced by high-latitude tyrannosaurs throughout the region.

Lastly, we are pleased to contribute this work to a volume celebrating the career of Dr. Louis Jacobs. In his role as a bold scientist, explorer, and mentor at Southern Methodist

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University, Professor Jacobs has inspired a force of new paleontologists who, through their own efforts, have furthered our understanding of the history of life on this planet. As Aniakchak National Monument is one of the least visited National Park units within the United States, it is fitting to contribute this work to a volume dedicated to a paleontologist who has made a career of exploring places where few had gone before him.

METHODS

Photographic data of the tyrannosaur track described here were obtained using a digital camera in the field. A three-dimensional model of the track was created using the software Agisoft Metashape Standard v1.7.3. In the software, sixty photos from different angles were added, aligned, and used to build a dense cloud with texture. The trimmed data of the 3D model was exported and saved as an obj. file. This obj. file was then imported into another software, Cloud-Compare v2.13 alpha, to create a heat map of the track.

GEOGRAPHIC AND GEOLOGIC BACKGROUND

Aniakchak National Monument and Preserve (ANIA), comprises approximately 240,000 hectares and is one of the least-visited parks within the United States National Park Service system (Fig. 1). Established in 1978, the park is centered around the massive Aniakchak Caldera, a circular volcanic feature approximately 10 kilometers wide with walls ranging from a few hundred meters to over a thousand meters in height. Much of the landscape seen today has been shaped by Holocene-era volcanic activity that included the collapse of the magma chamber beneath the caldera around 3,590 cal. B.P., along with ten other volcanic events that occurred between 7,000 BP and 1931 (Hubbard, 1931; Jaggar, 1932; Miller and Smith, 1987; Beget et al., 1992; Bacon et al., 2014). Aside from the Holocene volcanic deposits and the Pleistocene sedimentary deposits, sedimentary rocks within Aniakchak National Monument range in age from the Upper Jurassic (Naknek Formation) to Eocene

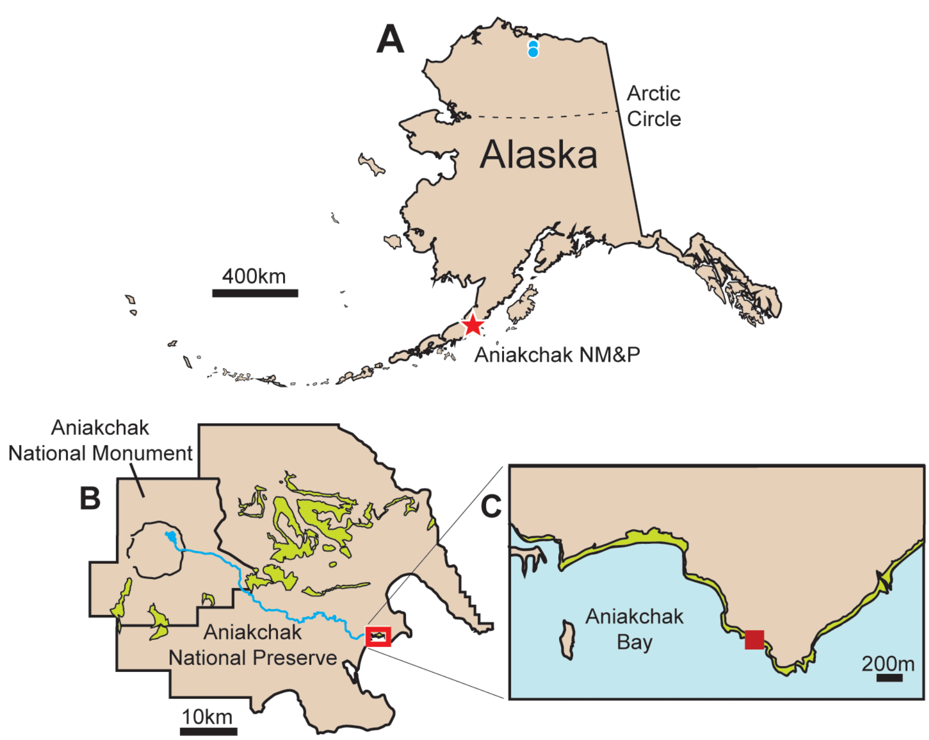

FIGURE 1. Location of Aniakchak National Monument, the study area for this report. Blue dots in **A** represent locations of primary bonebeds in correlative Prince Creek Formation. The green band in **B** represents coastal exposures of Chignik Formation. Red square in **C** represents the location where the track was found.

