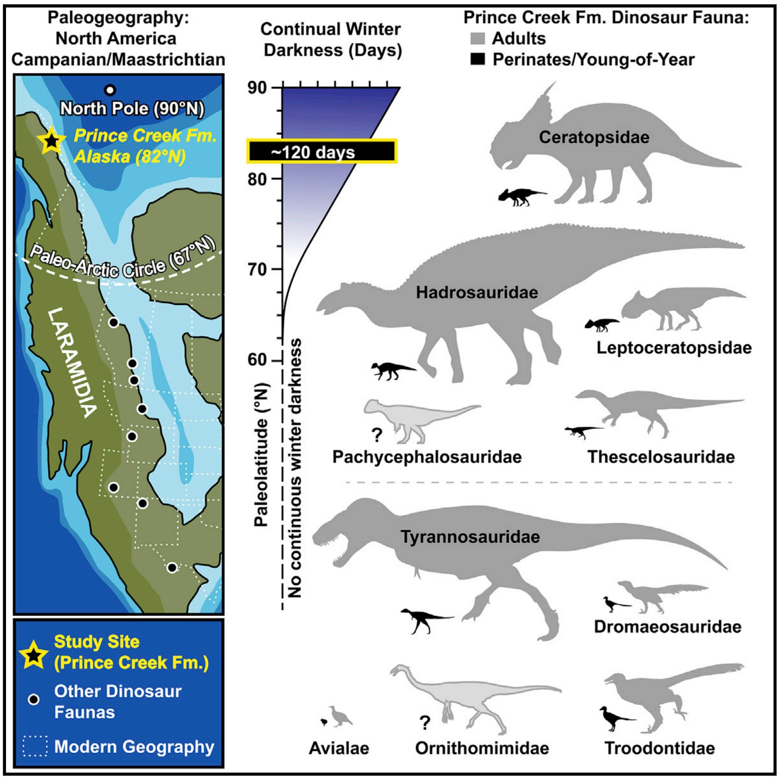
Article

Current Biology

Nesting at extreme polar latitudes by non-avian dinosaurs

Graphical abstract



Highlights

- Perinatal dinosaurs reported from the Late Cretaceous of northern Alaska
- A diverse assemblage of dinosaur species reproduced in the Arctic
- Large- and small-bodied taxa were nonmigratory year-round residents
- Paleoenvironmental constraints suggest polar-specific life history strategies

Authors

Patrick S. Druckenmiller,
Gregory M. Erickson,
Donald Brinkman, Caleb M. Brown,
Jaelyn J. Eberle

Correspondence

psdruckenmiller@alaska.edu

In brief

Druckenmiller et al. document reproduction in a diverse assemblage of herbivorous and carnivorous dinosaurs from polar paleolatitudes of the Late Cretaceous Prince Creek Formation. Both large- and small-bodied dinosaurs were nonmigratory year-round residents and likely exhibited polar-specific life history strategies, including endothermy.

Druckenmiller et al., 2021, Current Biology *31*, 1–10

https://doi.org/10.1016/j.cub.2021.05.041

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

Current Biology

CellPress

Article

Nesting at extreme polar latitudes by non-avian dinosaurs

Patrick S. Druckenmiller,[1,2,7,*] **Gregory M. Erickson,**[3] **Donald Brinkman,**[4] **Caleb M. Brown,**[4] **and Jaelyn J. Eberle**[5,6]
[1]University of Alaska Museum, 1962 Yukon Drive, Fairbanks, AK 99775, USA
[2]Department of Geosciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
[3]Department of Biological Science, Florida State University, 319 Stadium Drive, FL 32306, USA
[4]Royal Tyrrell Museum of Palaeontology, Drumheller, AB T0J 0Y0, Canada
[5]Univerity of Colorado Museum of Natural History, 265 UCB, Boulder, CO 80309, USA
[6]Department of Geological Sciences, University of Colorado, Boulder, CO 80309, USA
[7]Lead contact
*Correspondence: psdruckenmiller@alaska.edu
https://doi.org/10.1016/j.cub.2021.05.041

SUMMARY

The unexpected discovery of non-avian dinosaurs from Arctic and Antarctic settings has generated considerable debate about whether they had the capacity to reproduce at high latitudes—especially the larger-bodied, hypothetically migratory taxa. Evidence for dinosaurian polar reproduction remains very rare, particularly for species that lived at the highest paleolatitudes (>75°). Here we report the discovery of perinatal and very young dinosaurs from the highest known paleolatitude for the clade—the Cretaceous Prince Creek Formation (PCF) of northern Alaska. These data demonstrate Arctic reproduction in a diverse assemblage of large- and small-bodied ornithischian and theropod species. In terms of overall diversity, 70% of the known dinosaurian families, as well as avialans (birds), in the PCF are represented by perinatal individuals, the highest percentage for any North American Cretaceous formation. These findings, coupled with prolonged incubation periods, small neonate sizes, and short reproductive windows suggest most, if not all, PCF dinosaurs were nonmigratory year-round Arctic residents. Notably, we reconstruct an annual chronology of reproductive events for the ornithischian dinosaurs using refined paleoenvironmental/plant phenology data and new insights into dinosaur incubation periods. Seasonal resource limitations due to extended periods of winter darkness and freezing temperatures placed severe constraints on dinosaurian reproduction, development, and maintenance, suggesting these taxa showed polar-specific life history strategies, including endothermy.

INTRODUCTION

Beginning in the 1950s, non-avian dinosaur remains (hereafter dinosaurs) were discovered in the Arctic and Antarctic,[1,2] regions once thought to experience adverse environmental conditions unexpected for reptilian occupation.[3–5] This led to hypotheses that some or all of these dinosaurs were either year-round polar inhabitants or alternatively that at least large-bodied species migrated to such settings, taking advantage of seasonally abundant warm season resources and possibly to reproduce.[3,6,7] Direct evidence for high-latitude dinosaurian reproduction in the form of perinatal teeth and bones, embryos, brooding individuals, or eggs is rare. Furthermore, most of these few localities also lacked exceptionally adverse environmental conditions at any time of year. Specifically, from Laurasia, hadrosaurid (duck-billed dinosaurs) and theropod (primarily carnivorous dinosaurs) eggshell fragments were recovered from the Upper Cretaceous Kakanaut Formation of northeastern Russia.[8] The site lies at ~70°–75°N paleolatitude and experienced ~45 days of continuous winter darkness with moderate mean annual temperatures (MATs) of ~10°C (50°F).[8] From Gondwana, femora of very young indeterminate ornithopods have been found in mid-Cretaceous formations in southeastern Australia. Specifically, perinatal remains from the Griman Creek Formation occur at a South Temperate paleolatitude of 60°S that experienced a moderately warm climatic regime (MAT = ~14°C [°57 F]).[9] Neonate to yearling individuals are also known from the Eumeralla and Wonthaggi Formations of Australia at a paleolatitude of ~70°S, where the light regime was similar to the Kakanaut Formation.[9] The paleotemperature estimates for these formations are poorly constrained (−6°C [21°F] up to +10°C [50°F] MAT), but the presence of ectothermic taxa typically found in warmer temperate zones (e.g., temnospondyls, crocodylomorphs, and testudines) strongly supports the warmer estimates.[9,10]

In contrast, a notable high-latitude dinosaur assemblage where extreme and adverse winter conditions definitively occurred is found in the Upper Cretaceous Prince Creek Formation (PCF) of northern Alaska.[1,2] Deposition of the PCF occurred at 80°–85°N paleolatitude[11,12] and records the northernmost known extent of dinosaurian occupation (Figure 1). Owing to the exceptionally high latitude, where winter forage was limited, the PCF experienced a highly seasonal polar light regime and climatic extremes unlike that experienced by other dinosaurian faunas. Specifically, the formation was deposited under a

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

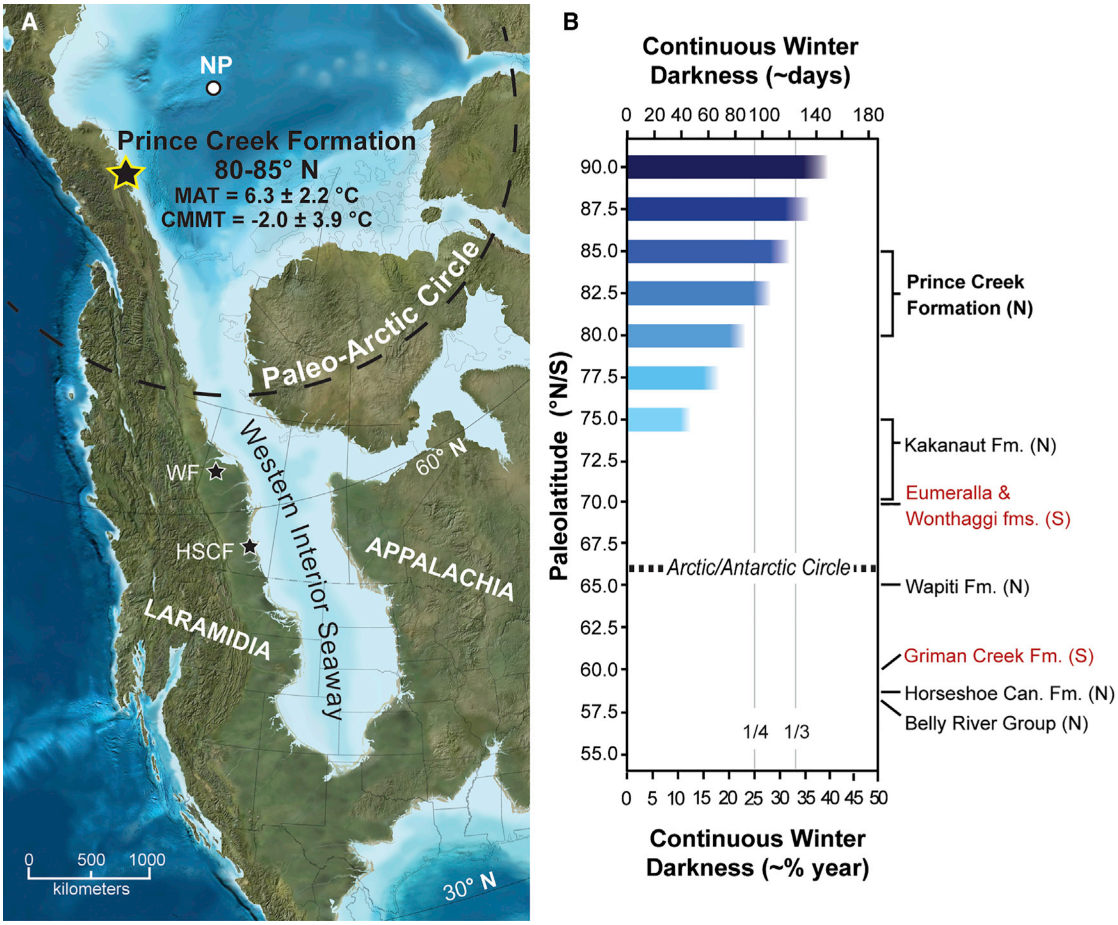


Figure 1. Location and paleoenvironmental conditions for the Prince Creek Formation

(A) North American paleogeography at 72 Ma.

