Spicer, R. A., Valdes, P., Hughes, A., Yang, J., Spicer, T. E. V., Herman, A. B., & Farnsworth, A. (2019). New insights into the thermal regime and hydrodynamics of the early Late Cretaceous Arctic. *Geological Magazine*. <https://doi.org/10.1017/S0016756819000463>

Peer reviewed version

Link to published version (if available):
[10.1017/S0016756819000463](https://doi.org/10.1017/S0016756819000463)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Cambridge University Press at <https://www.cambridge.org/core/journals/geological-magazine/article/new-insights-into-the-thermal-regime-and-hydrodynamics-of-the-early-late-cretaceous-arctic/D561B4623B27F69E65727D98E682CFDB> . Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

New insights into the thermal regime and hydrodynamics of the early Late Cretaceous Arctic

ROBERT SPICER ^{1,2*}, PAUL VALDES³, ALICE HUGHES², JIAN YANG⁴, TERESA SPICER⁴, ALEXEI HERMAN⁵, ALEXANDER FARNSWORTH³

¹School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, MK7 6AA, UK.

²Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, P.R. China.

³School of Geographical Sciences, University of Bristol, Bristol BS81SS, UK.

⁴State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, P.R. China.

⁵Geological Institute, Russian Academy of Sciences, Moscow 119017, Russia.

• Corresponding author: r.a.spicer@open.ac.uk

Keywords: Polar warmth, palaeoclimate, CLAMP, ecosystem, Alaska, Russia, plant fossils

20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39

Abstract – The Arctic is warming faster than anywhere else of comparable size on Earth, impacting global climate feedbacks and the Arctic biota. However, a warm Arctic is not novel. The Late Cretaceous fossil record of the region enables a detailed reconstruction of polar environmental conditions, and a thriving extinct ecosystem, during a previous 'hothouse' global climate. Using leaf form (physiognomy) and tree ring characteristics we reconstruct Cenomanian to Coniacian polar thermal and hydrological regimes over an average annual cycle at eight locations in north-eastern Russia and northern Alaska. A new high spatial resolution (~1 km) WorldClim2 calibration of the Climate-Leaf Analysis Multivariate Program (CLAMP) yields similar, but often slightly warmer, results to previous analyses, but also provides more detailed insights into the hydrological regime through the return of annual and seasonal vapour pressure deficit (VPD), potential evapotranspiration (PET) estimates and soil moisture, as well as new thermal overviews through measures of thermicity and growing degree days. The new results confirm the overall warmth of the region, particularly close to the Arctic ocean, but reveals strong local differences that may be related to palaeoelevation in the Okhotsk-Chukotka Volcanogenic Belt in north-eastern Russia. While rainfall estimates have large uncertainties due to year-round wet soils in most locations, new measures of VPD and PET show persistent high humidity, but with notably drier summers at all the Arctic sites.

1. Introduction

The Arctic is warming faster than almost all other parts of our planet (IPCC 2014). This phenomenon is consistent with 'polar amplification' (Lee 2014) where any change in planetary scale net radiation balance, irrespective of whether ice is present at the poles or not, produces larger temperature changes at higher latitudes than in equatorial regions. Polar amplification is no better illustrated than in the Arctic during past episodes of extreme

Deleted: and t

47 warmth, such as in the early Late Cretaceous. Polar amplification makes Arctic palaeoclimate
48 proxies sensitive recorders of global change phenomena, and by studying warm Arctic
49 conditions we can derive the most reliable insights into future climate, and linked biospheric
50 responses, at high northern latitudes.

51 The current warming of the Arctic is dramatic and perhaps inevitably most
52 investigations into the [Late Cretaceous](#) palaeoclimate of the region have focussed on the
53 ancient thermal regime (e.g. Spicer & Parrish 1986; Spicer & Corfield 1992; Herman &
54 Spicer 1996a, 1997a; Amiot et al. 2004; Spicer & Herman 2010; Herman, Spicer & Spicer
55 2016), but arguably more important is the polar hydrological cycle. In today's 'coldhouse'
56 world a strong polar high-pressure cell leads to a relatively dry Arctic and only low
57 temperatures, and thus low evaporation, prevents widespread aridity. However, in a warmer
58 world a weaker polar high, and thus a weaker polar front, would have profound implications
59 for global atmospheric circulation (including phenomena such as polar vortex outbreaks) and
60 the water cycle.

61 It is possible that in the Late Cretaceous a warm Arctic Ocean generated vigorous
62 ocean-atmosphere feedbacks that helped sustain that ocean warmth while also producing a
63 more or less permanent Arctic cloud cap (Spicer et al. 2014), but atmospheric hydrology is
64 poorly constrained through a lack of reliable proxies. The focus of this work is to re-examine
65 the Arctic early Late Cretaceous climate and introduce new quantitative proxy palaeo-
66 humidity measurements in order to characterise better the polar environment at times of
67 global warmth.

68 Late Cretaceous Arctic sediments of Alaska and north-eastern Russia, collectively
69 referred to here as the North Pacific Region (NPR) (Fig. 1), host a wealth of palaeontological
70 evidence attesting to a highly diverse extinct ecosystem thriving under a temperate and humid
71 climate at palaeolatitudes as high as 82 °N ([Fig. 2](#)). The rich plant fossil record from the NPR

72 has been investigated for more than a century (see background reviews in
73 <http://arcticfossils.nsii.org.cn>) and is well documented [in a large body of work](#) (e.g. Hollick
74 1930; Samylina 1963; Lebedev 1965; Smiley 1966; Budantsev 1968; Samylina 1968; Smiley
75 1969a, b; Samylina 1973; Samylina 1974a, [b](#); Filippova [1975a, b](#); Krassilov 1975; Lebedev
76 1976; Samylina 1976; Kiritchkova & Samylina 1978; Krassilov 1978; Filippova 1979; Scott
77 & Smiley 1979; Detterman & Spicer 1981; Budantsev 1983; Spicer & Parrish 1986; Spicer
78 1986; Lebedev 1987; Spicer [Wolfe & Nichols](#) 1987; Spicer 1987; Filippova 1988;
79 Golovneva 1988; Grant [Spicer & Parrish](#) 1988; Parrish & Spicer 1988a, [b](#); Samylina 1988;
80 Filippova 1989; Lebedev & Herman 1989; Herman 1990; Spicer & Chapman 1990; Spicer &
81 Parrish 1990a; Spicer & Parrish 1990b; Golovneva 1991a, b; Herman 1991; Herman &
82 Lebedev 1991; Herman & Shchepetov 1991; Samylina & Shchepetov 1991; Shchepetov
83 1991; Golovneva & Herman 1992; Lebedev 1992; Shchepetov, Herman & Belaya 1992;
84 Spicer & Corfield 1992; Spicer [Parrish & Grant](#) 1992; Filippova & Abramova 1993; Herman
85 1993; Spicer, Rees & Chapman 1993; Filippova 1994; Golovneva 1994a, [b](#); Herman 1994;
86 Herman & Spicer 1995; Shchepetov 1995; Herman & Spicer 1996b; Herman & Spicer 1997a,
87 b; Golovneva 2000; Herman 2002; [Herman, Spicer & Kvacek 2002](#); Spicer et al. 2002;
88 Craggs 2005; Herman 2007; Herman et al. 2009; [Golovneva & Alekseev 2010](#); Spicer &
89 Herman 2010; [Tomsich et al. 2010](#); [Golovneva, Shchepetov & Alekseev 2011](#); Herman 2011,
90 [2013](#); [Alekseev, Herman & Shchepetov 2014](#); [Shchepetov & Golovneva 2014](#); [Golovneva,](#)
91 [Herman & Shchepetov 2015](#); [Golovneva & Shchepetov 2015](#); [Herman et al. 2016](#); [Herman,](#)
92 [Spicer & Spicer 2016](#); [Herman & Solokova 2016](#); [Vasilenko, Maslova & Herman 2016](#);
93 [Shchepetov & Herman 2017](#); [Nikitenko et al. 2017, 2018](#); [Herman et al. 2019](#)). While not
94 exhaustive, these works attest to the richness and intensity of study that the Cretaceous Arctic
95 floras have attracted despite the logistic difficulties of working in remote regions. A brief
96 synthesis is given here.

Deleted: Samylina 1974b;

Deleted: 1975b

Deleted: Filippova 1975a;

Deleted: a

Deleted: et al.

Deleted: [et al.](#)

Deleted: Parrish & Spicer 1988b;

Formatted: Highlight

Deleted: a

Deleted: [et al.](#)

Formatted: Highlight

Deleted: Golovneva 1994a;

Deleted: et al.

Deleted: so only

Deleted: a

Deleted: overview

[Figure 1 near here]

[Figure 2 near here]

Deleted:

1.a. Early Late Cretaceous Arctic Forests

In the early Late Cretaceous at latitudes above the palaeo-Arctic Circle (~66 °N) forests were conifer-dominated and at high latitudes almost exclusively deciduous (Parrish & Spicer 1988b; Spicer & Parrish 1990b; Spicer & Herman 2001; Spicer et al. 2002; Spicer & Herman 2010; Herman, Spicer & Spicer 2016). Key canopy-forming taxa were predominantly *Cephalotaxopsis*, *Elatocladus*, *Pityophyllum*, *Araucarites*, *Sequoia reichenbachii* and *Pagiophyllum*, while angiosperms were most abundant as understorey elements and along stream sides (Spicer & Herman 2010; Herman, Spicer & Spicer 2016), but were non-existent or rare in swamp or mire forests (Spicer, Parrish & Grant 1992). Evergreen elements were regionally comparatively rare and restricted to conifers such as *Araucarites*, *Pagiophyllum* and *Geinitzia* (<http://arcticfossils.nsii.org.cn>) characterised by having small hook- and scale-like xeromorphic leaves that reduced water loss during winter dormancy. Ground cover consisted mostly of ferns and sphenophytes (Herman, Spicer & Spicer 2016), but towards the end of the Late Cretaceous, even at the highest latitudes, herbaceous angiosperms (probably annuals and preserved only as pollen) contributed to the ground cover especially in areas disturbed by wildfires or along river margins (Frederiksen, Ager & Edwards 1988; Herman, Spicer & Spicer 2016). A comprehensive illustrated catalogue of Late Cretaceous polar forest megafossils is available online at <http://arcticfossils.nsii.org.cn>.

