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# Environmental constraints on terrestrial vertebrate behaviour and reproduction in the high Arctic of the Late Cretaceous

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ABSTRACT

Reconstructions of temperature and moisture regimes based on fossil leaves, combined with tree ring studies, detail the light regime, length of the growing season, and summer and winter temperatures of the Late Cretaceous Arctic. Such constraints have important implications for dinosaur feeding and reproductive behaviour, and the capacity to reside year-round in near-polar environments.

At the highest palaeolatitudes where dinosaurs have been found (82–85 °N) winter darkness lasted for ~120 days and the spring and autumn twilight periods for ~15 days. A mostly cloud and mist-shrouded environment witnessed a mean annual temperature (MAT) of 6–7 °C, a warm month mean temperature (WMMT) of 14.5 ± 3.1 °C and a cold month mean temperature (CMMT) of −2 ± 3.9 °C. Growth rings in wood suggest summer temperatures frequently fell below +10 °C. Winter temperatures as low as −10 °C were likely for short periods. Spring bud break in late February to early March and leaf fall in early October limited the time when fresh food was available in any quantity to not more than 6 months.

The diversity of Arctic dinosaur body sizes implies a range of overwintering strategies but year-round residency requires reproduction. Burrowing and enclosed nest building no doubt facilitated overwintering for small animals, but for larger dinosaurs shelter was problematical. No dinosaur egg remains have yet been found as far north as 82° palaeolatitude, but they occur 6° further south in the Early Maastrichtian Kakanaut Formation, Northeastern Russia. Here the winter darkness was shorter (45 days), and the temperature regime warmer (MAT 10 °C, WMMT 19 °C, CMMT +3 °C). The growing season (temperatures > 10 °C) was ~6.3 months and fresh food was available in quantity for slightly longer. These summer temperatures constrain the thermal regime of nest environments and suggest sophisticated nest management and possibly brooding strategies for the necessary rapid incubation and hatching before the onset of winter.



## 1. Introduction

The Arctic Late Cretaceous terrestrial fossil record is extraordinarily rich by any measure. Information on the flora, fauna and climate at the highest northern palaeolatitudes where there was land (~70–85 °N) is preserved in the deposits of Northern Alaska and Northeastern Russia; collectively referred to here as the North Pacific Region (NPR). The exceptional abundance, preservation, diversity and geological context of fossils contained in these rocks illuminate the structure, composition and dynamics of a unique extinct high latitude ecosystem. This ecosystem has no true modern analogue: it existed under a polar light regime similar to that of the present day but experienced a temperature regime far warmer than now. Quantifying the Late Cretaceous polar climate and understanding the constraints it imposed on the near-polar terrestrial biota is the principal goal of our work reported here.

Climate (temperature and moisture regimes), light, nutrient (food) availability, and, in the case of animals, shelter are all critical factors that determine the geographic range of an organism. While these factors impose important constraints throughout the life cycle of an organism it is during the reproductive phase that they exert the strongest limitations.

In general animals are poor indicators of environmental conditions because they have the ability to escape adversity by hibernating or aestivating, migrating, possessing thermal homeostatic mechanisms and moderating their immediate surroundings (e.g. nest building). Plants, however, have more limited options for isolating themselves from their surroundings. They can enter dormancy (either seasonal, or over a longer term as a propagule such as a seed or buried rhizome), but migration via seed dispersal is slow, often omnidirectional, and progress at each stage of the migration depends on an individual surviving for long periods in a fixed location until reproductive maturity is achieved. Unlike animals, plants are spatially fixed and far more integrated with the environment in which they live. Consequently

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plants record those conditions both through the kinds of species that survive in a given location and through the architecture (physiognomy) they display.