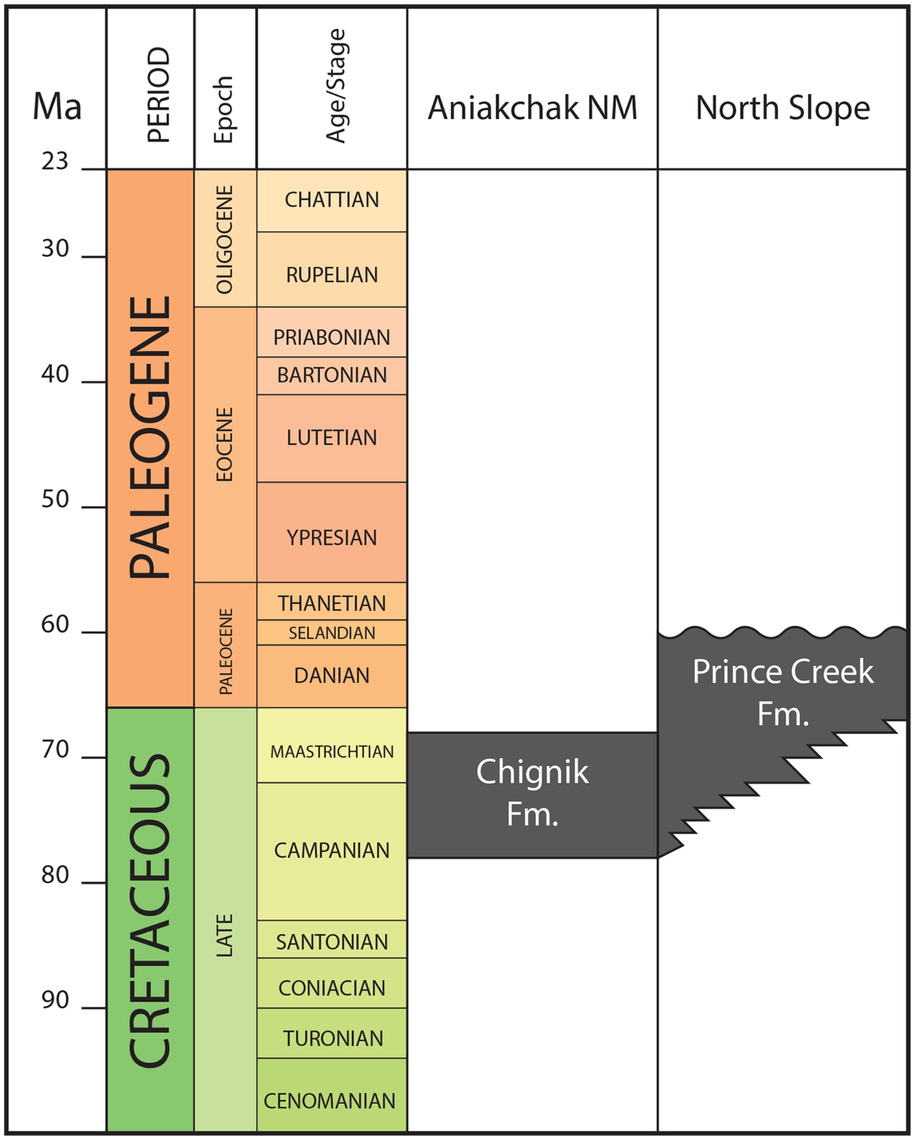

FIGURE 2. Stratigraphic correlation of Chignik and Prince Creek formations (modified from Fiorillo, 2018).

(Tolstoi Formation) and are also preserved in the park (Detterman et al., 1981; Wilson et al., 1999).