Formatted: Not Highlight

Deleted: et al.

Formatted: Not Highlight

Preserved standing isolated trees (Herman, Spicer & Spicer 2016) and even “fossil forests” are not uncommon in Late Cretaceous floodplain successions of the NPR. Stands of

138 straight upright trunks up to 4.5 m tall and 0.7 m in diameter have been reported from
139 northern Alaska (Decker et al. 1997) and evidence that these represent mire forests comes
140 from the observation they are rooted in coals and carbonaceous mudstones. These standing
141 trees attest not only to the stature, and structure of the mire forests, but periodic extremely
142 high sedimentation rates, suggesting intense rainfall events, river channel breakouts and
143 associated flooding.

144 Occasionally fossil wood is structurally preserved and to-date all wood specimens
145 recovered have been coniferous with well-developed growth rings, typically showing sharp
146 transitions between summer growth and winter dormancy (Parrish & Spicer 1988a; Spicer &
147 Parrish 1990a; Herman, Spicer & Spicer 2016). Summer-wood rings in Cenomanian age trees
148 tend to be wide with typically >100 cells produced each growing season and few false rings
149 (Parrish & Spicer 1988a; Herman, Spicer & Spicer 2016) showing that growth was largely
150 uninterrupted during the summer season, but Maastrichtian woods have narrow early
151 (summer) rings with few smaller cells and numerous false rings indicative of frequent
152 interruptions to growth, most likely caused by temperatures falling below 10 °C (Spicer &
153 Parrish 1990a; Spicer & Herman 2010; Herman, Spicer & Spicer 2016).

154 **1.b. Insolation and General Thermal Regime**

155 As far as can be determined Earth's rotational and magnetic poles were roughly coincidental
156 in the Late Cretaceous and obliquity, and thus the high latitude light regime, was similar to
157 that of today (Lottes 1987) meaning that Arctic winters in near-polar settings were
158 characterised by several months of darkness (Figs 3, 5). Despite this lack of direct insolation
159 polar winters along the coastlines of the Arctic Ocean were surprisingly warm, experiencing
160 temperatures that remained above freezing for much of the time (Spicer & Parrish 1990b;
161 Herman & Spicer 1996a, 1997a; Herman, Spicer & Spicer 2016). While the temperature

Deleted: 2

Formatted: Font color: Custom
Color(142,170,219)

Deleted: 4

Formatted: Font color: Custom
Color(142,170,219)

Formatted: Font color: Custom
Color(142,170,219)

164 regime of the Late Cretaceous Arctic has been well characterised through multiple proxies,
165 the hydrological system is less well constrained.

166 1.c. Research Scope

167 In this work we re-examine the thermal regime of this extinct early Late Cretaceous
168 (Cenomanian to Coniacian) polar ‘Lost World’ in the light of new high spatial resolution (~1
169 km) WorldClim2 (Fick & Hijmans 2017; <http://www.worldclim.org/>) calibrations of the non-
170 taxonomic leaf physiognomic proxy known as CLAMP (<http://clamp.ibcas.ac.cn>), but the
171 main focus is to explore new insights into the hydrological regime. We examine not only
172 precipitation and soil moisture capacity, but humidity in terms of specific humidity (SH),
173 relative humidity (RH), vapour pressure deficit (VPD) and potential evapotranspiration
174 (PET). VPD and PET are investigated in respect of annual average values and seasonal
175 variations.

176

177 2. Methods and Materials

178 Individual plants are spatially static so they have to be well adapted to their local
179 environment or they die as a direct result of environmental stress or competition from those
180 better equipped to withstand the prevailing conditions. These adaptations, preserved in the
181 abundant early Late Cretaceous plant fossil record of the NPR, can be used to determine past
182 conditions either as average annual or seasonal climate, as in the case of leaf form, or as a
183 near-daily record of environmental change encoded as variations in wood growth (tree rings).
184 By using both leaf form and tree ring data (Herman, Spicer & Spicer 2016) we can quantify
185 the early Late Cretaceous high Arctic atmospheric conditions ~~over seasonal or even sub-~~
186 ~~seasonal~~ temporal resolutions.

Deleted:)

Deleted:)

Deleted: down to a

Deleted:

Deleted: measured in weeks (Herman et al. 2016)

The principal leaf-based palaeoclimate proxy for assessing a range of climate variables is known as CLAMP (Climate-Leaf Analysis Multivariate Program) (<http://clamp.ibcas.ac.cn>) (Wolfe 1993; Kovach & Spicer 1996; Yang et al. 2011, 2015). CLAMP utilises the universal relationships that exist between leaf form in woody dicotyledonous plants and an array of climate variables. On a global scale aggregate leaf form in a stand of vegetation is more strongly determined by climate than by taxonomic composition (Yang et al. 2015), and through a combination of pleiotropy and integrated developmental pathways all leaf traits are correlated with each other (Pigliucci 2003) and an array of climate variables (Wolfe 1993; Wolfe & Spicer 1999; Yang et al. 2011, 2015). Using a multivariate statistical engine CLAMP decodes these relationships and, by scoring fossil leaf traits the same way as for living vegetation growing under known climatic regimes, estimates of past conditions can be obtained (<http://clamp.ibcas.ac.cn>).

No proxy is perfect, so a multiproxy approach should be used where possible. For the high Late Cretaceous Arctic CLAMP and oxygen isotopes from marine (Zakharov et al. 1999, 2011) and non-marine vertebrate remains (Amiot et al. 2004) [all](#) give broadly similar estimates (Herman & Spicer 1997a; Amiot et al. 2004; Spicer & Herman 2010; Herman, Spicer & Spicer 2016), increasing confidence in the fidelity of [all](#) the proxies. However, all proxies depend on modern observations for their calibration and several modern observational datasets are available, each with its own characteristics.

2.a. CLAMP Calibration

Previous CLAMP analyses of Late Cretaceous Arctic leaves have been based on modern gridded climate observations recorded between 1961 and 1990 at a spatial resolution of 0.5 x 0.5° (New, Hulme & Jones 1999), with interpolations and altitude corrections to the exact location of the vegetation stands comprising the CLAMP training sets

217 (https://www.paleo.bristol.ac.uk/ummodel/scripts/html_bridge/clamp_UEA.html). This
218 calibration dataset is known as GridMet_3br (<http://clamp.ibcas.ac.cn>). Higher spatial
219 resolution data are also available using the same observational network of meteorological
220 stations. One such dataset is that of WorldClim2 (<http://worldclim.org/version2>) (Fick &
221 Hijmans 2017), which interpolates average meteorological observations between 1970 and
222 2000 on to a spatial grid approximating to 1 km².

223 One advantage of using WorldClim2 for calibration is that numerous environmental
224 variables have been mapped on to the same grid, so by using CLAMP the range of
225 environmental signals decoded from leaf form can be extended. The new temperature-related
226 environmental variables that correlate strongly with leaf form are 1) the compensated
227 thermicity index (THERM.), 2) growing degree days above 0 °C (GDD_0), 3) growing
228 degree days above 5 °C (GDD_5), 4) minimum temperature of the warmest month
229 (MIN_T_W) and 5) maximum temperature of the coldest month (MAX_T_C). New
230 humidity-related variables are 6) mean annual vapour pressure deficit (VPD.ANN), 7) mean
231 summer vapour pressure deficit (VPD.SUN), 8) mean winter vapour pressure deficit
232 (VPD.WIN), 9) mean spring vapour pressure deficit (VPD.SPR), 10) mean autumn vapour
233 pressure deficit (VPD.AUT), 11) mean annual potential evapotranspiration (PET.ANN), 12)
234 potential evapotranspiration during the warmest month (PET.WARM), 13) potential
235 evapotranspiration during the coldest month (PET.COLD), 14) soil moisture capacity
236 (SOIL.M) and 15) the number of months when the mean temperature is above 10 °C. This
237 last metric serves as a further comparison between the WorldClim2 data and previous
238 calibrations because it should return values similar to those indicating the length of the
239 growing season (LGS). [For easy reference Table 1 summarises all the CLAMP metrics](#)
240 [presented here.](#)

Figures 6–10, graphs A–Z, illustrate the CLAMP regression models for each of the climate variables to show not only the relative position on the regression of the NPR fossil locations but also the scatter of the modern training data and thus the precision of the CLAMP predictions. All regression models are derived from the leaf physiognomy/climate relationships in 4D space as used in earlier CLAMP analyses (Herman & Spicer 1996b; 1997a; Spicer & Herman, 2010).

Formatted: Not Highlight

2.b. Climate Variable Definitions

Descriptions and regression models for the 11 standard CLAMP climate variables (mean annual temperature - MAT, warm month mean temperature - WMMT, cold month mean temperature - CMMT, length of the growing season - LGS, growing season precipitation - GSP, mean monthly growing season precipitation - MMGSP, precipitation during the three consecutive wettest months - 3WET, precipitation during the three consecutive driest months - 3DRY, mean annual relative humidity - RH. ANN, mean annual specific humidity - SH. ANN and mean annual moist enthalpy - ENTH) are given in the CLAMP website (<http://clamp.ibcas.ac.cn>) and summarised in Table 1. Here we describe the newly added climate variables.

Deleted: Figure 5, parts a–c, illustrates the CLAMP regression models for each of the climate variables (Fig. 5, graphs A–Z) to show not only the relative position on the regression of the NPR fossil locations but also the scatter of the modern training data and thus the precision of the CLAMP predictions. All regression models are derived from the leaf physiognomy/climate relationships in 4D space as used in earlier CLAMP analyses (Herman & Spicer 1996b; 1997a; Spicer and Herman, 2010).