(B) Comparison of polar light regime as approximated by the relative extent of continuous winter darkness by latitude (measured in number of days and percentage of year).

CMMT, cold month mean temperature; MAT, mean annual temperature; N, north; NP, North Pole; WF, Wapiti Formation; HSCF, Horseshoe Canyon Formation; S, south.

climatic regime with up to ~120 days of continuous winter darkness, and an MAT of just 6.3°C ± 2.2°C (43.3°F ± 4.0°F), suggesting the dinosaurs, if winter residents, endured freezing winter conditions with occasional snowfall.[13] This formation preserves large and small taxa, including herbivorous hadrosaurids (duck-billed dinosaurs), ceratopsians (horned dinosaurs), thescelosaurids (small bipedal ornithopods/neornithischians), and pachycephalosaurids (dome-headed dinosaurs), as well as carnivorous tyrannosaurids, deinonychosaurs, and ornithomimosaurians.[2,14] Notably, although a diversity of endothermic mammals and birds also occur in the PCF,[15] terrestrialized ectotherms (e.g., lissamphibians, testudines, choristodires, squamates, and crocodilians) that are commonplace in warmer, contemporaneous lower latitude formations are absent,[5] likely due to the paleoclimatic conditions. With the exception of the Kakanaut Formation, the PCF is distinct from other high-latitude dinosaur-bearing formations where several of these thermally restricted ectothermic taxa are present.[9,10]

The PCF has figured prominently in the development of both the "year-round" and "migratory" hypotheses regarding high-latitude occupation by dinosaurs.[3,7] It has been posited that as permanent residents the smaller (<30 kg) PCF dinosaurs, presumably incapable of long distance treks, must have hibernated during the winter (perhaps in burrows), whereas larger forms fasted or gained sustenance on the limited seasonal forage.[16,17] Alternatively, the migratory hypothesis proposes that large herding megaherbivores (e.g., most hadrosaurids and ceratopsids) were primarily summer PCF occupants.[3,18] This hypothesis posits that in the autumn, populations trekked as much as 3,200 km, crossing up to 30° of latitude to lower latitudes where more equable climatic conditions existed and foliage had recovered from the previous year's foraging. In the spring, they returned north to the Arctic, feeding on the poleward-moving wave of vernal productivity brought about by increases in day length and temperature. Predators (e.g., tyrannosaurids) perhaps followed the migrating herbivores throughout their annual treks.[3,18] The migratory hypothesis, like the year-round scenario, envisions smaller taxa overwintering in the Arctic owing to their small sizes. Although sexually immature, post-nestling-stage individuals (*sensu* Horner and Currie[19]) of large

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

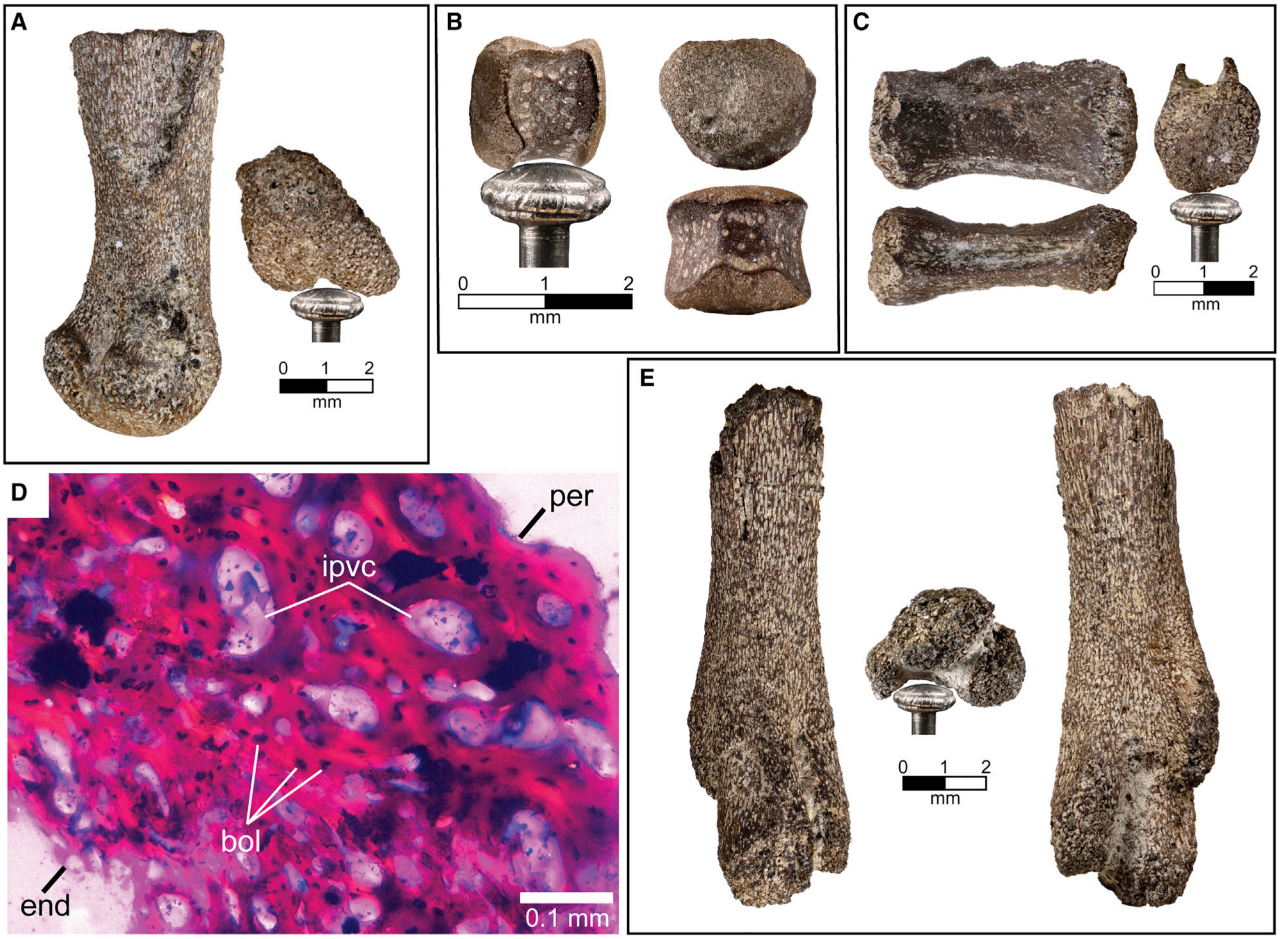


Figure 2. Perinatal skeletal elements of Prince Creek Formation dinosaurs

(A) Medial and distal views of distal femur(?), Ornithischia indet. (UAMES 41721).

(B) Lateral, articular, and ventral views of caudal centrum, Ornithischia indet. (UAMES 41633).

(C) Lateral, ventral, and articular views of caudal centrum, Theropoda indet. (UAMES 51934).

(D) Transverse thin section of Ornithischia indet. long bone (UAMES 52384) showing the extreme porosity attributable to large, irregularly shaped vascular canals and the incompletely formed primary vascular canals on both the endosteal and periosteal surfaces.

(E) Extensor, distal, and flexor views of distal tarsometatarsus, Avialae indet. (UAMES 41722).

bol, bulbous osteocyte lacunae; end, endosteal surface; ipvc, incipient primary vascular canals; per, periosteal surface. See also Figures S1 and S2.

hadrosaurids,[20] ceratopsids,[21] and dromaeosaurid taxa[22] have been described from the PCF, direct evidence of their reproduction in the paleo-Arctic in the form of eggs, perinatal remains, or brooding individuals has not been reported.

A three-decade-long field program and extensive microfossil analyses in the PCF led to recovery of numerous minute dinosaurian skeletal elements and teeth (Figures 2, 3, and S1–S5). These discoveries led us to consider whether the remains represent very young animals indicative of high-latitude nesting. We first diagnose the remains using taxonomically informative anatomical features and then determine their ontogenetic status based on surficial morphology, histological indices, and inter- and/or intraspecific scaling comparisons with adults. We use these data to test the "year-round" and "migratory" hypotheses and, in combination with refined paleoenvironmental data for the PCF,[11,13] glean insights into polar-specific dinosaurian life history strategies.

RESULTS

The minute PCF fossil bones consist of long bones, vertebrae, and cranial elements ($n > 100$). Several of the elements are referable to Ornithopoda indet., Thescelosauridae, Theropoda indet., and Deinonychosauria (Figures 2 and S2). Representative specimens for each taxon exhibit features consistent with perinatal or young-of-the-year[23] developmental status: (1) the long bones and vertebral elements have poorly formed articular surfaces that when viewed with incident light microscopy show calcified cartilage caps[24,25] (Figures 2A–2D and S2); (2) transverse and longitudinal plane petrographic histological analyses of the long bones show highly vascularized woven endochondral bone, calcified cartilage epiphyses, bulbous osteocyte lacunae, and a lack of annual growth lines[24–26] (Figures 2D and S2); and (3) the surfaces of all elements show extremely porous surface textures from the trapping of incompletely formed primary vascular