These Mesozoic and younger rocks are part of the Peninsular Terrane, a structural unit encompassing much of southwestern Alaska. Paleomagnetic reconstructions based on the Upper Cretaceous and Lower Tertiary volcanic rocks of this terrane suggest that the sediments of the Chignik Formation were initially deposited at nearly their current latitude of approximately 57^{o} North (Hillhouse and Coe, 1994). The Chignik Formation was named by Atwood (1911) for rocks exposed in the vicinity of Chignik Lagoon, approximately 75 kilometers southwest of our study site in Aniakchak Bay. The formation has a maximum stratigraphic thickness of approximately 600 m in the type area of Chignik Bay (Detterman et al., 1996). Outside of the type area, deposit thicknesses start to change significantly, thinning rapidly to the northeast and southwest (Detterman et al., 1996).

Based on the presence of marine bivalves, the age of the Chignik Formation was interpreted as late Campanian to early Maastrichtian (Detterman et al., 1996). These data suggest then, that the Chignik Formation exposed in Aniakchak Bay is approximately correlative with dinosaur-bearing sections in the Prince Creek Formation along the

FIGURE 3. Annotated outcrop photograph illustrating the depositional settings for where the track in this report was found.

Colville River of northern Alaska (Fig. 2, Fiorillo, 2018).

Fiorillo and Parrish (2004) originally measured a 280 m section of the Chignik Formation in the study area in Aniakchak Bay. Their documentation was later expanded by extending this section to encompass slightly more of the local marine context and adding additional details of the sedimentology (Fiorillo et al., 2019). Detailed sedimentological work on the upper 300 m of the section indicates that the entire section represents a tidally influenced estuary-fill. Marine shoreface deposits are incised by a thick sandstone package interpreted as a multi-story, meandering fluvial channel valley-fill. This is overlain by outer estuary deposits, containing two thick red paleosols, culminating in estuary mouth sands with disarticulated bivalve shells. This succession is overlain by an inner estuarine succession containing weakly developed paleosols, tidal channels, tidal flats, and thin coals, overlain by a tidally influenced alluvial succession containing small meandering fluvial channels, floodplain successions, and thin, grey and red paleosols (Fiorillo et al., 2019, 2022). The tyrannosaurid track was found in a large block (approximately 60 cm by 75 cm) on a prominent point along the coast (Fig. 3). Based on size and lithological characteristics, the block is likely derived from a 4 m-thick, multi-story channel sandstone that overlies a thick, red, upper estuarine paleosol. Sand and mud tidal flats and splay deposits overlie and interfinger with the other facies in this vicinity.

TRACK DESCRIPTION

A single large tridactyl, mesaxonic track was found in 2022 which is preserved in epirelief (Fig. 4). The digits are long and linear, and the preserved digits taper to points. Digits III and IV are well preserved, while digit II is incomplete. In addition to the sharply terminated distal end, digit III also has a slight sinusoidal curve. The length of the track is 55 cm, with the lengths of digits II, III, and IV are respectively, 26 cm, 55 cm, and 35 cm. The outer digits (digits II and IV) are diverged to 27 and 26 degrees from digit III, respectively. The morphology of this track allows attribution as a large non-avialan theropod.

Given the track length of 55 cm, using an equation of 4X the track length as an estimate of hip height, and 3.75X the hip height as an estimate of body length (Alexander, 1976; Henderson, 2003; Fiorillo and Tykoski, 2016), this track was made by a non-avialan theropod approximately 825 cm in length, or over 8 meters. Such a body length is approximately 60% larger than previously recognized from this ichnofauna (Fiorillo et al., 2019). There are a great number of tridactyl non-avian theropod ichnotaxa. It is not the purpose of this paper to review all of the nuances distinguishing these various taxa and debates on ichnotaxon validity such as the discussions surrounding *Buekeburgichnus* and *Megalosauripus* (e.g., Thulborn, 2001; Castenera et al., 2014; Razzolini et al., 2017).