Formatted: Highlight

The compensated thermicity index (THERM.) is given by

$$\text{THERM.} = ((T + m + M) \cdot 10) \pm C \quad (1)$$

where T is the mean annual temperature, m is the minimum temperature of the coldest month, M is the maximum temperature of the coldest month and C is a ‘compensation value’. Calculating C is complicated and depends on continentality, which is simply a measure of the difference between the WMMT and the CMMT. In the extratropical zones of the World (northern and southern 27° parallels, respectively) THERM. is designed to equilibrate the large differences in temperature that occur between winter cold and summer warmth in

275 continental climates compared to those small differences that occur in maritime climates.
276 Details of how C is calculated are given in the Worldwide Bioclimatic Classification System
277 (www.globalbioclimatics.org) (Rivas-Martinez, Sanchez-Mata & Costa 1999).

278 GDD_0 is a measure of the cumulative heat available to plants and is the sum of the
279 mean monthly temperatures for months with mean temperatures greater than 0 °C multiplied
280 by number of days above that temperature.

281 GDD_5 is the sum of mean monthly temperatures for months with mean temperature
282 greater than 5 °C multiplied by number of days above that temperature.

283 VPD reflects the ease of losing water to the atmosphere and as such affects
284 transpiration as well as evaporation. It is the difference between the actual water vapour
285 pressure and the water vapour pressure at saturation. At saturation (VPD=0 kPa) water will
286 condense out to form clouds, dew or films of water on surfaces, including leaves. VPD
287 combines temperature and relative humidity so, unlike relative humidity, vapour-pressure
288 deficit has a simple nearly straight-line relationship to the rate of evapo-transpiration and
289 other measures of evaporation. Because of this, plant distribution (Huffaker 1942) and leaf
290 physiognomy are more strongly reflective of VPD. ~~ANN~~ than RH. ~~ANN~~ (Fig. ~~7~~, ~~1~~, ~~1~~). This
291 suggests strong leaf trait adaptations to overcoming transpiration depression at low VPDs.

292 Also, VPD is strongly correlated with stomatal conductance and carbon isotope fractionation
293 (e.g. Oren et al. 1999; Bowling et al. 2002; Katul, Palmroth & Oren 2009). As well as annual
294 mean VPD (VPD.ANN), seasonal VPD estimates (spring – VPD.SPR, summer – VPD.SUM,
295 autumn – VPD. AUT and winter – VPD.WIN) are also given by CLAMP.

296 Potential evapotranspiration (PET) is an expression of the ability of the atmosphere to
297 remove water through evapotranspirational processes assuming no limits on plant water
298 supply. Such an assumption appears valid in the case of the early Late Cretaceous Arctic as
299 evidenced by the widespread occurrence of thick coals indicative of raised mires (Sable &

Deleted: Sb

Deleted: I

Deleted: J

303 Stricker 1987; Grant, Spicer & Parrish 1988), gleyed palaeosols and isotopic analysis (Ufnar
 304 et al. 2004). PET combines the energy available for evaporation and the capacity of the lower
 305 atmosphere to move evaporated water vapour away from the land surface, for example by
 306 winds and convective processes. Because solar radiation provides the energy for evaporation,
 307 PET is lower on cloudy days, in winter and at higher latitudes. Like VPD, PET can be
 308 thought of as an indication of how difficult it is for a plant to transpire, a process that is
 309 essential for moving water and nutrients from the soil to the leaves. Because of this, and as
 310 with VPD, leaf physiognomy correlates well with PET (Fig. 8, Q; Fig. 9, V & W) particularly
 311 at low PET values. Although herbaceous plants transpire less than woody plants because they
 312 have a lower leaf surface area, the PET reference measure is based on uniformly short grass
 313 completely covering the ground. PET estimates for the warmest month (PET.WARM, Fig. 9,
 314 V) and coldest month (PET.COLD, Fig. 9, W) are given as well as the mean annual PET
 315 (PET.ANN, Fig. 8, Q).

316 In the work presented here we introduce a new CLAMP calibration based on
 317 WorldClim2 that we call WorldClim2_3br. As well as using the WorldClim2 gridded climate
 318 data for the standard CLAMP climate variables, we add the 15 new climate variables
 319 considered above. The new WorldClim2-based climate training set (WorldClim2_3br) and
 320 the accompanying modern leaf physiognomic (Physg3brcAZ) data files are given in the
 321 *Supplementary Materials*.

323 2.c. Fossil Assemblages

324 Here we re-analyse eight well-documented fossil leaf assemblages (see
 325 <http://arcticfossils.nsii.org.cn>) from across the NPR (Figs. 1 & 2) spanning the Cenomanian
 326 to Coniacian. All have been previously analysed for the standard CLAMP climate variables

Deleted: 5

Deleted: c

Deleted: -S

Deleted: 5c

Deleted: R

Deleted: 5c

Deleted: S

Deleted: 5

Deleted: c

Deleted: WorldClim3

337 calibrated using low spatial resolution modern gridded climate data (GridMet_3br) (Spicer &
338 Herman 2010; Herman, Spicer & Spicer 2016). We use the same modern vegetation trait
339 scores as used previously (Physg3brcAZ) but with the new WorldClim2_3br ~1 km² gridded
340 data and with 15 new environmental variables. Where palaeolatitudes are quoted they are
341 derived from GeTech.Plc palaeogeographies ([an example of which is shown in Fig. 2](#)) used
342 in climate modelling (<http://www.bridge.bris.ac.uk/resources/simulations>). These
343 palaeogeographies time-integrate a range of geological data and include plate kinematics.
344 CLAMP scoresheets for these fossil assemblages are given in the *Supplementary Materials*.

346 **3. Results and Discussion**

347 Tables [2-4](#) present results obtained for the fossil assemblages using the new WorldClim2_3br
348 CLAMP calibration as well [as](#) (for comparison) previously obtained results that used low
349 spatial resolution GridMet_3br CLAMP calibration. The GridMet_3br results are given in
350 parentheses. Figures [6-10, graphs A-Z](#), show the CLAMP regression models for the new
351 WorldClim2_3br calibration and the positions of the fossil sites on the regression model. The
352 regression models indicate the relationship between leaf physiognomy and the individual
353 climate variable and thus the precision of the predictions. They also indicate the positions of
354 the values for each fossil assemblage for each climate variable relative to those for modern
355 vegetation. Note that despite essentially the same observational network of meteorological
356 stations underpinning both gridded datasets, GridMet_3br and WorldClim2_3br calibrations
357 rarely yield identical results. These differences are purely a function of the different gridding
358 processes between the GridMet_3br and WorldClim2_3br and a slightly different period of
359 climate observations: 1961–1990 in the case of GRIDMet_3br and 1970–2000 for
360 WorldClim2_3br. Such differences define the maximum predictive precision possible for any

Deleted: 1

Deleted: 3

Deleted: 5a-e

364 proxy using modern gridded climate observations for calibration because they are a measure
365 of how well we can quantify modern climate.
366

367 **3.a. Thermal regime**

368 While not identical, the two calibrations yield similar results regarding the thermal regime
369 and the differences are smaller than, or the same as, the uncertainties. They show clearly that
370 despite the lack of winter insolation terrestrial CMMTs across the Arctic NPR region, even at
371 latitudes as high as ~80 °N, rarely fell below freezing. This might appear surprising for the
372 highest palaeolatitudes (Novaya Sibir – 81.6 °N, North Slope Alaska – 77 °N) that
373 experienced more than three months of continuous winter darkness (Fig. 3), but these sites
374 were close to the Arctic Ocean coastline and several lines of evidence point to the Arctic
375 Ocean being warm with winter sea surface temperatures of ~6 °C (Herman & Spicer 1997a),
376 or even approaching 10 °C as indicated here by the winter coastal plain temperatures of the
377 North Slope, Alaska.
378

379 [Table 2 near here]
380

381 The estimates for the length of the growing season are also consistent with the light
382 regimes at different palaeolatitudes (Figs. 3–5). Because leaf load is directly related to
383 transpiration and the humidity regime, we have attempted to estimate the timing of bud break
384 and leaf fall in the predominantly deciduous NPR vegetation. Bud break and leaf fall likely
385 occurred in early March and late October respectively in the Cenomanian Vilui Basin
386 (palaeolatitude 72 °N, LGS 7.5 months) when mean temperatures rose above 10 °C and there
387 was at least 8 hours of direct sunlight (Fig. 5).
388

Deleted: 2

Deleted: 1

Deleted: 2

Deleted: 4

Deleted: 4

394 [Figure 3 near here]

Deleted: 2

395

396 In Grebenka, also Cenomanian but at 74 °N, the growing season is similar with a

397 slightly warmer winter despite the slightly higher latitude (Fig. 4). The Penzhina assemblage

Deleted: 3

398 (Plat. 72 °N) has a shorter growing season of around 5 months due to the lower winter

399 temperature (Fig. 5). The 10 °C mark was not passed until almost mid-April when there were

Deleted: 4

400 16 hours of direct sunlight during each 24-hour period and the growing season lasted until

401 late September when temperatures dipped below 10 °C and daylight hours approached 12.

402 The foliage traits of the highest palaeolatitude assemblage, Novaya Sibir (Turonian, Plat. ~82

403 °N), suggest that bud break occurred in early April and growth continued until the beginning

404 of October, a growing period of 5.8 months. The Coniacian North Slope assemblage from the

405 northern Alaska palaeo-floodplain has the longest growing season (7.5 months) despite its

406 palaeolatitude of ~78 °N. This is because winter temperatures barely dipped below 10 °C

407 (Table 2, Fig. 3) and although the mean air temperature would have passed 10 °C in mid

Deleted: 1

408 February and dipped below 10 °C in early November, a period of ~8.5 months, growth must

Deleted: 2

409 have been moderated by insolation. With relatively warm conditions maintained by a nearby

410 warm Arctic Ocean we estimate that a minimum of 4 hours of direct sunlight per 24-hour

411 period is likely to have been the critical driver for leaf expansion and abscission, meaning

412 that bud burst likely took place in late February and leaf fall in early-mid October. Early Late

413 Cretaceous North Slope tree ring characteristics (Parrish & Spicer 1988a) indicate the rapid

414 onset of growth and a prolonged and uninterrupted summer growth period.