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

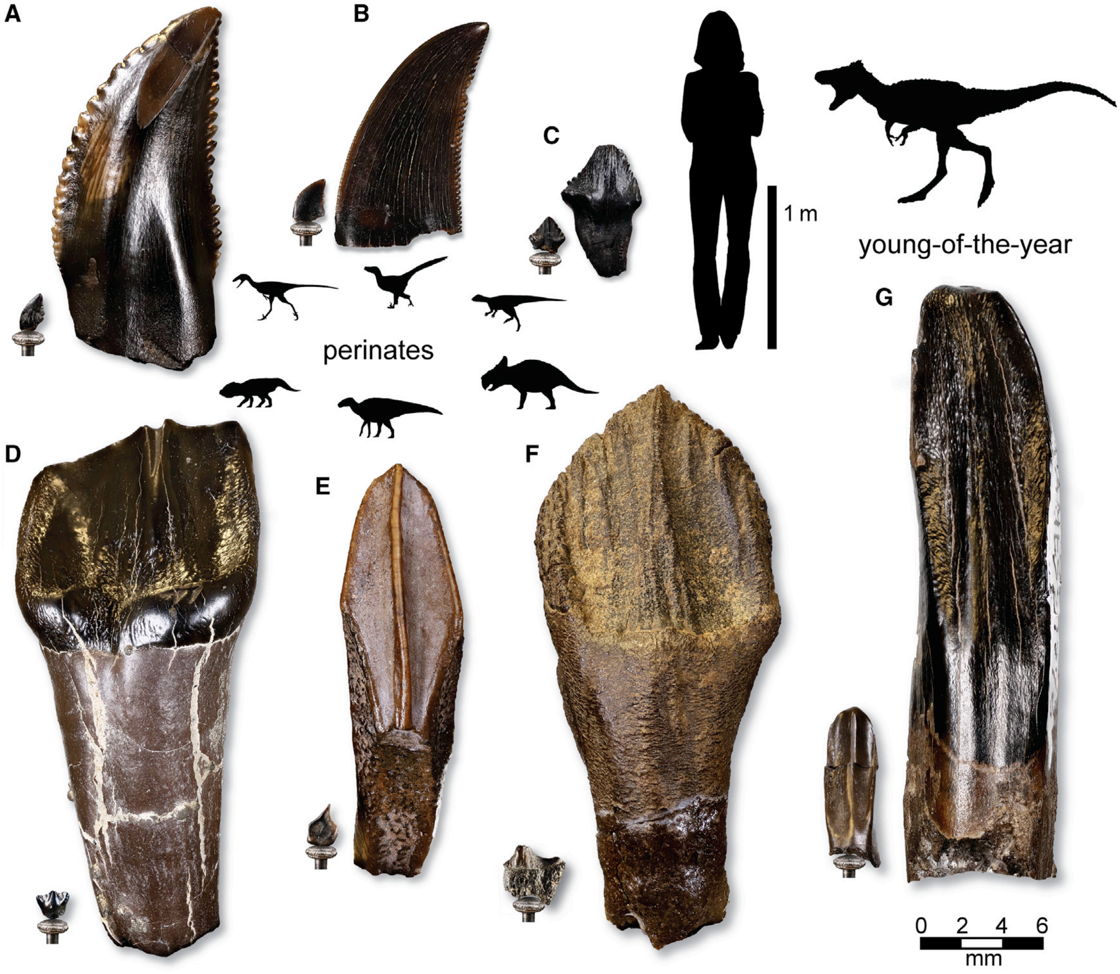


Figure 3. Comparative sizes of immature and mature teeth from Prince Creek Formation dinosaurs

(A) Troodontidae indet. (UAMES 52268, UAMES 51652).

(B) Saurornitholestinae indet. (UAMES 52292, UAMES 29574).

(C) Thescelosauridae indet. cheek teeth (UAMES 52230, UAMES 52272)

(D) Leptoceratopsidae indet. (UAMES 42720, UAMES 39298).

(E) Hadrosauridae (cf. *Ugrunaaluk*) (UAMES 42739, UAMES 12491).

(F) Ceratopsidae (cf. *Pachyrhinosaurus*) (UAMES 52467, UAMES 29413).

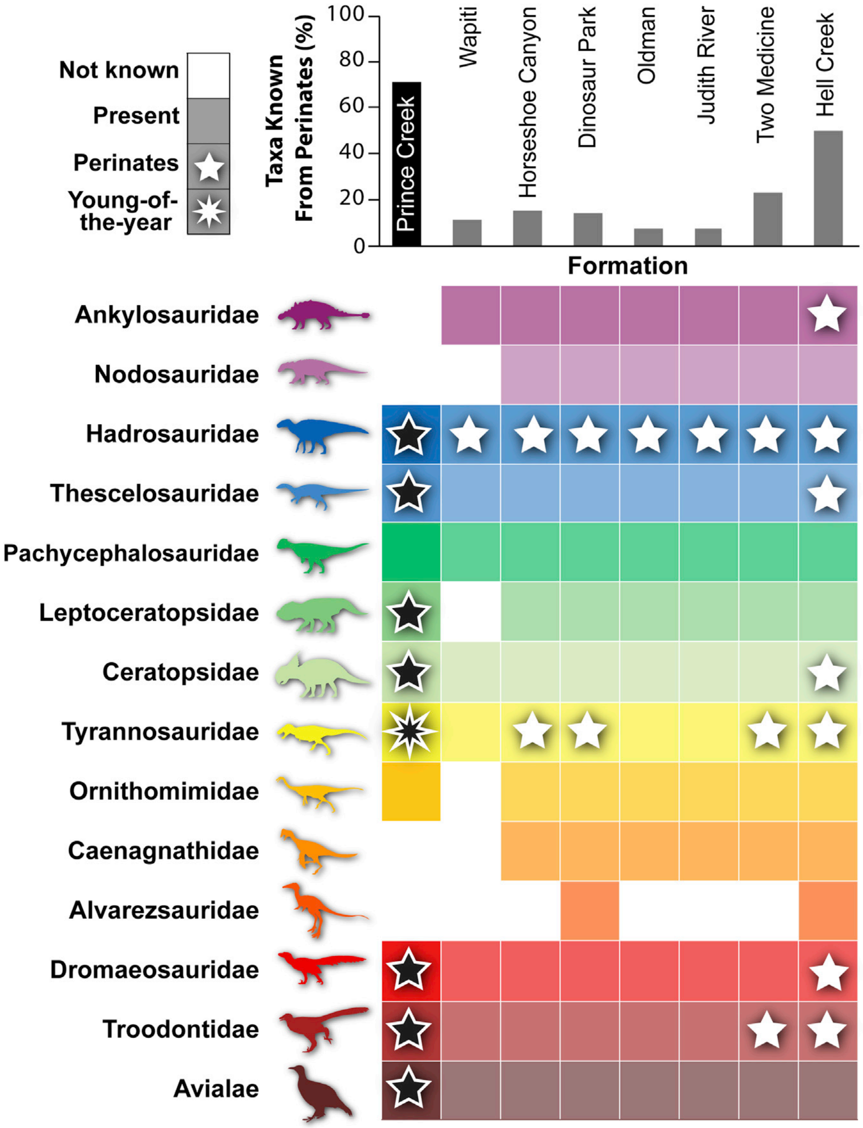
(G), Tyrannosauridae (cf. *Nanuqsaurus*) premaxillary teeth (UAMES 17610, UAMES 29370). See also Figures S1 and S3–S5 for magnified views of teeth and further examples.

canals at the periosteal surfaces (also seen in the histologic sections;[24,27] Figures 2A–2D and S2). Notably, four small avian dinosaur (Avialae; bird) tarsometatarsi were also recovered that show comparable surface textures indicative of perinatal developmental status (Figure 2E).

More specifically, very small teeth representing both small- and large-bodied taxa were also recovered (Figures 3 and S3–S5). These provide more refined taxonomic assignments of the small PCF specimens than the skeletal elements. At least four ornithischian taxa are represented including Hadrosauridae (likely the large [6+ m total length] edmontosaurine *Ugrunaaluk kuukpikensis*/"*Edmontosaurus regalis*," the most common PCF hadrosaurid)[20] (Figures 3E and S4), Ceratopsidae (likely the large [5+ m total length] neoceratopsian *Pachyrhinosaurus perotorum*, the only known PCF ceratopsid)[28] (Figures 3F and S3), Leptoceratopsidae[29] (Figures 3D and S3), and Thescelosauridae[5] (Figures 3C and S3). At least three theropods, Troodontidae[5,30] (Figures 3A and S3), Dromaeosauridae[31] (Figures 3B and S3), and Tyrannosauridae (likely the large [5+ m total length] *Nanuqsaurus hoglundi*)[32] (Figures 3G and S3), are also present. The teeth, some of which are among the smallest known for these clades, show they come from very young individuals. Our scaling estimations for these taxa indicate diminutive body sizes inconsistent with later developmental stages (juveniles or adults) of small-bodied taxa.

Collectively, the osteological and dental data demonstrate the occurrence of perinatal and young-of-the-year from both large- and small-bodied dinosaurs in the PCF. These data represent the first direct evidence for dinosaurian reproduction for both large and small taxa at an extremely high (>75°N) latitude polar

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041



	Prince Creek	Wapiti	Horseshoe Canyon	Dinosaur Park	Oldman	Judith River	Two Medicine	Hell Creek
Ankylosauridae		▨	▨	▨	▨	▨	▨	★
Nodosauridae			▨	▨	▨	▨	▨	▨
Hadrosauridae	★	★	★	★	★	★	★	★
Thescelosauridae	★	▨	▨	▨	▨	▨	▨	★
Pachycephalosauridae	▨	▨	▨	▨	▨	▨	▨	▨
Leptoceratopsidae	★		▨	▨	▨	▨	▨	▨
Ceratopsidae	★	▨	▨	▨	▨	▨	▨	★
Tyrannosauridae	✷	▨	★	★	▨	▨	★	★
Ornithomimidae	▨		▨	▨	▨	▨	▨	▨
Caenagnathidae			▨	▨	▨	▨	▨	▨
Alvarezsauridae				▨				▨
Dromaeosauridae	★	▨	▨	▨	▨	▨	▨	★
Troodontidae	★	▨	▨	▨	▨	▨	★	★
Avialae	★	▨	▨	▨	▨	▨	▨	▨

Figure 4. Comparative occurrence of perinatal remains from Late Cretaceous (Campanian-Maastrichtian) formations in the northern portion of Laramidia

Data sources, by formation: Prince Creek (this study); Wapiti;[34] Horseshoe Canyon;[35,36] Dinosaur Park and Oldman;[36–38] Judith River;[38] Two Medicine;[36,38–41] Hell Creek.[38,42]

environment. Whether all PCF dinosaurs nested in the Arctic is currently unknown. Nevertheless, at least 13 dinosaurian species are known from the formation, but most are rare. Our findings show that minimally seven of these taxa, including large species that are consistently recovered from the PCF, reproduced in the Arctic. Our data also reveal the first direct evidence for polar reproduction by Mesozoic avialans. This represents the oldest unambiguous record for nesting by birds in any polar region, preceding other evidence for such behavior by ∼25 million years.[33]

Compared to other North American Late Cretaceous formations, particularly fossiliferous units from the northern portion of Laramidia, the PCF preserves an exceptionally high percentage of developmentally very young dinosaurs relative to known familial-level diversity. In total, perinatal material was recovered from seven dinosaur families, as well as birds, representing 70% of those known to occur in the PCF (Figure 4). The only PCF families not currently recognized by perinates are Pachycephalosauridae, the neonates of which are unknown globally, and Ornithomimidae, which lack teeth and make their discovery less likely. This high proportion of very young animals in the PCF, in both absolute and relative terms, is greater than that currently known for any North American Cretaceous formation, and potentially globally for the Mesozoic.