A similarly aged theropod track, *Bellatoripes*, warrants some discussion as it was described from Wapiti Formation (upper Campanian – lower Maastrichtian) in northeastern British Columbia (McCrea et al., 2014). The diagnosis for this taxon is generally broad for individual tracks, with characters such as longer than wide, and digits that are thick proximally but taper strongly digitally. The diagnosis includes pace length, stride length, pace angulation and trackway width. The track described here, though most similar to *Bellatoripes* in a very broad sense (Fig. 4), is isolated rather than part of a trackway so a fuller, more detailed, comparison with this ichnotaxon is not available. Further, as northern theropod footprints, though it is tempting that these tracks may be the same ichnogenus, it remains that there is approximately 2000 km between northeastern British Columbia and southwestern Alaska, and it would be unwise to invoke a geographic justification for attribution.

Instead, we focus instead on a subjective comparison of this track to two of the more commonly discussed theropod ichnotaxa, *Grallator* and *Eubrontes*. Several authors have quantified the differences between these two ichnogenera (Weems, 1992; Olson et al., 1998; Smith and Farlow, 2003). In general, the most significant aspect distinguishing these two ichnogenera is the relative length of digit III in relation to digits II and IV, and the track length as a whole. Smith and Farlow (2003) relied more on simple ratios between digits III and II, and digits III and IV which allowed them to distinguish the two ichnotaxa by *Grallator* having a proportionately longer digit III than *Eubrontes*. Because of the incomplete nature of digit II in the specimen described here, we only compare the simple ratios for digits III and IV (Table 1) for *Grallator* and *Eubrontes* with the track described here. Comparison of the digit III/IV length ratio for the Aniakchak track described here with those provided by Smith and Farlow (2003) shows the Alaska track to have a greater affinity with *Grallator* than with *Eubrontes*.

TABLE 1. Average ratios of digit lengths for *Grallator* and *Eubrontes* based on original sample data (17 and 16 tracks, respectively) from Smith and Farlow [54], as well as the ratios for the Aniakchak track (ANIA) described here. Note that the ratios indicate that digit III is proportionately longer in *Grallator* than in *Eubrontes*. Based on these ratios, the Aniakchak track is assigned to the ichnogenus *Grallator*

Taxon	III:IV
Grallator	1.22
Eubrontes	0.93
Grallator (ANIA)	1.57

DISCUSSION

The paleontological survey work in Aniakchak National Monument continues to increase the dinosaur track record from the Alaska Peninsula and provide new insights into high-latitude dinosaur biodiversity and adaptation to life in the North. The discovery of dinosaurs in the high latitudes initially puzzled researchers and one of the early ideas to explain these discoveries in such extremely seasonal latitudes was that these Arctic dinosaurs must have undergone large-scale migrations to cope with the extreme nature of the ancient high-latitude environment (Fiorillo, 2018). While it is no longer thought that dinosaurs survived the winter using seasonal migrations like caribou (Fiorillo and Gangloff, 2001; Chinsamy et al., 2012; Fiorillo et al., 2014), evidence does suggest that dinosaurs migrated between what is now modern Asia and North America through Alaska during the Cretaceous (Russell, 1993; Cifelli et al., 1997; Sereno, 2000; Fiorillo, 2008; Zanno, 2010; Fiorillo and Adams, 2012; Fiorillo et al., 2018b; Kobayashi et al., 2019). The fossil records of Alaska and eastern Asia show some of the most robust evidence for this dispersal route with the close phylogenetic relationship between *Edmontosaurus* and *Kamuysaurus* (Kobayashi et al., 2019), as well as with the enigmatic theropods, the Therizinosauridae (Fiorillo et al., 2018b).