415 ▼ Deleted: 1

416 3.b. Relative Palaeoelevations

417 The differences in thermal regime between the various leaf fossil assemblages used in our

418 analyses depend not only on their palaeo-position but also on their relative elevations above

425 sea level. Clues to these elevational differences come from the moist enthalpy estimates
426 (Table 3). The North Slope assemblage is known to represent near sea level conditions
427 because the plant-bearing units inter-finger with marine sediments (Mull, Houseknecht &
428 Bird 2003), and as would be expected this site yields the highest moist enthalpy value
429 indicative of the lowest elevation. The site with the lowest moist enthalpy value (highest
430 elevation) is in the Okhotsk-Chukotka Volcanogenic Belt (Arman) and the difference
431 between the two enthalpy values is 20 kJ/kg (Table 3) which translates to a height difference
432 of ~2 km (Forest, Molnar & Emanuel 1995; Spicer 2018). However, this difference is not
433 spatially or temporally corrected. The Arman site has been estimated to have been at ~0.6 km
434 using the Kaivayam assemblage as a sea level datum and the GridMet_3br calibration
435 (Herman 2018). Using the new WorldClim2_3brc raises this surface height estimate for the
436 Arman flora to $\sim 0.9 \pm 0.8$ km. Based on the relative palaeo-enthalpy estimates all the NPR
437 localities likely were below 1 km elevation, but detailed analysis awaits future moist enthalpy
438 fields derived from integrating proxy and palaeoclimate modelling.

440 [Figure 4 near here]

442 [Figure 5 near here]

444 **3.c. Precipitation**

445 Table 3 shows the estimated precipitation regime derived from leaf form. In general, the
446 wetter the climate the less well leaf physiognomy predicts the precipitation regime (Figs. 6 &
447 7, E-H). Many of the Arctic angiosperm leaves are large (Herman 1994), which is an
448 advantageous adaptation to low and predominantly diffuse sunlight situations provided that
449 water is abundant. Abundant thick Late Cretaceous coals (Sable & Stricker 1987), many of

Deleted: 2

Deleted: 2

Deleted: 3

Deleted: 4

Deleted: 2

Deleted: 5a

Deleted: ,

Deleted: b

458 which represent raised mires (Youtcheff, Rao & Smith 1987; Grant, Spicer & Parrish 1988),
459 and isotope analyses (Ufnar et al. 2004) all suggest that early Late Cretaceous Arctic annual
460 precipitation was high.

461

462 [Table 3 near here]

463

464 Although we can be certain that in general the Late Cretaceous Arctic was wet,
465 deriving accurate precipitation estimates from high latitude palaeofloras is problematic for
466 several reasons. Firstly, leaf fossils are invariably preserved in aquatic environments where
467 low oxygen limits decay. The limited distance that leaves can be transported from their
468 growth site before burial (Spicer 1981; Ferguson 1985; Spicer & Wolfe 1987) means that the
469 source plants most likely grew in locations where the water table was high year-round. The
470 estimate of soil moisture capacity for the NPR fossil assemblages (Table 3, SOIL M, Fig. 9,
471 U) also suggests moist soils. Moreover, this water may not reflect local precipitation but
472 conditions in the headwaters of the river catchment many tens if not hundreds of kilometres
473 away. Secondly, even if the water table was maintained by local precipitation, the soil system
474 stores water and buffers seasonal variations in water availability, meaning that 3WET and
475 3DRY estimates represent seasonality in rainfall only poorly. Thirdly, at high latitudes where
476 light and temperature impose dormancy and seasonal leaf-shedding, rainfall in the dormant
477 period is unlikely to be reflected in leaf physiognomy. This is not the case, however, for
478 winter temperatures.

479 Winter temperatures are to some extent encoded in leaf physiognomy (Fig. 6, C)
480 because young leaves have to be adapted to rapidly warming spring conditions, the rate of
481 warming being determined in large part by the CMMT (Spicer, Herman & Kennedy 2004).
482 However, below observed winter temperatures of -10 °C this extrapolative encoding, which

Deleted: 2

Deleted: 2

Deleted: 5d

Deleted: 5a

487 tends to yield winter temperatures that are too warm (Spicer, Herman & Kennedy 2004), does
488 not apply at all to winter precipitation where soil moisture may be high year-round but
489 inaccessible to the plant in early spring if the soil is frozen. The GSP estimate (note not the
490 mean annual precipitation) of between 50 and 125 cm is quite low where the regression
491 model shows little scatter (Fig. 6, E), but because the growing season is often less than half
492 the year this indicates that overall the annual precipitation could have been at least double
493 that indicated. Although CLAMP routinely returns estimates for precipitation during the
494 three wettest (3WET) and three driest months (3DRY), these values may be unreliable
495 because of the marked growth seasonality. In view of the arguments just given for wet soils it
496 is noteworthy that there is a marked difference in the 3WET:3DRY ratio, which for all
497 assemblages except Vilui B return ratios near 4:1.

Deleted: 5a

498 ▼
499 The wet soils would necessarily mute these ratios, so the fact that they are pronounced
500 suggests even more extreme rainfall seasonality than the values suggest and that the Arctic
501 may have experienced a ‘monsoonal’ climate in the early Late Cretaceous. An essentially
502 ‘summer wet’ (wet:dry ratio 3:1) has been proposed for the Arctic in the Eocene based on
503 isotopic analysis of fossil wood interpreted to have been evergreen (Schubert et al. 2012), but
504 an ‘ever wet’ precipitation regime for this Epoch is indicated by leaf form (West, Greenwood
505 & Basinger 2015) based on predominantly deciduous angiosperm taxa. To really understand
506 the hydrological regime in a warm Arctic requires, as far as is possible, decoupling the soil
507 water environment from that of the atmosphere.

Deleted:
[Figure 5 a near here]

[Figure 5 b near here]

[Figure 5 c near here]

509 3.d. Humidity

510 Until now CLAMP has routinely returned only two humidity measures: mean annual relative
511 humidity (RH.ANN) and mean annual specific humidity (SH.ANN). SH is simply the amount

519 of water in grams contained within a kilogram of dry air and as such is a measure of the
520 absolute water content of the air. Leaf form appears to code for mean annual SH quite well in
521 that the CLAMP regression model (Fig. 7, J) shows relatively little scatter compared to that
522 of mean annual RH (Fig. 7, I). RH is a measure of the amount of water in the atmosphere
523 relative to what it can hold and as such is highly dependent upon temperature. As the scatter
524 in Fig. 7, I shows leaf form does not correlate well with RH so CLAMP predictions of RH
525 carry a lot of uncertainty.

Deleted: 5b

Deleted: 5b

Deleted: 5b

526 A better measure of humidity, one that reflects the force opposing transpiration, is
527 vapour pressure deficit (VPD). VPD is the difference between the amount of moisture
528 actually in the air and how much moisture the air could potentially hold when it is saturated
529 and, like SH, is not measured in relation to temperature. High VPD values are found in arid
530 environments while low VPDs reflect air close to saturation and thus a high resistance to
531 transpiration.

Deleted: ¶
[Figure 5 d near here]¶

532 Figs. 7 & 8, L-P, show that at low VPD values leaf form correlates very well with
533 VPD, presumably because leaves have to possess adaptations to enhance transpiration, while
534 in high VPD situations transpiration can take place easily without the need for specific leaf
535 trait spectra to increase transpiration. Thus, there is more scatter in the CLAMP regressions at
536 high VPDs. So, unlike precipitation, CLAMP estimates of VPD in moist regimes are
537 generally more precise than in dry regimes.

Deleted: [Figure 5 e near here]¶

Deleted: 5b

Deleted: and

Deleted: c

538 [Table 4 near here]

Deleted: 3

539 Table 4 shows that all the Arctic early Late Cretaceous leaf assemblages indicate low
540 VPDs (<5 kPa) in spring, autumn and winter but, because autumn and winter are times when
541 leaves are senescent or shed, these values have to be interpreted with caution. The spring and

Deleted: 3

553 summer values are likely to be the most reliable because this is when the leaves are
554 functional. The highest summer VPDs are those from fossil assemblages in NE Russia
555 (Greibenka, Arman, Tylpegyrgynai) and these assemblages also point to the lowest annual RH
556 values, while the lowest summer VPD and annual values are revealed in assemblages from
557 the Arctic Ocean coastal areas (Novaya Sibir, North Slope), the Yukon-Koyukuk Basin and
558 the Vilui Basin. These assemblages also indicate the highest RH.ANN values. Of all the
559 Arctic fossil sites those bordering the Arctic Ocean and nearest the palaeo-pole (Novaya Sibir
560 and North Slope) have the lowest VPDs, the only exception being the North Slope that has a
561 VPD.WIN value similar to those of Grebenka and Arman. These assemblages also indicate
562 the warmest winter temperatures (Fig. 3). However, even assemblages indicating the driest
563 summers have very low VPDs compared to most modern vegetation in the calibration (Figs.

564 7 & 8, L-P), indicating an overall extremely wet atmosphere compared to that experienced
565 by most vegetation in the modern CLAMP training sets.

566 PET is a measure of how easily the atmosphere removes water from a surface and so,
567 like VPD, indicates the ease with which transpiration can take place. Also, like VPD, PET
568 shows a close relationship with leaf trait spectra at low PET values i.e. wet regimes. All NPR
569 fossil assemblages fall in the lower half of the regressions showing that they experienced
570 similar PETs as modern vegetation in the more humid half of the 3br training set. The
571 PET.WARM and PET.COLD values also show that any dry season was in the summer,
572 presumably because higher temperatures and convective winds favoured greater evaporation.