DISCUSSION

The high proportional representation of perinatal and young-of-the-year dinosaurs at the family level is an unexpected outcome of this study and establishes the PCF as a globally significant unit for investigating dinosaur reproduction. This is all the more remarkable when considering the relatively small areal extent of surficial outcrop of the PCF. Compared to extensive badland exposures of many Campanian and Maastrichtian rock units (e.g., Dinosaur Park and Hell Creek formations), dinosaur-bearing outcrops of the PCF are limited to a narrow ∼20 km band of near-vertical river-cut exposures along one bank of the Colville River. As such, our field investigations have necessarily focused on finding new micro- and macrofossil horizons such as those from which most of the perinatal remains are found. Our collection methods also use very fine mesh screens (≥500 μm), leading to the discovery of even the smallest bones and teeth. Although the vast majority of materials reported in this study are derived from time-averaged fossil assemblages, their small size, delicate nature, and quality of preservation suggest a limited degree of transport[43] and deposition of perinatal remains in close proximity to nesting areas. Given deposition within the distalmost portions of a coastal plain environment,[44,45] coastal settings appear to have been important areas of landscape use by developmentally young animals, although comparative sites from more inland Arctic settings are currently unknown.

The recovery of perinatal and young-of-the-year individuals of putative migratory megaherbivores (Hadrosauridae and Ceratopsidae) and megacarnivores (Tyrannosauridae), when viewed in conjunction with a refined understanding of the PCF environmental conditions, also provides a natural test of the "year-round" versus "migratory" hypotheses. Temperatures conducive to the incubation of eggs maximally spanned just 7 months in the PCF.[13] New evidence reveals prolonged

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

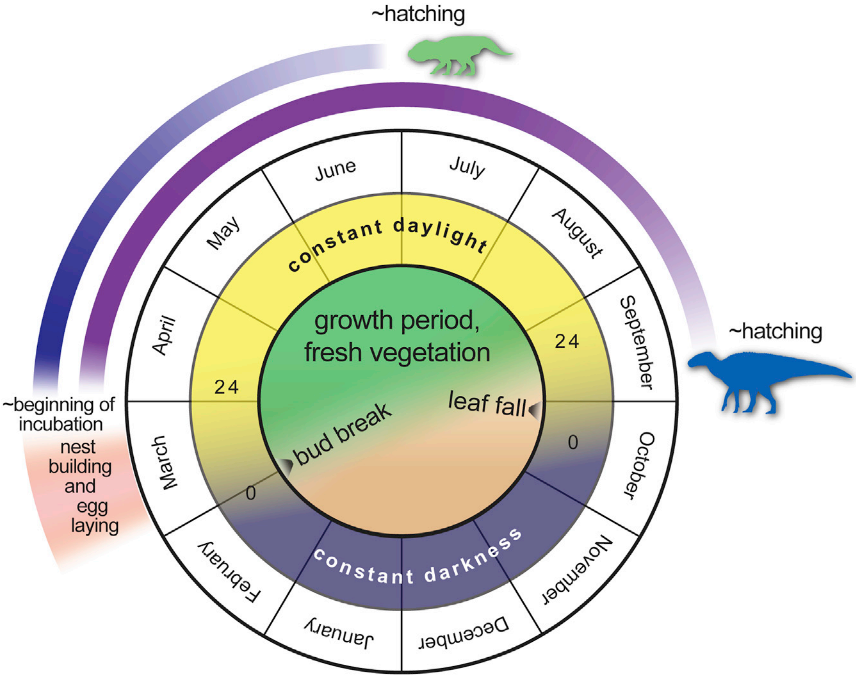


Figure 5. Reproductive phenology of Prince Creek Formation dinosaurs

Hypothetical annual chronology of reproductive events for two polar (∼82°N) dinosaurs (Hadrosauridae and Leptoceratopsidae) at 72 Ma. See text for discussion. Data for light, temperature, and plant phenology adapted from Herman et al.[13]

(∼2.5- to 6-month) incubation periods for non-avian dinosaurs, with larger eggs taking longer to incubate.[46] Prolonged incubation would have provided negligible post-hatching time for the young (especially in larger taxa) to attain sizes necessary to undertake long migrations, likely forcing residency throughout the polar winter. Hence, the results strongly support the "year-round" hypothesis. Nesting in the PCF by small-bodied, presumably non-migratory taxa, such as leptoceratopsids, thescelosaurids, and dromaeosaurids, is predicted by both the "migratory" and "non-migratory" hypotheses, but our data nevertheless provide the most compelling evidence that both small and large taxa nested in the paleo-Arctic.

The conclusion that PCF dinosaurs were year-round Arctic residents is supported by ancillary evidence based on subadult and adult fossils. Specifically, contrasts of dental and skeletal growth lines between subadult and adult PCF dinosaurs and close relatives from lower latitude temperate zone formations reveal distinctive differences, suggesting the PCF taxa were endemic to the Arctic.[47,48] Additionally, remains of most, if not all, PCF dinosaurian taxa identified to the species level, as well as several unnamed taxa, have not been found in lower latitude contemporaneous formations, suggesting Arctic faunal provinciality.[47,49]

Year-round occupancy at very high latitudes would have likely exerted pronounced selective pressures on dinosaurs, necessitating polar-specific life history strategies. In the face of annual environmental extremes, polar dinosaurs may have employed a mix of dietary, reproductive, behavioral, and anatomical strategies that are currently unrecognized or poorly understood. PCF vegetation consisted of an open canopied forest dominated by deciduous conifers and angiosperms with an understory of ferns and horsetails.[11,50] The polar light regime and marked seasonal temperature variations affected primary productivity and would have placed severe constraints on food availability and overwintering behaviors of dinosaurs. At ∼82°N, complete winter darkness lasted 4 months (approximately mid-October until approximately mid-February), with bounding vernal and autumnal twilight periods spanning ∼15 days[13] (Figure 5). During the winter months, organisms experienced cold month mean temperatures of −2.0°C ± 3.9°C, short periods as low as −10°C, and occasional bouts of snowfall.[11] Spring bud break occurred no earlier than approximately late February or early March and leaf fall was in approximately early October. This would have limited the availability of most fresh vegetation as a food resource for herbivores to just 6 months maximally.

These seasonal environmental limitations, coupled with new insights into the incubation periods for ceratopsians and hadrosaurids, provide a novel opportunity to understand the hypothetical annual chronology of reproductive events for relatively small and large PCF dinosaurs (Figure 5). Incubation periods for the ceratopsian *Protoceratops andrewsi* (1.8 m adult length) and the hadrosaurid *Hypacrosaurus stebingeri* (9.1 m adult length) were ∼83 days (2.8 months) and ∼171 days (5.8 months), respectively.[46] In the PCF, we have identified perinatal to adult remains of an undescribed leptoceratopsid ceratopsian[29] approximately the same adult body size as *Protoceratops andrewsi*. Assuming an incubation period similar to *Protoceratops* beginning no later than approximately early April, nest building and egg laying could have commenced shortly after bud break in approximately early to mid-March. Hatching would have occurred near summer solstice in approximately mid- to late June. Approximately 4 months would have remained before the onset of full-day winter darkness in approximately early October. For PCF hadrosaurids (both a lambeosaurine and saurolophine are known),[2,20] extended incubation periods would have likely occupied most of the summer growing season. Assuming an incubation period similar to *Hypacrosaurus* beginning by approximately early April, hatching would have occurred as late as approximately mid- to late September, only a month before the last sunrise of the year. If the incubation period was either a month shorter or incubation began a month earlier, neonatal hadrosaurids would still have entered the winter season and continuous darkness at a very small body size, even assuming growth rates comparable to those at lower latitudes. For dinosaurs at lower latitudes, it is not known how many broods were produced and whether they did so throughout the year. Given temporal constraints

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

conducive for producing viable young and prolonged incubation periods, high Arctic PCF dinosaurs likely had opportunities to lay just a single viable brood per year.

It is intriguing to consider possible overwintering strategies that enabled PCF dinosaurs to exist in this challenging environment. For larger, presumably non-hibernating megaherbivorous taxa such as hadrosaurids and ceratopsids, fasting was a possibility, as large size provides advantages over small taxa with regard to lower relative metabolic rates, surface to mass scaling advantages, and greater absolute reserves of somatic tissues that can be used for survival. It is also possible that the consumption of low-quality forage following the shedding of deciduous leaves (perhaps bark,[51] ferns, horsetails, or moss[52]) may have served as winter subsistence. In the case of smaller taxa such as thescelosaurids and leptoceratopsids, hibernation or torpor was a possible strategy, potentially using burrows for both shelter during the winter and protection of young. Burrowing behavior is reported in the Cretaceous orodromine *Oryctodromeus*[17] from Montana, USA, and suggested for the Cretaceous protoceratopsid *Protoceratops* from Mongolia.[53] Putative dinosaur burrows from high-latitude deposits of the Otway Group in Victoria, Australia, have also been described as a possible adaptation to survival in polar conditions.[54]

In extant birds, feathers of various forms show diverse functionality depending on the taxon (e.g., flight, camouflage, display, insect traps, shedding parasite loads), but almost invariably possess types that serve some role in insulation.[55] Although feather preservation is currently unknown in the PCF, it has recently been found in other formations that preserve representatives of each of the theropod groups identified in the PCF, namely Ornithomimisauria,[56] Deinonychosauria,[57,58] and even Tyrannosauroidea[59] (most notably the large, downy-covered tyrannosauroidean *Yutyrannus huali* from the cool, temperate Yixian Formation of China[60]). Given these considerations, it is plausible that insulator feathers helped to facilitate their winter polar occupation.

During deposition of the PCF, terrestrial polar faunas did not experience temperatures as cold as those in the Arctic today. However, climatic conditions did impose constraints on faunal composition similar to modern Arctic environments, where endothermic taxa (birds and mammals) are the dominant terrestrial vertebrates, and ectothermic tetrapods such as squamates and lissamphibians (i.e., salamanders, frogs, and caecilians) are non-existent or very rare. The apparent absence of the ectothermic terrestrial taxa from the PCF, but richness in avian (at least three species), mammalian (four-five taxa[5,61]), and dinosaurian taxa (~13 species), supports a growing body of evidence that at least some dinosaurs (coelurosaurian theropods and cerapodan ornithischians) were endothermic.[26] We posit that this served as a critical exaptation enabling the dinosaurs' Late Cretaceous high-latitude occupation.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead Contact
  - Materials Availability
  - Data and Code Availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Notes on the taphonomy of microfossil horizons
  - Dinosaurs of the Prince Creek Formation
- METHOD DETAILS
  - Specimen preparation
  - Photography and Measurements
  - Histological analysis
  - Polar light regime and estimations of continuous winter darkness
  - Estimation of ontogenetic status and scaling comparisons

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.05.041.