Light, temperature and moisture are key environmental variables that affect plant growth throughout the year. With a good quantitative understanding of these parameters and how they varied through the annual cycle it is possible to frame growth constraints and hence the resources available for the heterotrophic components of that ecosystem. Detailed study of the plant fossil record provides a wide diversity of information relating to the composition, structure and dynamics of the extinct plant communities, as well as quantitative and qualitative data on the ancient climate and light regime. Here we summarise the Late Cretaceous Arctic palaeobotanical record and use it to understand better the constraints on near-polar dinosaur reproduction.

### 1.1. Introduction to the Late Cretaceous Arctic Plant Fossil record

The plant fossil record of the Late Cretaceous in the NPR is well documented (e.g. Smiley, 1966, 1969a,b, 1972a,b; Vakhrameev, 1966, 1991; Samylina, 1974, 1988; Krassilov, 1975, 1998; Vakhrameev and Akhmetiev, 1977; Kiritchkova and Samylina, 1978; Budantsev, 1983; Lebedev, 1987; Spicer et al., 1987; Grant et al., 1988; Parrish and Spicer, 1988a,b; Spicer and Parrish, 1990a,b; Herman and Lebedev, 1991; Shczepetov et al., 1992; Filippova and Abramova, 1993; Golovneva, 1994a,b, 1998; Herman, 1994, 1999a,b, 2002, 2011, 2013; Golovneva and Herman, 1998; Spicer and Herman, 2001, 2010; Herman and Spicer, 2002, 2010; Spicer et al., 2002; Craggs, 2005) and the richness of the plant megafossil record (Fig. 1) has allowed the construction of detailed phytostratigraphic correlations throughout the NPR (Herman, 1993, 1999a, 2011, 2013; Golovneva, 1994a,b; Spicer and Herman, 2010), the evolution of the Arctic flora and the dynamics of vegetation change through geologic time.

#### 1.1.1. Phytostratigraphy

The first phytostratigraphic scheme, based on phases in the evolution of the Late Cretaceous flora, was suggested for the Anadyr–Koryak sub-region of Northeastern Russia by Herman (1993, 1999a) and Golovneva (1994a, b) enhanced the resolution of the scheme within the Maastrichtian. This phytostratigraphic scheme now encompasses not only the rich palaeofloras of Northeastern Russia but also those of Northern Alaska (Spicer and Herman, 2010; Herman, 2011, 2013), and provides the framework for studying both the composition and the dynamics of the ancient Arctic forests.

The basic terminological construct of the phytostratigraphic scheme we have adopted is from Herman (2013) and is summarised in Fig. 2. The fundamental unit in this terminology is a '***florule***', which refers to an individual plant fossil assemblage at a given site. In Smiley's original usage (Smiley, 1966, 1969a, b, 1972a, b) it is not clear if this included a combination of several burial layers from several different sediment types or if it referred only to one burial layer. Based on its usage, and re-examination by us of many of Smiley's localities in the field, it is likely that it refers to collections made from several different sedimentary facies and burial layers within a given rock unit (e.g. a formation or subdivision of a formation) at a single location. A group of assemblages comprising florules from several locations at close stratigraphic intervals comprise a '***taphoflora***' (= floral assemblage), which characterises