573 Taking Figures 3-5 together it is noticeable that Figure 4 shows the highest
574 humidities and that these occur at palaeolatitude ~75 °N from sites (Greibenka and
575 Tylpegyrgynai) that were not immediately adjacent to the Arctic Ocean, but closer to the
576 north Pacific. These high humidities may be a function of a cool northern Pacific gyre

Deleted: 5

Deleted: c

Deleted: 5 b

Deleted: and

Deleted: c

Deleted: 2

Deleted: 4

Deleted: 3

585 (Herman & Spicer 1996a, 1997a) or reflect a more northward and diffuse palaeoposition of
586 the polar front, which today is located at ~60 °N as a consequence of a strong polar high.

587

588 4. Conclusions

589 4.a. Thermal regime.

590 The new WorldClim2_3br CLAMP calibration confirms earlier isotopic (Amiot et al. 2004),

591 vegetation (Parrish & Spicer 1988b) and leaf physiognomic analyses (Herman & Spicer

592 1996b, 1997a; Spicer & Herman 2010) from the NPR, demonstrating a thermal regime that

593 may be broadly characterised as 'temperate' even at palaeolatitudes as high as ~80 °N where

594 freezing temperatures were of limited duration and severity. The precision of the

595 palaeoclimate regime estimates are constrained by the uncertainties associated with our

596 inability to quantify precisely modern climate. These uncertainties, which will differ between

597 calibration suites depending on calibration sampling distribution, density and temporal

598 coverage, apply to any palaeoenvironmental proxy that relies on calibrations using the

599 modern conditions and should not be ignored when making inter-proxy comparisons or

600 interpreting past environments. In the analyses presented here MAT estimates differ by up to

601 0.6 °C, WMMT by up to 0.9 °C and CMMT by up to 1.5 °C depending purely on the

602 underlying modern gridded climate data.

603

604 4.b. Palaeoelevation

605 No terrestrial palaeotemperature comparisons can be meaningful without taking into

606 account differences in the surface height at which the estimates are made. In the case of the

607 early Late Cretaceous NPR it is clear that some thermal differences between assemblages can

608 be attributed to relative elevational differences, but that no site was likely to have been above

609 1 km. However, a 1 km elevation range can translate into MAT differences of several

Deleted: and

Deleted: and

Deleted: and

Deleted: region

614 degrees Celsius depending on early Late Cretaceous near polar terrestrial lapse rates. This
615 aspect of the NPR palaeoclimate, and better characterisation of Late Cretaceous moist
616 enthalpy fields, await future modelling work.

617

618 **4.c. Precipitation and humidity**

619 The precipitation regime throughout the NPR, overall appears moderately wet with
620 most sites indicating summer (growing season) precipitation ~0.5 m, but **apparently** with
621 marked seasonal variations. Compared to all the sites in the modern calibration data humidity
622 is high year-round, but with most evaporative stress occurring in the summer. PET (Table 4)
623 never exceeds rainfall even in the summer growth period (Table 3), leading to year-round
624 saturated soils. Drought was not limiting to growth in any of the NPR early Late Cretaceous
625 localities and CMMTs (Table 2) were never low enough for long enough to freeze the soil to
626 below tree rooting depth.

Deleted: region

Deleted: 3

Deleted: 2

Deleted: 1

627 Our new insights into annual and seasonal atmospheric humidity in the warm early
628 Late Cretaceous Arctic supports the concept of a very humid near-polar regime markedly
629 different from today's frigid desert under a strong polar high-pressure cell and with a
630 corresponding strong polar front at ~60 °N. It is likely **that** the polar front in the early Late
631 Cretaceous was displaced towards the pole and more diffuse than at present. A key
632 component of the weaker polar high was the warm Arctic Ocean that, as evidenced by year-
633 round high humidities, generated a vigorous hydrological cycle, which in turn helped
634 maintain the polar warmth.

Deleted:

635 The vegetation and climate records entombed in the extensive Late Cretaceous
636 sediments of the Arctic point towards what the North polar region is likely to experience as
637 overall anthropogenic global warming progresses. Polar amplification will rapidly drive the
638 Arctic from a place where at present precipitation is sparse under a cold strong polar high-

644 pressure system to a region that is wet and polar air masses become increasingly loosely
645 constrained as warming proceeds and the polar high weakens. The hydrological cycle is
646 likely to become invigorated through warming-induced evaporation and enhanced
647 transpiration from greater vegetation cover and complexity. Eventually this will result in a
648 near permanent polar cloud cap, high humidity and frequent fog occurrences over both land
649 and sea, further enhancing warming.

651 **Acknowledgements.** The research was performed within the framework of the State program
652 no. 0135-~~2019-0044~~ of the Geological Inst., Russian Acad. Sci. and partly supported by the
653 Russian Foundation for Basic Research project no. 19-05-00121 (AH). CLAMP recalibration
654 was made possible through NSFC-NERC joint research program (41661134049 and
655 NE/P013805/1) (PJV) and an XTBG International Fellowship for Visiting Scientists (RAS).

657 **Declarations of Interest**

658 All authors declare no competing interests.

660 Online Supplementary Material at <http://journals.cambridge.org/geo>

663 **References**

664 ALEKSEEV, P.I., HERMAN, A.B. & SHCHEPETOV, S.V. 2014. New angiosperm genera from
665 Cretaceous sections of Northern Asia. *Stratigraphy and Geol. Correlation*, **22**(6), 606–
666 617.

668 AMIOT, R., LECUYER, C., BEUFFETAUT, E., F., F., LEGENDRE, S. & MEARTINEAU, F. 2004.

669 Latitudinal temperature gradient during the Cretaceous Upper-Campanian-Middle
670 Maastrichtian: $\delta O18$ record of continental vertebrates. *Earth and Planetary Science*
671 *Letters*, **226**, 255–272.

Deleted: 2016

Deleted: 0001

Commented [RAS1]: Alexei - what other works should go in here? It would be good to add more recent Russian ones.

Formatted: Indent: Left: 0 cm, Hanging: 1 cm, Line spacing: single

Deleted: -

675 BOWLING, D.R., MCDOWELL, N.G., BOND, B.J., LAW, B.E. & EHLERINGER, J.R. 2002. ¹³C
676 content of ecosystem respiration is linked to precipitation and vapor pressure deficit.
677 *Oecologia*, **131**, 113–124.

678 BUDANTSEV, L.Y. 1968. Late Cretaceous flora of the Vilui Depression. *Botanicheskii*
679 *Zhurnal*, **53**, 3–16.

680 BUDANTSEV, L.Y. 1983. *Istoriya Arkticheskoi Flory Epokhi Rannego Kainofita (Arctic Flora*
681 *History in the Early Cenophytic Epoch)*. Nauka, Leningrad.

682 CRAGGS, H.J. 2005. Late Cretaceous climate signal of the Northern Pekulney Range Flora of
683 northeastern Russia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **217**, 25–46.

684 DECKER, P.L., WILSON, G.C., WATTS, A.B. & WORK, D. 1997. Growth position petrified trees
685 over-lying thick Nanushuk Group coal, Lili Creek, Lookout Ridge Quadrangle, North
686 Slope Alaska. In: Clough, J.G. & Larson, F. (eds) *Short Notes on Alaskan Geology*
687 *1997*. Alaska Division of Geological and Geophysical Surveys, 63–70.

688 DETTERMAN, R.L. & SPICER, R.A. 1981. New stratigraphic assignment for rocks along
689 Igilatvik (Sabbath) Creek, William O. Douglas Wildlife Range, Alaska. U.S.
690 Geological Survey in Alaska, accomplishments during 1979. *U.S. Geological Survey*
691 *Circular*, **823-B**, 11–12.

692 FERGUSON, D.K. 1985. The origin of leaf-assemblages - new light on an old problem. *Review*
693 *of Palaeobotany and Palynology*, **46**, 117–188.

694 FICK, S.E. & HIJMANS, R.J. 2017. Worldclim2: New 1-km spatial resolution climate surfaces
695 for global land surfaces. *International Journal of Climatology*, **37**, 4302–4315,
696 <http://doi.org/https://doi.org/10.1002/joc.5086>.

697 FILIPPOVA, G.G. 1975a. Flora of the Lower Cretaceous deposits of the Umkuveem and
698 Ainakhkurgan Depressions. *Materialy po geologii i poleznym iskopayemym Severo-*
699 *Vostoka SSSR*, **22**, 23–35.

Deleted: -

Deleted: -

Deleted: -

Deleted: -

704 FILIPPOVA, G.G. 1975b. On the age of the volcanogenic deposits of the left bank of the
 705 Palyavaam River (Chukotka). *Proceedings of the Institute of Biology and Pedology,*
 706 *Far Eastern Scientific Centre, USSR Academy of Sciences, New Series [Trudy Biologo-*
 707 *Pochvennogo Instituta DVNTs AN SSSR, Novaya Seriya], 27, 55–59.*
 708 FILIPPOVA, G.G. 1979. Cenomanian flora of the Grebenka River and its stratigraphic
 709 significance *Dalnevostochnaya Paleofloristika (Palaeofloristics of the Far East)*. Trudy
 710 Biologo-Pochvennogo Instituta DVNTs Akademii Nauk SSSR, Novaya Seriya, **53**, 91–
 711 115.
 712 FILIPPOVA, G.G. 1988. Grebenka floristic assemblage in the Anadyr River basin (Chukotka).
 713 *Tikhookeanskaya Geologiya*, **17**, 50–60.
 714 FILIPPOVA, G.G. 1989. New data on the Grebenka Flora from the Anadyr River Basin
 715 *Vulkanogennyi Mel Dalnego Vostoka (Volcanogenic Cretaceous of the Far East)*. DVO
 716 Akademii Nauk SSSR, Vladivostok, 76–87.
 717 FILIPPOVA, G.G. 1994. Coniacian flora of the northern part of the Pekulnei Range. *Kolyma*,
 718 *March 1994*, 13–21.
 719 FILIPPOVA, G.G. & ABRAMOVA, L.N. 1993. *Late Cretaceous flora of North-eastern Russia*.
 720 Nedra, Moscow.
 721 FOREST, C.E., MOLNAR, P. & EMANUEL, K.E. 1995. Palaeoaltimetry from energy
 722 conservation principles. *Nature*, **343**, 249–253.
 723 FREDERIKSEN, N.O., AGER, T.A. & EDWARDS, L.E. 1988. Palynology of Maastrichtian and
 724 Paleocene rocks, lower Colville River region, North Slope of Alaska. *Canadian*
 725 *Journal of Earth Sciences*, **25**, 512–527.
 726 GOLOVNEVA, L.B. 1988. Novyi rod *Microconium* (Cupressaceae) iz pozdнемelovykh
 727 otlozhenii Severo-Vostoka SSSR (A new genus *Microconium* (Cupressaceae) form the

Deleted: -

Deleted: -

Deleted: -

Formatted: Font: Not Bold

Deleted: -

Formatted: Font: Not Bold

Deleted: -

Formatted: Font: Not Bold

Deleted: -

734 Late Cretaceous deposits of the North-East of the USSR). *Botanicheskii Zhurnal*, **73**(8),
735 1179–1184 (in Russian). Deleted: -

736 GOLOVNEVA, L.B. 1991a. Novyi rod *Palaeotrapa* (Trapaceae?) i novye vidy *Quereuxia* iz
737 rarytinskoi svity (Koryakskoye nagor'ye, maastrikht-danii (The new genus
738 *Palaeotrapa* (Trapaceae?) and new species *Quereuxia* from the Rarytkin Formation
739 (the Koryak Upland, Maastrichtian - Danian)). *Botanicheskii Zhurnal*, **76**(4), 601–610 Deleted: -
740 (in Russian).