ACKNOWLEDGMENTS

We thank K. May, R. Missler, D. Stewart, K. Anderson, Z. Perry, J. Rousseau, C. Heninger, K. Johnson, R. Troll, M. Kunz, J. Keeney, B. Breithaupt, B. King, R. VanderHoek, J. Havens, K. Solt, P. Gignac, D. Kay, C. Spurlock, A. Harper, N. Sheplak, C. Calvert, T. Hunt, N. Whalen, F. Therrien, D. Ksepka, as well as the US Bureau of Land Management, State of Alaska Department of History and Archaeology, and North Slope Bureau for permitting and logistical support. We thank three anonymous reviewers whose comments improved the paper. Taxon silhouettes used in Figures 4 and 5 (and graphical abstract) were obtained from Phylopic (http://phylopic.org/) under Public Domain Dedication 1.0 license and Creative Commons Attribution-ShareAlike 3.0 Unported license (https://creativecommons.org/licenses/by-sa/3.0/), with images scaled and/or reflected. Art by Tasman Dixon, Andrew A. Farke, "FunkMonk," Scott Hartman, Jaime Headden, T. Michael Keesey, George Edward Lodge, Gareth Monger, Nobu Tamura, and Emily Willoughby. This work was supported by National Science Foundation grants EAR 1226730 (to P.S.D. and G.M.E.) and EAR 1736515 (to P.S.D., G.M.E., and J.J.E.).

AUTHOR CONTRIBUTIONS

P.S.D. and G.M.E. designed the research project; P.S.D., G.M.E., and J.J.E. collected the field data and conducted microfossil analyses; P.S.D., G.M.E., D.B., and C.M.B. analyzed the data and wrote the paper; and all authors reviewed and revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as a member of the LGBTQ+ community.

Received: March 16, 2021
Revised: April 26, 2021
Accepted: May 18, 2021
Published: June 24, 2021

REFERENCES

1. Rich, T.H., Vickers-Rich, P., and Gangloff, R.A. (2002). Paleontology. Polar dinosaurs. Science *295*, 979–980.
2. Gangloff, R.A. (2012). Dinosaurs under the Aurora (Indiana University Press).

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

3. Hotton, N. (1980). An alternative to dinosaur endothermy. In A Cold Look at the Warm-Blooded Dinosaurs, R. Thomas, and E. Olsen, eds. (Westview Press), pp. 311–350.
4. Ostrom, J.H. (1980). The evidence for endothermy in dinosaurs. In A Cold Look at the Warm-Blooded Dinosaurs, R. Thomas, and E. Olsen, eds. (Westview Press), pp. 5–54.
5. Clemens, W.A., and Nelms, L.G. (1993). Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. Geology *21*, 503–506.
6. Russell, D.A. (1989). In An Odyssey in Time: The Dinosaurs of North America (Northword Press).
7. Bell, P.R., and Snively, E. (2008). Polar dinosaurs on parade: a review of dinosaur migration. Alcheringa *32*, 271–284.
8. Godefroit, P., Golovneva, L., Shchepetov, S., Garcia, G., and Alekseev, P. (2009). The last polar dinosaurs: high diversity of latest Cretaceous arctic dinosaurs in Russia. Naturwissenschaften *96*, 495–501.
9. Kitchener, J.L., Campione, N.E., Smith, E.T., and Bell, P.R. (2019). High-latitude neonate and perinate ornithopods from the mid-Cretaceous of southeastern Australia. Sci. Rep. *9*, 19600.
10. Poropat, S.F., Martin, S.K., Tosolini, A.M.P., Wagstaff, B.E., Bean, L.B., Kear, B.P., Vickers-Rich, P., and Rich, T.H. (2018). Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. Alcheringa *42*, 157–229.
11. Spicer, R.A., and Herman, A.B. (2010). The Late Cretaceous environment of the Arctic: a quantitative reassessment based on plant fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. *295*, 423–442.
12. Hay, W.W., DeConto, R.M., Wold, C.N., Wilson, K.M., Voigt, S., Schulz, M., Wold, A.R., Dullo, W.C., Ronov, A.B., Balukhovsky, A.N., and Söding, E. (1999). Alternative global Cretaceous paleogeography. In The Evolution of the Cretaceous Ocean/Climate System, E. Barrera, and C. Johnson, eds. (Geological Society of America), pp. 1–47.
13. Herman, A.B., Spicer, R.A., and Spicer, T.E.V. (2016). Environmental constraints on terrestrial vertebrate behaviour and reproduction in the high Arctic of the Late Cretaceous. Palaeogeogr. Palaeoclimatol. Palaeoecol. *441*, 317–338.
14. Fiorillo, A.R. (2018). Alaska Dinosaurs: An Ancient Arctic World (CRC Press).
15. Gangloff, R.A. (1994). The record of Cretaceous dinosaurs in Alaska: an overview. In 1992 Proc. Int. Conf. Arct. Margins, pp. 399–404.
16. Parrish, J.M., Parrish, J.T., Hutchison, J.H., and Spicer, R.A. (1987). Late Cretaceous vertebrate fossils from the North Slope of Alaska and implications for dinosaur ecology. Palaios *2*, 377–389.
17. Varricchio, D.J., Martin, A.J., and Katsura, Y. (2007). First trace and body fossil evidence of a burrowing, denning dinosaur. Proc. Biol. Sci. *274*, 1361–1368.
18. Russell, D.A. (1973). The environments of Canadian dinosaurs. Can. Geogr. J. *87*, 4–11.
19. Horner, J.R., and Currie, P.J. (1994). Embryonic and neonatal morphology of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. In Dinosaur Eggs and Babies, K. Carpenter, K.F. Hirsch, and J.R. Horner, eds. (Cambridge University Press), pp. 310–356.
20. Mori, H., Druckenmiller, P.S., and Erickson, G.M. (2016). A new Arctic hadrosaurid from the Prince Creek Formation (Lower Maastrichtian) of northern Alaska. Acta Palaeontol. Pol. *61*, 15–32.
21. Fiorillo, A.R., and Tykoski, R.S. (2013). An immature *Pachyrhinosaurus perotorum* (Dinosauria: Ceratopsidae) nasal reveals unexpected complexity of craniofacial ontogeny and integument in *Pachyrhinosaurus*. PLoS ONE *8*, e65802.
22. Chiarenza, A.A., Fiorillo, A.R., Tykoski, R.S., McCarthy, P.J., Flaig, P.P., and Contreras, D.L. (2020). The first juvenile dromaeosaurid (Dinosauria: Theropoda) from Arctic Alaska. PLoS ONE *15*, e0235078.
23. DeAngelis, D.L., and Grimm, V. (2014). Individual-based models in ecology after four decades. F1000Prime Rep. *6*, 39.
24. Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.-Y., Zylberberg, L., and de Ricqlès, A. (1990). Microstructure and mineralization of vertebrate skeletal tissues. In Biomineralization: Patterns and Evolutionary Trends, *Volume 1*, J.G. Carter, ed. (Van Nostrand Reinhold), pp. 471–530.
25. Horner, J.R., de Ricqlès, A., and Padian, K. (2000). Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. J. Vertebr. Paleontol. *20*, 115–129.
26. Erickson, G.M. (2014). On dinosaur growth. Annu. Rev. Earth Planet. Sci. *42*, 675–697.
27. Erickson, G.M., Rauhut, O.W.M., Zhou, Z., Turner, A.H., Inouye, B.D., Hu, D., and Norell, M.A. (2009). Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. PLoS ONE *4*, e7390.
28. Fiorillo, A.R., and Tykoski, R.S. (2012). A new Maastrichtian species of the centrosaurine ceratopsid *Pachyrhinosaurus* from the North Slope of Alaska. Acta Palaeontol. Pol. *57*, 561–573.
29. Erickson, G.M., Sidebottom, M.A., Kay, D.I., Turner, K.T., Ip, N., Norell, M.A., Sawyer, W.G., and Krick, B.A. (2015). Wear biomechanics in the slicing dentition of the giant horned dinosaur *Triceratops*. Sci. Adv. *1*, e1500055.
30. Fiorillo, A.R. (2008). On the occurrence of exceptionally large teeth of *Troodon* (Dinosauria: Saurischia) from the Late Cretaceous of northern Alaska. Palaios *23*, 322–328.
31. Fiorillo, A.R., and Gangloff, R.A. (2000). Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on Arctic dinosaur paleoecology. J. Vertebr. Paleontol. *20*, 675–682.
32. Fiorillo, A.R., and Tykoski, R.S. (2014). A diminutive new tyrannosaur from the top of the world. PLoS ONE *9*, e91287.
33. Jadwiszczak, P. (2010). New data on the appendicular skeleton and diversity of Eocene Antarctic penguins. In Morphology and Systematics of Fossil Vertebrates, D. Nowakowski, ed. (DN Publisher), pp. 45–51.
34. Fanti, F., and Miyashita, T. (2009). A high latitude vertebrate fossil assemblage from the Late Cretaceous of west-central Alberta, Canada: evidence for dinosaur nesting and vertebrate latitudinal gradient. Palaeogeogr. Palaeoclimatol. Palaeoecol. *275*, 37–53.
35. Ryan, M.J., Currie, P.J., Gardner, J.D., Vickaryous, M.K., and Lavigne, J.M. (1998). Baby hadrosaurid material associated with an unusually high abundance of *Troodon* teeth from the Horseshoe Canyon Formation, Upper Cretaceous, Alberta, Canada. Gaia Ecol. Perspect. Sci. Soc. *133*, 123–133.
36. Funston, G.F., Powers, M.J., Whitebone, S.A., Brusatte, S.L., Scannella, J.B., Horner, J.R., and Currie, P.J. (2021). Baby tyrannosaurid bones and teeth from the Late Cretaceous of western North America. Can. J. Earth Sci. Published online January 25, 2021. https://doi.org/10.1139/cjes-2020-0169.
37. Tanke, D.H., and Brett-Surman, M.K. (2001). Evidence of hatchling- and nestling-size hadrosaurs (Reptilia: Ornithischia) from Dinosaur Provincial Park (Dinosaur Park Formation: Campanian), Alberta. In Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie, D.H. Tanke, and K. Carpenter, eds. (Indiana University Press), pp. 206–218.
38. Carpenter, K., and Alf, K. (1994). Global distribution of dinosaur eggs, nests, and babies. In Dinosaur Eggs and Babies, K. Carpenter, K.F. Hirsch, and J.R. Horner, eds. (Cambridge University Press), pp. 15–30.
39. Horner, J.R., and Weishampel, D.B. (1988). A comparative embryological study of two ornithischian dinosaurs. Nature *332*, 256–257.
40. Varricchio, D.J., Jackson, F., Borkowski, J.J., and Horner, J.R. (1997). Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. Nature *385*, 247–250.
41. Horner, J.R. (1999). Egg clutches and embryos of two hadrosaurian dinosaurs. J. Vertebr. Paleontol. *19*, 607–611.