Late Maastrichtian tridactyl tracks measuring over 70-80

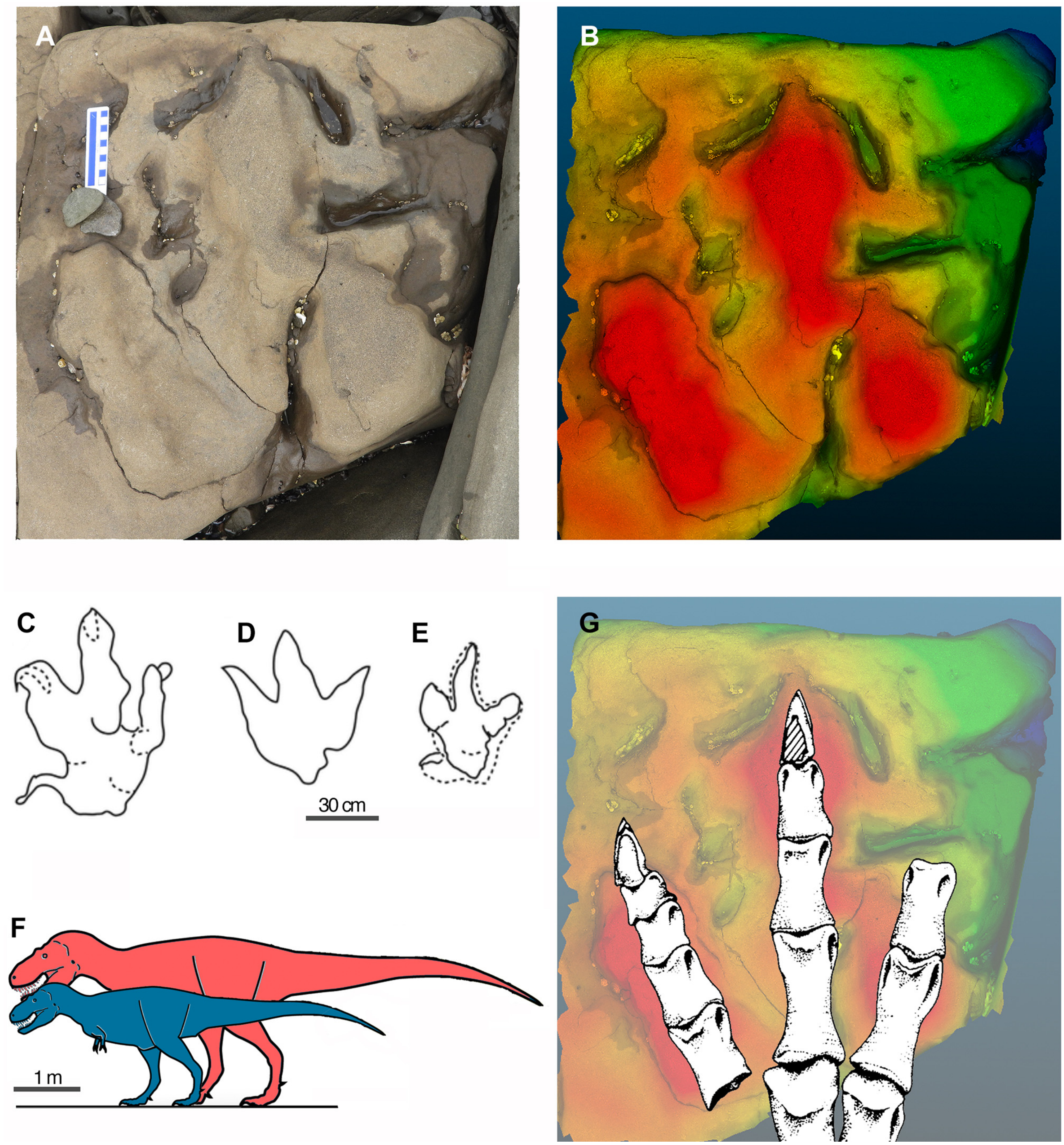

FIGURE 4. Composite track figure. **A**. Tyrannosaur track as found in the field. **B**. Heat map which illustrates the general morphology of the track. **C – E**. Track outlines from Razzolini (2016) of ichnogenera *Tyrannosauripus*, *Bellatoripes*, *Bueckeburgichnus*, respectively. **F**. Comparison of body size between *Nanuqsaurus* and *Albertosaurus* (modified from Fiorillo & Tykoski, 2014). The larger *Albertosaurus* serves as a proxy for the trackmaker in this study. G. Pes of *Albertosaurus* (Molnar, 1980) overlain on Aniakchak footprint to illustrate the compatibility between track and skeletal structure of large theropod.