741 GOLOVNEVA, L.B. 1991b. Vidy roda *Trochodendroides* (Cercidiphyllaceae) v maastrikht-
742 datskoi rarytinskoi flore Koryakskogo nagor'ya (The species of the genus
743 *Trochodendroides* (Cercidiphyllaceae) in Maastrichtian - Danian Rarytkin Flora of the
744 Koryak Upland). *Botanicheskii Zhurnal*, **76**(3), 427–436 (in Russian). Deleted: -

745 GOLOVNEVA, L.B. 1994a. Maastrichtian–Danian Floras of Koryak Uplands. *Trudy*
746 *Botanicheskogo Instituta, VL Komarova*, **13**, 1–145. Deleted: -

747 GOLOVNEVA, L.B. 1994b. The flora of the Maastrichtian–Danian deposits of the Koryak
748 Uplands, northeast Russia. *Cretaceous Research*, **15**, 89–100. Deleted: -

749 GOLOVNEVA, L.B. 2000. The Maastrichtian (Late Cretaceous) climate in the Northern
750 Hemisphere. In: Hart, M.B. (ed) *Climates: past and present*. Geological Society of
751 London Special Publication, London, **181**, 43–54. Deleted: -

752 GOLOVNEVA, L.B., & ALEKSEEV, P. I. 2010. The genus *Trochodendroides* Berry in the
753 Cretaceous floras of Siberia. In: Budantsev, L. Yu. (ed.), *Palaeobotany*, Vol. **1**, 120–166
754 [in Russian, English summary].
755 Deleted: -
756 GOLOVNEVA, L.B. & HERMAN, A.B. 1992. New data on composition and age of flora of the
757 Koryak Formation (Borth-eastern Russia). *Botanicheskii Zhurnal*, **77**(7), 60–71. Deleted: -

Deleted: -

Deleted: -

Deleted: -

Deleted: -

Deleted: -

Deleted: -

Formatted: Small caps

Formatted: Line spacing: Double

Formatted: Font: Bold

Formatted: Check spelling and grammar

Formatted: Normal, Line spacing: single

Deleted: -

- 765 GOLOVNEVA, L.B., HERMAN, A.B., & SHCZEPETOV, S.V. 2015. The genus *Menispermites*
766 *Lesquereux* (angiosperms) in the Cretaceous Grebenka Flora of Northeastern Russia.
767 *Paleontological Journal*, **49**(4), 429–437.
- 768 GOLOVNEVA, L.B. & SHCZEPETOV, S.V. 2015. Floristic assemblages from Upper Cretaceous
769 deposits of East Chukotka. In: *Paleobotanika (Palaeobotany)*, Vol. **6**. St. Marafon,
770 Petersbourg, 96–119 [in Russian].
- 771 GOLOVNEVA, L.B., SHCZEPETOV, S.V., & ALEKSEEV, P.I. 2011. Chingandzha Flora (Late
772 Cretaceous, North-eastern Russia): systematic composition, palaeoecological features
773 and stratigraphic significance. In: *Lectures in Memory of A.N. Kryshstofovich*, Iss. **7**, 37–
774 61 [in Russian].
- 775 GRANT, P.R., SPICER, R.A. & PARRISH, J.T. 1988. Palynofacies of northern Alaskan
776 Cretaceous coals. *7th International Palynological Congress Brisbane, Abstracts*
777 *Volume*, **60**.
- 778 HERMAN, A.B. 1990. Late Cretaceous Floras and Climate of the Anadyr-Koryakian
779 Subregion (North-East USSR). *Proceedings of the Symposium "Paleofloristic and*
780 *Paleoclimatic Changes in the Cretaceous and Tertiary*, **73**, 79.
- 781 HERMAN, A.B. 1991. Cretaceous angiosperms and phytostратigraphy of North-Western
782 Kamchatka and Yelistratov Peninsula. In: Herman, A.B. & Lebedev, E.L. (eds)
783 *Stratigraphy and flora of the Cretaceous of north-western Kamchatka*. Nauka,
784 Moscow, **5**, 141.
- 785 HERMAN, A.B. 1993. Late Maestrichtian flora from the Emima-Ill'naivaam Interfluvium, the
786 northeastern Koryak Highland, and its stratigraphic significance. *Stratigraphy and*
787 *Geological Correlation*, **1**, 427–434.

Formatted: Small caps

Formatted: Small caps

Formatted: Font: Bold

Formatted: Small caps

Formatted: Normal

Formatted: Font: Bold

Formatted: Check spelling and grammar

Formatted: Font: Bold

Deleted: -

Deleted: -

Deleted: -

791 HERMAN, A.B. 1994. Late Cretaceous Arctic platanoids and high latitude climate. *In*: Boulter,
792 M.C. & Fisher, H.C. (eds) *Cenozoic Plants and Climates of the Arctic (NATO ASI Ser.,*
793 *I 27)*. Springer, Berlin, 151–159.

794 HERMAN, A.B. 2002. Late Early-Late Cretaceous floras of the North Pacific Region:
795 florogenesis and early angiosperm invasion. *Review of Palaeobotany and Palynology*,
796 **122**, 1–11.

797 HERMAN, A.B. 2007. Comparative paleofloristics of the Albian-early Paleocene in the
798 Anadyr-Koryak and North Alaska Subregions, Part 1: The Anadyr-Koryak Subregion.
799 *Stratigraphy and Geological Correlation*, **15**, 321–332.

800 HERMAN, A.B. 2011. *Al'bskaya – Paleotsenovaya Flora Severnoi Patsifiki (Albian –*
801 *Paleocene Flora of the North Pacific Region)*. GEOS, Moscow.

802 HERMAN, A.B. 2013. Albian – Paleocene Flora of the North Pacific: Systematic Composition,
803 Palaeofloristics and Phytostratigraphy. *Stratigraphy and Geological Correlation*, **21**(7),
804 689–747.

805 HERMAN, A.B. 2018. On the likely palaeoelevation of the Turonian-Coniacian Arman Flora
806 site (North-Eastern Asia). *Fossil Imprint*, **74**, 159–164.

807 HERMAN, A.B., AKHMETIEV, M.A., KODRUL, T.M., MOISEEVA, M.G. & IAKOVLEVA, A.I.
808 2009. Flora Development in Northeastern Asia and Northern Alaska during the
809 Cretaceous–Paleogene Transitional Epoch. *Stratigraphy and Geological Correlation*,
810 **17**, 79–97.

811 HERMAN, A.B., GOLOVNEVA, L.B., SHCZEPETOV, S.V., & GRABOVSKY, A.A. 2016. The Late
812 Cretaceous Arman Flora of Magadan Oblast, Northeastern Russia. *Stratigraphy and*
813 *Geological Correlation*, **24**(7), 651–760.

Deleted: -

Deleted: -

Deleted: -

Formatted: Small caps

Formatted: Normal

Deleted: ¶

Deleted: -

Formatted: Small caps

Formatted: Small caps

819 HERMAN, A.B., KOSTYLEVA, V.V., NIKOLSKII, P.A., BASILYAN, A.E., & KOTEL'NIKOV, A.E.
820 2019. New data on the Late Cretaceous flora of the New Siberia Island, New Siberian
821 Islands. *Stratigraphy and Geological Correlation*, 27(3).
822 HERMAN, A.B. & LEBEDEV, Y.L. 1991. *Stratigraphy and flora of the Cretaceous deposits of*
823 *North-West Kamchatka*. Academy of Sciences of the USSR Report **468**.
824 HERMAN, A.B. & SHCZEPETOV, S.V. 1991. The Mid-Cretaceous flora of the Anadyr river
825 basin (Tchukotka, NE Siberia). *Proceedings of the Pan-European Palaeobotanical*
826 *Conference, Palaeovegetational development in Europe*, 273–279.
827 HERMAN, A.B. & SPICER, R.A. 1995. Latest Cretaceous flora of northeastern Russia and the
828 “Terminal Cretaceous Event” in the Arctic. *Paleontological Journal*, **29**, 22–25.
829 HERMAN, A.B. & SOKOLOVA, A.B. 2016. Late Cretaceous Kholokhovchan Flora of
830 Northeastern Asia: Composition, age and fossil plant descriptions. *Cretaceous*
831 *Research*, 59, 249–271.
832 HERMAN, A.B. & SPICER, R.A. 1996a. Palaeobotanical evidence for a warm Cretaceous
833 Arctic Ocean. *Nature*, **380**, 330–333.
834 HERMAN, A.B. & SPICER, R.A. 1996b. *Nilssoniocladus* in the Cretaceous Arctic: new species
835 and biological insights. *Review of Palaeobotany and Palynology*, **92**, 229–243.
836 HERMAN, A.B. & SPICER, R.A. 1997a. New quantitative palaeoclimate data for the Late
837 Cretaceous Arctic: evidence for a warm polar ocean. *Palaeogeography,*
838 *Palaeoclimatology, Palaeoecology*, **128**, 227–251.
839 HERMAN, A.B. & SPICER, R.A. 1997b. The Koryak flora: did the early Tertiary deciduous
840 flora begin in the late Maastrichtian of northeastern Russia? *Mededelingen Nederlands*
841 *Instituut voor Toegepaste Geowetenschappen TNO*, **58**, 87–92.
842 HERMAN, A.B., SPICER, R.A. & KVACEK, J. 2002. In: Wagreich, M. (ed) *Aspects of*
843 *Cretaceous Stratigraphy and Palaeobiogeography. Proceedings 6th Internat.*

Formatted: Small caps

Formatted: Normal

Formatted: Font: Check spelling and grammar

Deleted: -

Deleted: -

Formatted: Small caps

Formatted: Font: Italic

Formatted: Font: Bold

Deleted: -

Deleted: -

Deleted: -

849 *Cretaceous Symposium, Vienna 2000*. Österreichische Akademie der Wissenschaften,
850 Schriftenreihe der Erdwissenschaftlichen Kommissionen, Vienna, **15**, 93–108.