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

42. Carpenter, K. (1982). Baby dinosaurs from the Late Cretaceous Lance and Hell Creek formations and a description of a new species of theropod. Contrib. to Geol. *20*, 123–134.
43. Fiorillo, A.R., McCarthy, P.J., and Flaig, P.P. (2010). Taphonomic and sedimentologic interpretations of the dinosaur-bearing Upper Cretaceous Strata of the Prince Creek Formation, Northern Alaska: Insights from an ancient high-latitude terrestrial ecosystem. Palaeogeogr. Palaeoclimatol. Palaeoecol. *295*, 376–388.
44. Flaig, P.P., McCarthy, P.J., and Fiorillo, A.R. (2011). A tidally influenced, high-latitude coastal-plain: the Upper Cretaceous (Maastrichtian) Prince Creek Formation, North Slope, Alaska. In From River to Rock Record, S.K. Davidson, S. Leleu, and C.P. North, eds. (SEPM Society for Sedimentary Geology), pp. 233–264.
45. Fiorillo, A.R., McCarthy, P.J., and Flaig, P.P. (2016). A multi-disciplinary perspective on habitat preferences among dinosaurs in a Cretaceous Arctic greenhouse world, North Slope, Alaska (Prince Creek Formation: Lower Maastrichtian). Palaeogeogr. Palaeoclimatol. Palaeoecol. *441*, 377–389.
46. Erickson, G.M., Zelenitsky, D.K., Kay, D.I., and Norell, M.A. (2017). Dinosaur incubation periods directly determined from growth-line counts in embryonic teeth show reptilian-grade development. Proc. Natl. Acad. Sci. USA *114*, 540–545.
47. Erickson, G.M., and Druckenmiller, P.S. (2011). Longevity and growth rate estimates for a polar dinosaur: a *Pachyrhinosaurus* (Dinosauria: Neoceratopsia) specimen from the North Slope of Alaska showing a complete developmental record. Hist. Biol. *23*, 327–334.
48. Chinsamy, A., Thomas, D.B., Tumarkin-Deratzian, A.R., and Fiorillo, A.R. (2012). Hadrosaurs were perennial polar residents. Anat. Rec. (Hoboken) *295*, 610–614.
49. Benson, R.B.J., Rich, T.H., Vickers-Rich, P., and Hall, M. (2012). Theropod fauna from southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. PLoS ONE *7*, e37122.
50. Brouwers, E.M., Clemens, W.A., Spicer, R.A., Ager, T.A., Carter, L.D., and Sliter, W.V. (1987). Dinosaurs on the north slope, Alaska: high latitude, latest cretaceous environments. Science *237*, 1608–1610.
51. Chin, K. (2007). the Paleobiological implications of herbivorous dinosaur coprolites from the Upper Cretaceous Two Medicine Formation of Montana: why eat wood? Palaios *22*, 554–566.
52. Erickson, G.M., Krick, B.A., Hamilton, M., Bourne, G.R., Norell, M.A., Lilleodden, E., and Sawyer, W.G. (2012). Complex dental structure and wear biomechanics in hadrosaurid dinosaurs. Science *338*, 98–101.
53. Longrich, N.R. (2010). The function of large eyes in *Protoceratops*: a nocturnal ceratopsian. In New Perspectives on Horned Dinosaurs: the Royal Tyrrell Museum Ceratopsian Symposium, M.J. Ryan, B.J. Chinnery-Allgeier, and D.A. Eberth, eds. (University of Indiana Press, Bloomington), pp. 308–327.
54. Martin, A.J. (2009). Dinosaur burrows in the Otway Group (Albian) of Victoria, Australia, and their relation to Cretaceous polar environments. Cretac. Res. *30*, 1223–1237.
55. Prum, R.O. (2005). Evolution of the morphological innovations of feathers. J. Exp. Zoolog. B Mol. Dev. Evol. *304*, 570–579.
56. Zelenitsky, D.K., Therrien, F., Erickson, G.M., DeBuhr, C.L., Kobayashi, Y., Eberth, D.A., and Hadfield, F. (2012). Feathered non-avian dinosaurs from North America provide insight into wing origins. Science *338*, 510–514.
57. Xu, X., Zhou, Z., Wang, X., Kuang, X., Zhang, F., and Du, X. (2003). Four-winged dinosaurs from China. Nature *421*, 335–340.
58. Turner, A.H., Makovicky, P.J., and Norell, M.A. (2007). Feather quill knobs in the dinosaur *Velociraptor*. Science *317*, 1721.
59. Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q., and Jia, C. (2004). Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. Nature *431*, 680–684.
60. Xu, X., Wang, K., Zhang, K., Ma, Q., Xing, L., Sullivan, C., Hu, D., Cheng, S., and Wang, S. (2012). A gigantic feathered dinosaur from the lower cretaceous of China. Nature *484*, 92–95.
61. Eberle, J.J., Clemens, W.A., Mccarthy, P.J., Fiorillo, A.R., Erickson, G.M., and Druckenmiller, P.S. (2019). Northernmost record of the Metatheria: a new Late Cretaceous pediomyid from the North Slope of Alaska. J. Syst. Palaeontology *17*, 1805–1824.
62. Burn, C.R. (1995). Where does the polar night begin? Can. Geogr. *39*, 68–74.
63. Makovicky, P.J. (2001). A *Montanaceratops cerorynchus* (Dinosauria: Ceratopsia) braincase from the Horseshoe Canyon Formation of Alberta. In Mesozoic Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie, D.H. Tanke, and K. Carpenter, eds. (Indiana University Press), pp. 343–362.
64. Baszio, S. (1997). Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of South Alberta, Canada. Cour. Forschungsinstitut Senckenb. *196*, 33–77.
65. Ryan, M.J., Evans, D.C., Currie, P.J., Brown, C.M., and Brinkman, D. (2012). New leptoceratopsids from the Upper Cretaceous of Alberta, Canada. Cretac. Res. *35*, 69–80.
66. Brown, B. (1914). *Leptoceratops*, a new genus of Ceratopsia from the Edmonton Cretaceous of Alberta. Bull. Am. Mus. Nat. Hist. *33*, 567–580.
67. Russell, D.A. (1970). A skeletal reconstruction of *Leptoceratops gracilis* from the upper Edmonton Formation (Cretaceous) of Alberta. Can. J. Earth Sci. *7*, 181–184.
68. Brinkman, D.B., Ryan, M.J., and Eberth, D.A. (1998). The paleogeographic and stratigraphic distribution of ceratopsids (Ornithischia) in the upper Judith River Group of western Canada. Palaios *13*, 160–169.
69. Erickson, G.M., and Zelenitsky, D.K. (2014). Osteohistology of *Hypacrosaurus stebengeri* teeth throughout ontogeny with comments on wear induced form and function. In Hadrosaurs, D. Eberth, and D.C. Evans, eds. (University of Indiana Press), pp. 422–432.
70. Prieto-Márquez, A. (2008). Phylogeny and historical biogeography of hadrosaurid dinosaurs (Florida State University), PhD dissertation.
71. Brown, C.M., Evans, D.C., Ryan, M.J., and Russell, A.P. (2013). New data on the diversity and abundance of small-bodied ornithopods (Dinosauria, Ornithischia) from the Belly River Group (Campanian) of Alberta. J. Vertebr. Paleontol. *33*, 495–520.
72. Boyd, C.A. (2015). The systematic relationships and biogeographic history of ornithischian dinosaurs. PeerJ *3*, e1523.
73. Butler, R.J., Upchurch, P., and Norman, D.B. (2008). The phylogeny of the ornithischian dinosaurs. J. Syst. Palaeontology *6*, 1–40.
74. Dieudonne, P.-E., Cruzado-Caballero, P., Godefroit, P., and Tortosa, T. (2020). A new phylogeny of cerapodan dinosaurs. Hist. Biol. Published online July 20, 2020. https://doi.org/10.1080/08912963.2020.1793979.
75. Brown, C.M., and Druckenmiller, P. (2011). Basal ornithopod (Dinosauria: Ornithischia) teeth from the Prince Creek Formation (early Maastrichtian) of Alaska. Can. J. Earth Sci. *48*, 1342–1354.
76. Sullivan, R.M. (2006). A taxonomic review of the Pachycephalosauridae (Dinosauria: Ornithischia). New Mex. Museum Nat. Hist. Sci. Bull. *35*, 347–365.
77. Egerton, V.M., Novas, F.E., Dodson, P., and Lacovara, K. (2013). The first record of a neonatal ornithopod dinosaur from Gondwana. Gondwana Res. *23*, 268–271.
78. Currie, P.J., Rigby, J.K., and Sloan, R.E. (1990). Theropod teeth from the Judith River Formation of southern Alberta. In Dinosaur Systematics: Approaches and Perspectives, K. Carpenter, and P.J. Currie, eds. (Cambridge University Press), pp. 107–125.
79. Varricchio, D.J., Horner, J.R., and Jackson, F.D. (2002). Embryos and eggs for the Cretaceous theropod dinosaur *Troodon formosus*. J. Vertebr. Paleontol. *22*, 564–576.
80. Makovicky, P.J., Norell, M.A., Clark, J.M., and Rowe, T. (2003). Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). Am. Mus. Novit. *3402*, 1–32.

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

81. Bever, G.S., and Norell, M.A. (2009). The perinate skull of *Byronosaurus* (Troodontidae) with observations on the cranial ontogeny of paravian theropods. Am. Mus. Novit. *3657*, 1–52.

82. Tsuihiji, T., Watabe, M., Tsogtbaatar, K., Tsubamoto, T., Barsbold, R., Suzuki, S., Lee, A.H., Ridgely, R.C., Kawahara, Y., and Witmer, L.M. (2011). Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. J. Vertebr. Paleontol. *31*, 497–517.

83. Erickson, G.M., Makovicky, P.J., Currie, P.J., Norell, M.A., Yerby, S.A., and Brochu, C.A. (2004). Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. Nature *430*, 772–775.

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Studied specimens		
Perinatal postcranial remains (distal femur, caudal centrum) of indeterminate ornithischian	University of Alaska Museum Earth Sciences Collection	UAMES 41721, UAMES 41633
Perinatal postcranial remains (caudal centrum) of indeterminate theropod	University of Alaska Museum Earth Sciences Collection	UAMES 51934
Perinatal ornithischian long bone sectioned for histology	University of Alaska Museum Earth Sciences Collection	UAMES 52384
Perinatal tarsometatarsus of Avialae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 41722
Perinatal and adult teeth of Troodontidae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 52268, UAMES 51652
Perinatal and adult teeth of Saurornitholestinae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 52292, UAMES 29574
Perinatal and adult teeth of Thescelosauridae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 52230, UAMES 52272
Perinatal and adult teeth of Leptoceratopsidae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 42720, UAMES 39298
Perinatal and adult teeth of Hadrosauridae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 42739, UAMES 12491
Perinatal and adult teeth of Ceratopsidae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 52467, UAMES 29413
Immature and adult teeth of Tyrannosauridae indet.	University of Alaska Museum Earth Sciences Collection	UAMES 17610, UAMES29370
Software and algorithms		
Stackshot 3X	Cognisys	https://cognisys-inc.com/motion-control/stackshot3x-pkgs.html
ZereneStacker v.1.04	Zerene Systems, LLC	https://www.zerenesystems.com
Photoshop CS6	Adobe	https://www.adobe.com

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources and reagents should be directed to and will fulfilled by the lead contact, Patrick Druckenmiller (psdruckenmiller@alaska.edu)

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

This study did not generate/analyze datasets.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The specimens reported here are housed in the University of Alaska Museum Earth Sciences Collection (UAMES) in Fairbanks, AK, USA. The data analyzed in this study were collected both from the literature and firsthand examination of fossils housed in public repositories. The following abbreviations denote museum collections where fossil material in this supplement is accessioned.