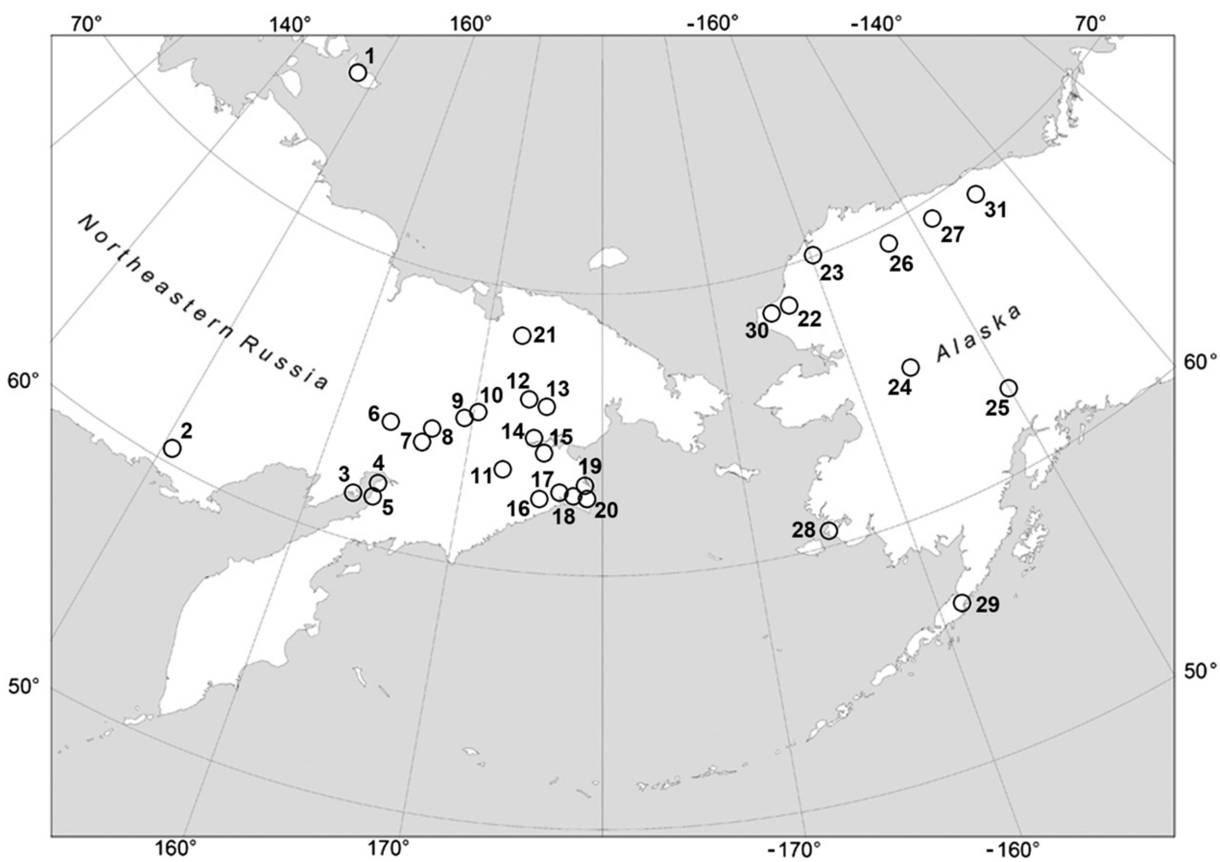


**Fig. 1.** Map of the North Pacific Region showing the major Cretaceous and Paleocene plant fossil yielding areas: 1) Novaya Sibir' Island, 2) Arman River, 3) Yelistratov Peninsula, 4) Cape Valizhgen, 5) Cape Konglomeratoviy, 6) Kholokhovchan River basin, 7) Grebenka River basin, 8) Chukotskaya and Bystraya rivers basin, 9) Ubienka and Krestovaya rivers basin, 10) Chineiveem River basin, 11) South-west Rarytkin Ridge, 12) Pekulnei Ridge, western slope, 13) Pekulnei Ridge, eastern slope, 14) Rarytkin Ridge, Anadyr River, 15) Rarytkin Ridge, Velikaya River basin, 16) Khatyrka River basin, 17) Pekulnei Lake, 18) Southern Bering Peninsula, 19) Ugol'naya Bay, 20) Amaam Lagoon, 21) Chauna, 22) Kokolik and Kukpowruk Rivers, 23) Kuk-Kaolak Area, 24) Yukon–Koyukuk Basin, 25) Cantwell, 26) Upper Colville and Chandler Rivers, 27) Lower Colville River, 28) Nelson and Nunivak islands, 29) Chignik Area, 30) Corwin Bluffs, and 31) Sagavanirktok River, Sagwon Bluffs.