851 HERMAN, A.B., SPICER, R.A. & SPICER, T.E.V. 2016. Environmental constraints on terrestrial
852 vertebrate behaviour and reproduction in the high Arctic of the Late Cretaceous.
853 *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **441**, 317–338.

854 HOLLICK, A. 1930. The Upper Cretaceous Floras of Alaska. *United States Geological Survey*
855 *Professional Paper*, **159**, 1–123.

856 HUFFAKER, C.B. 1942. Vegetational Correlations with Vapour Pressure Deficit and Relative
857 Humidity. *American Midland Naturalist*, **28**, 486–500.

858 IPCC (ed) 2014. *Synthesis Report. Contribution of Working Groups I, II and III to the Fifth*
859 *Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing*
860 *Team*. IPCC, Geneva, Switzerland, 151.

861 KATUL, G.G., PALMROTH, S. & OREN, R. 2009. Leaf stomatal responses to vapour pressure
862 deficit under current and CO₂-enriched atmosphere explained by the economics of gas
863 exchange. *Plant Cell Environment*, **32**, 968–979.

864 KIRITCHKOVA, A.I. & SAMYLINA, V.A. 1978. Korrelyatsiya nizhnemelovykh otlozhenii
865 Lenskogo ugleonosnogo basseina i Severo-Vostoka SSSR (Correlation of Lower
866 Cretaceous deposits of Lena coal-bearing basin and North-eastern USSR). *Soviet Geol.*,
867 **12**, 3–18.

868 KOVACH, W.L. & SPICER, R.A. 1996. Canonical correspondance analysis of leaf
869 physiognomy: a contribution to the development of a new palaeoclimatological tool.
870 *Palaeoclimates*, **2**, 125–138.

871 KRASSILOV, V.A. 1975. Climatic changes in Eastern Asia as indicated by fossil floras. II Late
872 Cretaceous and Danian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **17**,
873 157–172.

Deleted: -

Deleted: s

Deleted: -

Deleted: -

Deleted: -

879 KRASSILOV, V.A. 1978. Late Cretaceous gymnosperms from Sakhalin, U.S.S.R., and the
880 terminal Cretaceous event. *Palaeontology*, **21** (4), 893–905.

881 LEBEDEV, Y.L. 1965. Late Jurassic Flora of Zeia River and the Jurassic - Cretaceous
882 Boundary. *Academy of Sciences of the USSR*, **125**, 5–142.

883 LEBEDEV, Y.L. 1976. Evolution of Albian-Cenomanian floras of Northeast USSR and the
884 association between their composition and facies conditions. *International Geology*
885 *Review*, **19**, 1183–1190.

886 LEBEDEV, Y.L. 1987. Stratigraphy and age of the Okhotsk-Chukotsk volcanogenic belt.
887 *Academy of Sciences of the USSR*, **421**, 3–175.

888 LEBEDEV, Y.L. 1992. The Cretaceous floras of Northeastern Asia. *Izvestiya Akademii Nauk*,
889 *seriya geologicheskaya*, **4**, 85–96.

890 LEBEDEV, Y.L. & HERMAN, A.B. 1989. A new genus of Cretaceous angiosperms- *Dalembia*.
891 *Review of Palaeobotany and Palynology*, **59**, 77–91.

892 LEE, S. 2014. A theory for polar amplification from a general circulation perspective. *Asia-*
893 *Pacific Journal of the Atmospheric Sciences*, **50**, 31–43.

894 LOTTES, A.L. 1987. Paleolatitude determinations: comparison of palaeoclimatic and
895 palaeomagnetic methods. *Geological Society of America Abstracts with Program*, **19**,
896 749.

897 MULL. C.G., HOUSEKNECHT, D.W. & BIRD, K.J. 2003. Revised Cretaceous and Tertiary
898 stratigraphic nomenclature in the Colville Basin, Northern Alaska. *U.S. Geological*
899 *Survey Professional Paper*, **1673**, 1–51.

900 NEW, M., HULME, M. & JONES, P. 1999. Representing Twentieth-Century Space–Time
901 Climate Variability. Part I: Development of a 1961–90 Mean Monthly Terrestrial
902 Climatology. *Journal of Climate*, **12**, 829–856.

Deleted: -

Deleted: -

Deleted: -

Deleted: -

Deleted: -

Deleted: -

Deleted: -

910 NIKITENKO, B.L., DEVYATOV, V.P., LEBEDEVA, N.K., BASOV, V.A., GORYACHEVA, A.A.,
 911 PESTCHEVITSKAYA, E.B., & GLINSKIKH, L.A. 2017. Jurassic and Cretaceous
 912 stratigraphy of the New Siberian Archipelago (Laptev and East Siberian seas): facies
 913 zoning and lithostratigraphy. *Geologiya i Geofizika*, **58**(12), 1867–1885 (in Russian).
 914 NIKITENKO, B.L., DEVYATOV, V.P., LEBEDEVA, N.K., BASOV, V.A., FURSENKO, E.A.,
 915 GORYACHEVA, A.A., PESTCHEVITSKAYA, E.B., GLINSKIKH, L.A., & KHAFAEVA, S.N.
 916 2018. Jurassic and Cretaceous biostratigraphy and organic matter geochemistry of the
 917 New Siberian Islands (Russian Arctic). *Geologiya i Geofizika*, **59**(2), 211–230 (in
 918 Russian).

919 OREN, R., SPERRY, J.S., KATUL, G.G., PATAKI, D.E., EWERS, B.E., PHILLIPS, N. & SCHÄFER,
 920 K.V.R. 1999. Survey and synthesis of intra- and interspecific variation in stomatal
 921 sensitivity to vapour pressure deficit. *Plant Cell Environment*, **22**, 1515–1526.

922 PARRISH, J.T. & SPICER, R.A. 1988a. Middle Cretaceous wood from the Nanushuk Group,
 923 Central North Slope, Alaska. *Palaeontology*, **31**, 19–34.

924 PARRISH, J.T. & SPICER, R.A. 1988b. Late Cretaceous terrestrial vegetation: a near-polar
 925 temperature curve. *Geology*, **16**, 2–25.

926 PIGLIUCCI, M. 2003. Phenotypic integration: studying the ecology and evolution of complex
 927 phenotypes. *Ecology Letters*, **6**, 265–272.

928 RIVAS-MARTINEZ, S., SÁNCHEZ-MATA, D. & COSTA, M. 1999. *Itinera Geobotanica*, **12**, 3–
 929 316.

930 SABLE, E.G. & STRICKER, G.D. 1987. Coal in the National Petroleum Reserve in Alaska
 931 (NPRA): framework geology and resources. In: Tailleux, I. & Weimer, P. (eds) *Alaskan*
 932 *North Slope Geology*. Society of Economic Paleontologists and Mineralogists, Pacific
 933 Section, Bakersfield, California, **1**, 195–215.

Formatted: Small caps

Formatted: Small caps

Formatted: Normal

934 SAMYLINA, V.A. 1963. Mesozoic flora Aldan. *Academiya Nauk S.S.S.R., Paleobotanica*, ser.
935 8, 4, 59–139.

936 SAMYLINA, V.A. 1968. Early Cretaceous angiosperms of the Soviet Union based on leaf and
937 fruit remains. *J. Linnaean Soc. (Botany)*, **61**, 207–218.

938 SAMYLINA, V.A. 1973. Correlation of Lower Cretaceous continental deposits of Northeast
939 USSR based on palaeobotanical data. *Sovietskaya Geologiya*, **8**, 42–57.

940 SAMYLINA, V.A. 1974a. Florae Cretae Prioris Partium Boreali-orientalium URSS. *Academia*
941 *Scientiarum URSS*, 3–54.

942 SAMYLINA, V.A. 1974b. Early Cretaceous floras of Northeast USSR (problems of
943 establishing Cenophytic floras) [*Rannemelovye flory severo-vostoka SSSR. K probleme*
944 *stanovleniya flor Kainofita*]. Nauka, Leningrad.

945 SAMYLINA, V.A. 1976. The Cretaceous flora of Omsukchan (Magadan district). Komarov
946 Botanical Institute of the Academy of Sciences of the USSR.

947 SAMYLINA, V.A. 1988. *Arkagala stratoflora of northeastern Asia [Arkagalinskaya sratoflora*
948 *severo-vostoka Azii]*. Nauka, Leningrad.

949 SAMYLINA, V.A. & SHCZEPETOV, S.V. 1991. Ginkgovyye i chekanovskievyye iz
950 verkhmelovyykh otlozhenii Yeliseevskogo obnazheniiy na r. Grebyonka
951 (pravoberezh'ye r. Anadyr') (The ginkgoaleans and chekanowskialeans from the Upper
952 Cretaceous deposits of the Yeliseev outcrop on the Grebenka River (the right bank of
953 the Anadyr River)). *Botanicheskii Zhurnal*, **76**(7), 950–956 (in Russian).