AMNH; American Museum of Natural History, New York, New York, USA
IGM; Institute of Geology, Ulaanbaatar, Mongolia

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

MOR; Museum of the Rockies, Montana State University, Bozeman, Montana, USA
MPC; Mongolian Paleontological Center, Ulaanbaatar, Mongolia
MPM; Museo Padre Molina, Río Gallegos, Santa Cruz Province, Argentina
TMP; Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada
UALVP; University of Alberta Laboratory for Vertebrate Paleontology
UAMES; University of Alaska Museum of the North; Fairbanks, Alaska, USA

Notes on the taphonomy of microfossil horizons

The majority of small bones and teeth described in this study come from microvertebrate assemblages exposed in outcrops of the Prince Creek Formation along the Colville River. One of these sites, Pediomys Point, has been long known to produce small bones and teeth of fish, dinosaurs and mammals.[22,61] Three new microvertebrate sites provided much of the perinatal material described in this study. One, OJsaurus is located approximately 9 km downstream of Pediomys Point. Two others, Paul's Pearls and Jacob's Bed, are less than 1 km further downriver, are approximately 100 m apart and are separated by no more than 1 m of vertical stratigraphic section. (Exact locality data for all three sites is on record with the Bureau of Land Management Arctic Field Office). All are very similar to Pediomys Point in their lithology and architecture in being thin (2-15 cm thickness), silty to sandy, organic-rich lenticular bodies (see Rich et al.[1] for more detailed discussion of sedimentology). We interpret these lenses to be time-averaged lag deposits formed at the base of fluvial channels. Disarticulated skeletal elements from both large and small bodied individuals are preserved in the deposits, particularly at OJsaurus and Jacob's Bed. As a time-averaged deposit, these sites contain elements that have undergone varying degrees of weathering and transport. The majority of bones and teeth figured in this study preserve fragile structures such as articular condyles and delicate tooth roots and display undamaged surface textures indicative of minimal transport, although some elements exhibit slightly greater degrees of surface modification due to either weathering or rounding during transport. To date, there is no indication of eggshell preservation, possibly due to acidic pore waters.

Dinosaurs of the Prince Creek Formation

Currently, 13 non-avialan dinosaur taxa are recognized to occur in the Prince Creek Formation, but only four of these have been named at the species level. An unknown number of avialans are also present based on skeletal remains. A complete list is presented here:

- Ornithopoda
- Hadrosauridae
  - *Ugrunaaluk kuukpikensis* (“*Edmontosaurus regalis*”)
  - Lambeosaurinae indet.
- Thescelosauridae
  - Thescelosaurinae indet. (*Parksosaurus*-like)
  - Orodrominae indet. (*Orodromeus*-like)
- Ceratopsia
- Ceratopsidae
  - *Pachyrhinosaurus perotorum*
- Leptoceratopsidae indet.
- Pachycephalosauria
- Pachycephalosauridae
  - *Alaskacephale gangloffi*
- Theropoda
- Troodontidae indet.
  - *Troodon* sp.
- Dromaeosauridae
  - Dromaeosaurinae indet.
  - Saurornitholestinae indet.
  - *Richardoestesia* sp. (*R. isosceles*-like)
- Ornithomimosauria indet.
- Tyrannosauridae
  - *Nanuqsaurus hoglundi*
- Avialae indet.

METHOD DETAILS

Specimen preparation

Fossiliferous sediment was bulk-sampled in the field and then washed with water and sieved using 2.0 mm and 0.5 mm screens. The resulting fraction was visually inspected under a dissecting microscope.

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

Photography and Measurements

Photographs for focus-stacking were taken using a Canon digital camera (EOS 6D Mark II with 65 mm macro lens) fitted to macro-rail using Stackshot 3X (Cognisys) and processed using ZereneStacker v 1.04 and Adobe Photoshop CS6 software. Measurements of tooth dimensions were made with a Helios calipers and microscope slide grids (0.5 mm and 2.0 mm).

Histological analysis

Four indeterminate long bone elements representing Theropoda (n = 2) and Ornithopoda (n = 1) showing rugose periosteal surfaces were selected for histological microstructural characterization. Each was embedded in clear epoxy resin (Epoxyset; Allied High Tech Products, Rancho Dominguez, CA, USA). The diaphysis of the elements was sectioned in the transverse plane, using a slow-speed diamond saw (Isomet 1000; Buehler, Lake Bluff IL, USA). The distal end of the ornithopod long bone was also sectioned longitudinally. Each section was affixed to petrographic microscope slides using epoxy and then rotary-sanded (Rotopol 11; Struers, Cleveland, OH, USA) to ~100 μm thickness using descending grades (220-1,200 grit) of carbide sandpaper using water as a lubricant. They were then polished using alumina slurry. Each specimen was visualized and photographed using both incident light (SZX12; Olympus, Tokyo Japan) and polarized petrographic microscopy (BX60; Olympus, Tokyo Japan).

Polar light regime and estimations of continuous winter darkness

In Figure 1, we compare the estimated number of days of continuous winter darkness for several high latitude dinosaur-bearing sites. In general, the light regime of the Cretaceous polar regions are generally considered to be similar to those today for any given latitude.[13] Estimating the number of days of continuous winter darkness for various Cretaceous localities is primarily dependent on three factors: a) length of day and/or the number of days in the Cretaceous year; b) variation in orbital obliquity; and c) paleolatitude estimations for a given site. We use the end of civil twilight in modern polar environments as a basis for these calculations as this is the time of day when darkness forces the cessation of normal outdoor activities.[62]

Due to the gradual decline in Earth's rotational rate, the difference between Late Cretaceous and current parameters can be expressed in the length of day (23 h, 31 min versus 23 h 56 min; difference = 25 min), or days per year (372 days versus 365.24 days; difference = 7 days). These represent minor differences on the scale of 1.8% and have marginal effects on calculations of continual winter darkness in the polar Cretaceous. Likewise, variations in obliquity (axial tilt) are not believed to be outside those of known ranges. By far the largest effect on of solar insolation is caused by uncertainty of paleolatitude estimates. Even small uncertainties in paleolatitude have potentially large effects on the number of days winter darkness. For instance, a difference of 5 degrees (e.g., 80°N and 85°N) results in 91 versus 121 days of continual winter darkness, a difference of 25%.

Estimation of ontogenetic status and scaling comparisons

We first diagnose the minute bones and teeth using taxonomically informative anatomical features and then determine their ontogenetic status based on surficial morphology, histological indices and inter- and/or intraspecific scaling comparisons with adults. We then estimated skull and body size of the Prince Creek Formation teeth using scaling comparisons of more complete skeletal material with known embryos or young individuals from congeners or closely related taxa. Details of measurements and scaling methods for each taxon are provided below.

Ceratopsia: Leptoceratopsidae sensu *Makovicky*[63]

Our macro- and microfossil analyses have recovered numerous bones and teeth of an undescribed leptoceratopsid, ranging in size from very young to adult-sized individuals (Figures S3A–S3C). As is characteristic for leptoceratopsid teeth, the enameled side of the crown bear a prominent, slightly distally offset, apical ridge extending from the apex to the prominent basal cingulum to which it is confluent.[64] Unlike the Campanian-aged *Unescoceratops*,[65] secondary ridges do not extend from the marginal denticle along the lingual face of the crown. The teeth are also differentiated from Ceratopsidae as they only have a single root.

The largest maxillary and dentary teeth of the Prince Creek Formation taxon are comparable in size to those of adult *Leptoceratops gracilis* teeth (holotype AMNH 5205) from the Scollard Formation of Alberta,[66] indicating they had similar adult body lengths (~1.8 m[67]). UAMES 42720 is a dentary tooth crown (height = 1.0 mm (worn); mesiodistal length = 1.7 mm) and the smallest recovered in our screening efforts (Figure S3). We compared UAMES 42720 to *in ovo* embryonic teeth of the ceratopsian *Protoceratops andrewsi* (adult body length = 1.8 m) from the Djadochta Formation (Campanian) of Mongolia.[46] Crown dimensions of a left denary tooth (IGM 100/1021a; height = 1.8 mm; mesiodistal length = 2.2 mm) are actually larger than those of UAMES 42720 suggesting the Alaskan material belongs to an individual from a very early ontogenetic stage, likely a perinate and possibly an embryo.

Ceratopsia: Ceratopsidae

UAMES 52467 is a very small, worn ceratopsid tooth crown (enameled crown height = 1.0 mm; mesiodistal length = 3.0) (Figures S3D and S3E). It is referred to Ceratopsidae on the basis of having a prominent medial carina, coarsely textured enamel, a near-vertical wear facet and distinctive cellular cementum with large globous cementocytes.[29] UAMES 52467 is one of the smallest ceratopsid teeth yet reported, the only others of which we are aware having been reported from the Maastrichtian Hell Creek and Lance formations[42] (but see Brinkman et al.[68]). Comparative material of in ovo ceratopsid embryos are not known. Based on its extremely small size, even when compared to other small PCF ceratopsid teeth (see below), we consider this specimen to be from a perinatal individual.

UAMES 41664 is a small (crown height = 5.0 mm) unworn ceratopsid maxillary tooth crown. It is also referred to Ceratopsidae on the basis of overall morphology, the presence of double roots and having a thick layer of cellular cementum with large globous cementocytes[29] (Figure S5A). We refer it to the only named ceratopsid known in the formation, *Pachyrhinosaurus perotorum*.[28] UAMES 41664 is 26% the crown height of large, presumably mature ceratopsid teeth (e.g., UAMES 19655; 19.0 mm). Using the van Bertalanffy length-age growth curve for Prince Creek Formation *P. pertotorum*,[47] 26% of linear growth corresponds to the formation of the first growth band found in the femur of UAMES 3551. The first growth band presumably forms during the first winter season of life, approximately 6-8 months post-hatching. Thus, UAMES 41664 likely represents an individual more mature than a hatchling but less than one calendar year in age (i.e., young-of-the-year).