cm (approximately 68% larger than the track described here), *Tyrannosauripus* (Lockley and Hunt, 1994), have been attributed to the apex tyrannosaur, *Tyrannosaurus rex* (Lockley and Hunt, 1994; Manning et al., 2008). However, based on biostratigraphy, it has been shown that the Chignik Formation is older and is likely late Campanian to early Maastrichtian in age (Detterman et al., 1981; Fiorillo and Parrish, 2004; Fiorillo et al., 2019). Based on comparisons of its lengths with similar tridactyl tracks (e.g., Enriquez et al., 2022) from correlative ages, the track described here represents a full-sized (i.e., adult) tyrannosaur for its geologic age. So far, at least one hundred tracks of herbivorous dinosaurs, dominated by hadrosaurs, have been recorded from the section at this park (Fiorillo et al., 2019). This is the second definitive non-avian theropod track, suggesting a general rareness of carnivory in the estuarine environment of this region during the latest Cretaceous.

The well-known dinosaur remains in the Prince Creek Formation, approximately 1,500 kilometers farther north in Alaska, overlap in age with the dinosaur discoveries in the Chignik Formation (Fiorillo and Parrish, 2004; Flaig et al., 2014; Fiorillo, 2018). Considering recent work by others (Druckenmiller et al., 2021), we first review the study of the correlative tyrannosaur, *Nanuqsaurus* (Fiorillo and Tykoski, 2014). We then briefly review biogeographic patterns in body size changes in insular populations that are observed in modern vertebrates. We conclude by discussing the implications for the track described in this study.

Without providing the typical details of methods used to measure tooth crown height, and why taxa were chosen for comparisons, Druckenmiller et al. (2021) challenged the assertion that the tyrannosaurid, *Nanuqsaurus* (Fiorillo and Tykoski, 2014), described from the Kikak-Tegoseak Quarry in the Prince Creek Formation was of a diminutive nature. In the absence of such details in methodologies and practices, it is challenging to provide any in-depth understanding of any presented counter points from that study. What is of interest from the work by Druckenmiller et al. (2021) is the mention of additional, yet undescribed and unfigured, tyrannosaurid material from the Prince Creek Formation. But these specimens were collected across an approximately 20 km transect and therefore are unassociated and perhaps taxonomically distinct from each other. Further, even with the shallow dips of the strata that occur across the river exposures of the Prince Creek Formation (Flaig et al., 2011), given the range of radiometric dates reported through the formation (Phillips, 2003; Flaig et al., 2014) there is likely some significant geologic time represented over this transect, of the scale of 10^6 years, and of the scale of taxonomic turnover in dinosaurs (Dodson, 1990). Until such details are presented for critique, we instead focus here on the details presented in Fiorillo and Tykoski (2014) regarding an associated set of bones from a single quarry.

Though the skeletal remains are limited, *Nanuqsaurus* was diagnosed on characters such as thin, rostrally forked, spur of the fused parietals on the dorsal skull roof that overlaps and separates the frontals within the sagittal crest; a frontal with a long, rostrally pointed process separating the prefrontal and lacrimal facets; and the first two dentary teeth/alveoli much smaller than the remaining dentary teeth (Fiorillo and Tykoski, 2014). Despite the high percentage of missing skeletal data, Bremer support for this taxon and its taxonomic relationships to other tyrannosaurs was higher than Bremer support amongst more basal tyrannosaurs with more complete skeletal material (Fiorillo and Tykoski, 2014), indicating that despite the incomplete nature of the type material, the necessary skeletal remains for understanding the distinctiveness of the taxon were present for *Nanuqsaurus*. Further, the type material for *Nanuqsaurus* included the presence of a robust peg-in-socket articulation between the maxillae and nasals and was interpreted as a characteristic of a mature individual as it is a character shared by other tyrannosaurs (Fiorillo and Tykoski, 2014). From these data, Fiorillo and Tykoski (2014) estimated a skull length of approximately 60-70 cm and a body length of approximately 6 meters, suggesting an animal approximately half the body length of a full-sized *Tyrannosaurus rex* from the latest Maastrichtian and approximately two-thirds the body length of a correlative *Albertosaurus*.