Ornithopoda: Hadrosauridae

Small shed hadrosaurid teeth are common components of our microfossil analyses. UAMES 42739 is the smallest of this sample (partial mesiodistal length = 2.1 mm; complete labiolingual width = 1.5 mm) and is interpreted to be a shed and partially weathered tooth (Figure S4). In occlusal view it has an asymmetric shape and displays a combination of several morphological and histological features consistent with its referral to Hadrosauridae including: a prominent median ridge, a parasagittally oriented pulp cavity with longitudinal giant tubules, a broad zone of mantle dentine, transverse giant tubules, and von Ebner incremental lines that are most visible on the lingual side of the tooth.[52,69] The lack of a secondary carina on the lingual surface indicates it is likely a hadrosaurine.[70]

We compared UAMES 42739 to small, isolated teeth of *Edmontosaurus regalis* (Hadrosaurinae) from the Horseshoe Canyon Formation (Horsethief Canyon locality) of southern Alberta. Teeth from this site are considered to be from ''babies,'' broadly inferred to encapsulate an ontogenetic range spanning embryonic, hatchling and nestling-sized individuals.[35] Based on a small sample (n = 5; TMP 1997.036.0037; TMP 1997.036.0040; TMP 1997.036.0043; TMP 1997.036.0044; TMP 1997.036.0048), UAMES 42739 is considerably smaller in both mean mesiodistal length (4.8 mm) and mean labiolingual width (3.7 mm). UAMES 42739 is also smaller in labiolingual width than the two smallest teeth previously described from this site (1.75 mm; TMP 1997.036.0045 and TMP 1997.036.0054).[35] We also compared our material to young individuals of *Hypacrosaurus stebingeri* (Lambeosaurinae) from the Oldman Formation of Alberta, Canada. UAMES 42739 is smaller than a single rooted tooth of TMP 1987.079.0149, an embryonic dentary[46] (mesiodistal length = 4.7 mm; labiolingual width = 2.6 mm) and TMP 1987.077.0099, a histologically sampled, worn embryonic tooth[69] (mesiodistal length = 4.5 mm, labiolingual width 2.2 mm; 2.1mm excluding enamel). Although lambeosaurines typically have larger eggs than hadrosaurines, the very small size of UAMES 42739 compared to embryonic *Hypacrosaurus* suggests at the very least it is from a perinate and possibly an embryo.

Ornithopoda: Thescelosauridae sensu Brown et al.[71]

The phylogeny of small-bodied neornithischian (possibly ornithopod) taxa from the late Cretaceous of North America is poorly resolved. Some analyses recover these taxa (e.g., *Thescelosaurus*, *Parksosaurus*, *Orodromeus*, *Oryctodromeus*, *Zephyrosaurus*) as forming a true clade 'Thescelosauridae'[71] or 'Parksosauridae'[72], while other analyses recover these constituent genera nested within a number of clades, or a series of sister taxa.[73,74] Further, these genera are sometimes recovered within Ornithopoda,[73,74] and other time recovered outside of this group.[72] Here we follow the taxonomy of Brown et al.[71] and Boyd,[72] which under the phylogeny of Boyd[72] the node-based Thescelosauridae and stem-based Parksosauridae equally describe this group, with the understanding that our ideas of these relationships are likely to continue change with future analyses.

At least one thescelosaurid taxon similar to *Parksosaurus warreni*[75] is recognized in the Prince Creek Formation, with an estimated adult body length ~2.5 m. Thescelosaurid premaxillary and cheek teeth are relatively common elements of our microfossil analyses and can be morphologically distinguished from other ornithischian taxa.[75] UAMES 52230 is a very small cheek tooth of a thescelosaurid (crown height = 1.5 mm; crown mesiodistal length = 1.7 mm) (Figure S3I). Very young and adult-sized teeth (e.g., UAMES 52272; crown height 3.8 mm; crown mesiodistal length = 3.7 mm) can be distinguished from cheek teeth of other ornithischians based on a laterally compressed triangular crown with a swollen apical ridge and prominent mesial and distal denticles, and particularly the presence of a distolingual pocket, which is present in both very young and adult sized individuals of this taxon. Pachycephalosaurids, which are also heterodont, are known from the Prince Creek Formation (a single squamosal; the holotype specimen of *Alaskacephale gangloffi*[76]); however, a distolingual pocket is unknown from rooted teeth of any member of this clade. A second even smaller cheek tooth (UAMES 3579; crown height = 1.3 mm; crown mesiodistal length = 1.3 mm) is also likely assignable to Thescelosauridae based on the presence of an incipient distolingual pocket. Due to the lack of perinate/neonate thescelosaurid specimens, we compared the Alaskan teeth to those of *Talenkauen santacrucensis*, a medium-sized (~4.0 m adult body length) ornithopod from Cretaceous of Argentina.[77] Two probable neonate cheek teeth (MPM-10001B; worn crown height = 1.0 mm; crown mesiodistal length = 1.7 mm) of this taxon are known and found in association with the adult holotype specimen (MPM-10001).[77] Compared to adult material of the *T. santacrucensis* holotype, the neonate maxillary teeth are 10.7% as tall and 22% as wide, and the dentary teeth are 7.3% as tall and 15% as wide. The smallest Alaskan tooth crown (UAMES 3579) is 34% the height and 35% the width of the adult-sized teeth (UAMES 52272), proportional differences we attribute to the greater adult body size of *T. santacrucensis*. However, in terms of absolute size, UAMES 3579 is only slightly greater in height (but unworn) and slightly smaller in width than those of the *T. santacrucensis* neonates. Given both their absolute and proportional size differences, we interpret the smallest Alaskan thescelosaurid teeth to be perinates.

Theropoda: Troodontidae

UAMES 52268 is an isolated very small theropod tooth (crown height = 1.9 mm; fore-aft basal length [FABL] = ~1.3 mm) attributable to Troodontidae on the basis of overall shape and large denticle size relative to crown height[78] (Figure S3F). Shed adult-sized troodontid teeth are common elements in the Prince Creek Formation and are nearly twice the height and width of those of Judithian *Troodon* sp. from lower paleolatitudes in Alberta and Montana.[30] This suggests that the unnamed PCF taxon is absolutely larger with regard to adult body size.[47] We compared the Alaskan material to MOR 246-11, an *in ovo* embryo of *Troodon formosus* from

Please cite this article in press as: Druckenmiller et al., Nesting at extreme polar latitudes by non-avian dinosaurs, Current Biology (2021), https://doi.org/10.1016/j.cub.2021.05.041

the Two Medicine Formation of Montana.[79] Crowns from rooted embryonic maxillary teeth of MOR 246-11 are up to 1.0 mm in height and have a FABL of 0.7 mm (59% and 58% of UAMES 52268, respectively). The largest embryonic teeth of MOR 246-11 teeth are 20.2% the mean crown height of adult Judithian *Troodon* teeth (n = 27) from Montana and southern Alberta.[30] The crown height of UAMES 52268 is comparably smaller, being 19.4% the mean crown height of adult troodontid teeth (n = 67) from the Prince Creek Formation.

We also compared UAMES 52268 to IGM 100/972, a partial perinatal skull of the troodontid *Byronosaurus jaffei* from Ukhaa Tolgod, Upper Cretaceous Djadoctha Formation, Mongolia.[80,81] Crowns from rooted maxillary teeth of IGM 100/972 are up to 1.1 mm in height and have a FABL of 0.8 mm (65% and 67% of UAMES 52268, respectively). Crowns of perinatal maxillary teeth are 27.5% the height of adult rooted maxillary teeth in the holotype specimen of *B. jaffei* (IGM 100/983). Given the small absolute size of UAMES 52268 and that it is proportionately small compared to known troodontid perinates (whose adult size was considerably smaller), we interpret the Alaskan material to be perinatal.

Theropoda: Dromaeosauridae

UAMES 52292 is an isolated, very small theropod tooth crown (crown height = 2.3 mm; FABL = 1.6 mm). Based on its overall shape and relatively small denticle size and their proportions (e.g., denticles nearly as tall as they are long, curving distally at the tip, broad and chisel shaped)[78] we attribute this specimen to Dromaeosauridae (Figure S3G). Two dromaeosaurid taxa have been recognized from the Prince Creek Formation, a dromaeosaurine and a saurornitholestine.[31] Given that the Alaskan tooth is strongly labiolingually compressed, and that the denticles on the mesial carina are weakly developed and those on the distal carina are somewhat hook-shaped, UAMES 52292 is most likely attributable to Saurornitholestinae.

The crown height of UAMES 52292 is 23% the crown height of adult-sized saurornitholestine teeth from the Prince Creek Formation (UAMES 29575 = 10.1 mm; UAMES 29574 = 10.1 mm), comparable to the relative proportions of perinatal versus adult-sized teeth in troodontids (20.2%–27.5%; see above). To approximate skull length for UAMES 52292 we compared skull length to maxillary crown height proportions for UALVP 55700, a complete adult skull of *Saurornitholestes langstoni* from the Dinosaur Park Formation of Alberta (length = 220 mm; mean right maxillary crown height = 9.17 mm). Using a similar scaling factor, we estimate an approximate skull length of for UAMES 52292 to be just ~55 mm. The very small size and proportional estimations suggest UAMES 52292 belongs to a very young, perinatal or neonatal individual.

Theropoda: Tyrannosauridae

UAMES 17610 is an isolated tyrannosaurid (c.f. *Nanuqsaurus hoglundi*) premaxillary tooth crown (height = 8.4 mm) from the Prince Creek Formation (Kikak-Tegoseak Quarry; Figures S5C and S5D). It is one of the smallest known North American tyrannosaurid teeth. The tooth is ~32% the crown height of UAMES 29370, the largest, presumably adult-sized premaxillary tooth known from the Prince Creek Formation (crown height = 26.5 mm). We compared the Alaskan teeth to MPC-D 107/7, an articulated skull and partial skeleton of a juvenile *Tarbosaurus bataar* from the Nemegt Formation of Mongolia. Premaxillary crown height of UAMES 17610 is 73% that of MPC-D 107/7 (right, second premaxillary tooth = 11.5 mm[82]). Premaxillary crown height in MPC-D 107/7 is 3.9% skull length (= 290 mm). Applying the same tooth scaling factor, we estimate the skull length of UAMES 17610 at ~21 cm. MPC-D 107/7 is estimated to have been ~2.5 years old at death;[82] plotting at ~73% the size of MPC-D 107/7 onto the curve of Erickson et al.[83] suggests UAMES 17610 was from an individual at or within the first year of life, termed young-of-the-year.[23]

We also compared UAMES 17610 to TMP 1996.005.011, a very small premaxillary tooth (crown height = 8.5 mm) referred to *Albertosaurus sarcophagus* from the Horseshoe Canyon Formation of Alberta, Canada.[36] TMP 1996.005.011 has nearly the exact same crown height as UAMES 17610 and its developmental status is similarly interpreted as being likely a nestling or young juvenile.

We note that other Prince Creek Formation tyrannosaurid material in the UAMES collection do not support the assertion that *Nanuqsaurus* is a diminutive, small-bodied tyrannosaur.[32] Rather, adult-sized teeth and isolated postcranial elements suggest an adult body size more closely comparable to other North American tyrannosaurid taxa, such as *Albertosaurus sarcophagus*. As such, we interpret small tooth crown size in UAMES 17610 to be reflective of an early ontogenetic state and not related to small adult body size.