The evolution of body size changes within insular populations have been studied extensively across a variety of taxa (e.g., Van Valen, 1973; Heaney, 1978; Lomolino, 1985; 2005; Anderson and Handley, 2002; Pafilis et al., 2009; Lomolino et al., 2013, McFadden and Meiri, 2021; van der Geer et al., 2016; Stadler et al., 2022; Hayashi et al., 2023). It is widely recognized that the causes of these changes in body size within insular populations are the result of a combination of selective forces that include geographic characters as well as climate parameters (Heaney, 1978; Lomolino, 1985; 2005; Anderson and Handley, 2002; Lomolino et al., 2012, van der Geer et al., 2016), though there has been some challenges to the broader recognized patterns from some studies of mammalian carnivores and reptiles (Meiri et al., 2005; 2007; Itescu et al., 2018). Fiorillo and Tykoski (2014), followed the broader patterns recognized, and largely attributed the diminutive size of the high-latitude *Nanuqsaurus* when compared to correlative lower-latitude tyrannosaurs to the

FIGURE 5. Reconstruction comparing potential prey sizes, hadrosaurs, and the relative sizes of Aniakchak tyrannosaur (left), and *Nanuqsaurus* (right) in their respective environments. Artwork by Masato Hattori.

isolated depositional setting of the Prince Creek Formation, to the rising Brooks Range in northern Alaska, and suggested this mountain range may have largely separated this section of coastal plain from other parts of North America, and therefore functionally making it serve as an island.

Further, in the modern Arctic there are profound seasonal changes in light regime and such changes affect biological productivity and thus highly impact seasonal resource availability (Blix, 2005, 2016). It has been interpreted that a similarly varying light regime was present in the Cretaceous (e.g., Fiorillo, 2018). These inferred light conditions similarly created limited food resource availability for mega-herbivores, namely the hadrosaurs.

In a recent study (Fiorillo et al., 2022) compared paleoclimate conditions between the Cretaceous of northern Alaska which was at approximately 71°-85°N paleolatitude and the Cretaceous of southern Alaska which had a paleolatitude of approximately 57°N paleolatitude. Fiorillo and others (2022) demonstrated there was some variation in climate parameters, and that differences in conditions were different between northern and southern Alaska during the Cretaceous. Specifically, both mean annual temperature (~5-13°C) and mean annual precipitation (~661- ~1250 mm/year) varied across the region.

The track size of the predatory dinosaur described here contrasts with the projected body size of the diminutive *Nanuqsaurus*. In terms of interpreted body size from track length, the track length of 55 cm for the Aniakchak footprint provides an estimate of body length of greater than 8 meters (see above). This interpreted body length is consistent with the body length of correlative theropods, such as *Albertosaurus*, further to the south. *Albertosaurus* is known from several nearly complete specimens from the Red Deer River area of southern Alberta, Canada, and has a body length of approximately 9 m. This contrast in body size between the far northern tyrannosaur, *Nanuqsaurus*, and the tyrannosaur reported here from Aniakchak National Monument (Fig. 5), suggests a combination of geographic and climatic factors produced different selective pressures on the Tyrannosauridae between the northern and southern extremes of Alaska.

CONCLUSIONS

There are a growing number of records of dinosaurs from Cretaceous rocks around the state of Alaska. Nevertheless, very few fossil records of terrestrial vertebrates are known from the Mesozoic rocks of the southwestern part of the state. With the documentation of a large tyrannosaur track (55 cm long), this study adds new information on the dinosaur footprint record preserved in the Cretaceous Chignik Formation in Aniakchak National Monument of the Alaska Peninsula. This rock unit was deposited at approximately its current latitude of almost 57°N and thus the dinosaurs living in the region were living in the high latitudes.

The track size of the predatory dinosaur described here contrasts with the body size of the diminutive *Nanuqsaurus*, the tyrannosaurid known from bones from the approximately correlative Prince Creek Formation on the North Slope, some

1500 km further north in Alaska. This contrast in body size between the far northern tyrannosaur, and the tyrannosaur reported here suggests that the adaptative pressures of the very far north were different than those experienced in the lower high latitudes.

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AUTHOR CONTRIBUTIONS

ARF, YK, and PJM designed the project. ARF drafted the initial manuscript. All authors contributed to the data gathering, data analysis, and edited the manuscript.

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