954 SCHUBERT, B.A., JAHREN, A.H., EBERLE, J.J., STERNBERG, L.S.L. & EBERTH, D.A. 2012. A
955 summertime rainy season in the Arctic forests of the Eocene. *Geology*, **40**, 523–526.

956 SCOTT, R.A. & SMILEY, C.J. 1979. Some Cretaceous megafossils and microfossils from the
957 Nanushuk Group, northern Alaska: a preliminary report. *U.S. Geological Survey*
958 *Circular*, **794**, 89–111.

Formatted: EndNote Bibliography

Formatted: Font: Palatino

Deleted: SAMYLINA, V.A. 1968. Early Cretaceous angiosperms of the Soviet Union based on leaf and fruit remains. *J. Linnaean Soc. (Botany)*, **61**, 207–218.

962 SHCZEPETOV, S.V. 1991. *Mid Cretaceous flora of the Chauna Group (central Chukotka):*
 963 *stratigraphic setting, systematic composition, atlas of plants [Srednemelovaya flora*
 964 *Chaunskoi Serii (tsentral'naya Chukotka): stratigraficheskoye polozheniye,*
 965 *sistematicheskii sostav, stlas rastenii]*. Magadan.

966 SHCZEPETOV, S.V. 1995. *Nonmarine Cretaceous Stratigraphy of North-eastern Russia*
 967 *[Korrelyatsiya nemorskogo mela Severo-Vostoka Rossii]*. Severo-Vostochnyi
 968 kompleksnyi nauchno-issledovatel'skiy institut Sibirskogo otdeleniya Akademii nauk,
 969 Magadan, Magadan.

970 SHCZEPETOV, S.V., & GOLOVNEVA, L.B. 2014. The Late Cretaceous Zarya flora of the
 971 Northern Okhotsk region and phytostratigraphy of the lower part of the Okhotsk–
 972 Chukotka volcanogenic belt section. *Stratigraphy and Geological Correlation*, **22**(4),
 973 391–405.

974 SHCZEPETOV, S.V., & HERMAN, A.B. 2017. The formation conditions of the burial site of Late
 975 Cretaceous dinosaurs and plants in the Kakanaut River basin (Koryak Highlands,
 976 Northeastern Asia). *Stratigraphy and Geological Correlation*, **25**(4), 400–418.

977 SHCZEPETOV, S.V., HERMAN, A.B. & BELAYA, B.V. 1992. *Mid-Cretaceous flora of the right*
 978 *bank of the Anadyr River (stratigraphic setting, systematic composition, plant fossils*
 979 *atlas)*. Sev.-Vost. Kompl. Nauchn.-Issled. Inst. DVO AN SSSR, Magadan.

980 SMILEY, C.J. 1966. Cretaceous floras of the Kuk River area, Alaska, stratigraphic and
 981 climatic interpretations. *Geological Society of America Bulletin*, **77**, 1–14.

982 SMILEY, C.J. 1969a. Floral zones and correlations of Cretaceous Kukpowruk and Corwin
 983 Formations, northwestern Alaska. *American Association of Petroleum Geologists*
 984 *Bulletin*, **53**, 2079–2093.

Formatted: Font: Italic

Formatted: Small caps

Formatted: Small caps

Formatted: Normal

Formatted: Font: Check spelling and grammar

985 SMILEY, C.J. 1969b. Cretaceous Floras of the Chandler-Colville Region, Alaska, stratigraphy
986 and preliminary floristics. *American Association of Petroleum Geologists Bulletin*, **53**,
987 482–502.

988 SPICER, R.A. 1981. The sorting and deposition of allochthonous plant material in a modern
989 environment at Silwood Lake, Silwood Park, Berkshire. *USGS Prof. Pap.* 1143, 1–77.

990 SPICER, R.A. 1986. Comparative leaf architectural analysis of Cretaceous radiating
991 angiosperms. In: Spicer, R.A. & Thomas, B.A. (eds) *Systematic and Taxonomic*
992 *Approaches in Palaeobotany*. Systematics Association Special Volume, **31**, 223–233.

993 SPICER, R.A. 1987. Late Cretaceous Floras and terrestrial environment of Northern Alaska.
994 *Alaskan North Slope Geology*, **1**, 497–512.

995 SPICER, R.A. 2018. Phytopaleoaltimetry: Using Plant Fossils to Measure Past Land Surface
996 Elevation. In: Hoorn, C., Perrigo, A. & Antonelli, A. (eds) *Mountains, Climate and*
997 *Biodiversity*, (Wiley-Blackwell), 96–109.

998 SPICER, R.A., AHLBERG, A., HERMAN, A.B., KELLEY, S.P., RAIKEVICH, M.I. & REES, P.M.
999 2002. Palaeoenvironment and ecology of the middle Cretaceous Grebenka flora of
1000 northeastern Asia. *Palaeogeography Palaeoclimatology Palaeoecology*, **184**, 65–105.

1001 SPICER, R.A. & CHAPMAN, J.E. 1990. The evolution of high latitude floras, *Trends in Ecology*
1002 *and Evolution*, **5**, 279–284.

1003 SPICER, R.A. & CORFIELD, R.M. 1992. A Review of Terrestrial and Marine Climates in the
1004 Cretaceous and Implications for Modelling the Greenhouse Earth. *Geological*
1005 *Magazine*, **129**, 168–180.

1006 SPICER, R.A. & HERMAN, A.B. 2001. The Albian-Cenomanian flora of the Kukpowruk River,
1007 western North Slope, Alaska: stratigraphy and plant communities. *Cretaceous*
1008 *Research*, **22**, 1–40.

Deleted: -

Deleted: -

1011 SPICER, R.A. & HERMAN, A.B. 2010. The Late Cretaceous Environment of the Arctic: A
 1012 quantitative reassessment using plant fossils. *Palaeogeography, Palaeoclimatology,*
 1013 *Palaeoecology*, **295**, 423–442.

1014 SPICER, R.A., HERMAN, A.B. & KENNEDY, E.M. 2004. The Foliar Physiognomic Record of
 1015 Climatic Conditions During Dormancy: CLAMP and the Cold Month Mean
 1016 Temperature. *Journal of Geology*, **112**, 685–702.

1017 SPICER, R.A., HERMAN, A.B., YANG, J. & SPICER, T.E.V. 2014. Why Future Climate Change
 1018 is likely to be Underestimated: evidence from Palaeobotany. *Journal of the Botanical*
 1019 *Society of Bengal*, **67**, 75–88.

1020 SPICER, R.A. & PARRISH, J.T. 1986. Paleobotanical evidence for cool North Polar climates in
 1021 middle Cretaceous (Albian-Cenomanian) time. *Geology*, **14**, 703–706.

1022 SPICER, R.A. & PARRISH, J.T. 1990a. Late Cretaceous-early ~~Tertiary~~ palaeoclimates of
 1023 northern high latitudes: a ~~quantitative~~ view. *Journal of Geological Society, Lond.*, **147**,
 1024 329–341.

1025 SPICER, R.A. & PARRISH, J.T. 1990b. Latest Cretaceous woods of the central North Slope,
 1026 Alaska. *Palaeontology*, **33**, 225–242.

1027 SPICER, R.A., REES, P.M. & CHAPMAN, J.E. 1993. Cretaceous phytogeography and climate
 1028 signals. In: Allen J.R.L., Hoskins, B.J., Sellwood, B.W., Spicer, R.A., Valdes, P.J.
 1029 (eds), *Palaeoclimates and Their Modelling*. Royal Society/Chapman and Hall. 69–78.

1030 SPICER, R.A., PARRISH, J.T. & GRANT, P.R. 1992. Evolution of vegetation and coal-forming
 1031 environments in the Late Cretaceous of the North Slope of Alaska. In: McCabe P.J.,
 1032 Parrish J.T. (eds), *Controls on the Distribution and Quality of Cretaceous Coals*.
 1033 *Geol. Soc. Amer. Spec. Pap.*, No **267**, 177–192.

1034 SPICER, R.A. & WOLFE, J.A. 1987. Plant taphonomy of late Holocene deposits in Trinity
 1035 (Clair Engle) Lake, northern California. *Paleobiology*, **13**, 227–245.

Deleted: -

Deleted: -

Deleted: -

Deleted: Tertairy

Deleted: qunatitative

1041 SPICER, R.A., WOLFE, J.A. & NICHOLS, D. J. 1987. Alaskan Cretaceous-Tertiary floras and
1042 Arctic origins. *Paleobiology*, **13**, 73–83.

1043 TOMSICH, C.S., MCCARTHY, P.J., FOWELL, S.J. & SUNDERLIN, D. 2010. Paleofloristic and
1044 Paeoenevironmental information from a Late Cretaceous (Maastrichtian) flora of the
1045 lower Cantwell Formation near Sable Mountain, Denali National park, Alaska.
1046 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **295**, 389–408.

1047 UFNAR, D.F., LUDVIGSON, G.A., GONZÁLEZ, L.A., BRENNER, R.L. & WITZKE, B.J. 2004. High
1048 latitude meteoric $\delta^{18}\text{O}$ compositions: Paleosol siderite in the Middle Cretaceous
1049 Nanushuk Formation, North Slope, Alaska. *Geological Society of America Bulletin*,
1050 **116**, 463–473.

1051 VASILENKO, D.V., MASLOVA, N.P. & HERMAN, A.B. 2016. Galls on the *Compositiphyllum*
1052 *retinerve* (Herman) Herman et Kvaček (Angiosperms) from the Turonian of the
1053 Northwestern Kamchatka Peninsula, Russia. *Paleontological Journal*, **50**(6), 653–657.

1054 WEST, C.K., GREENWOOD, D.R. & BASINGER, J.F. 2015. Was the Arctic Eocene ‘rainforest’
1055 monsoonal? Estimates of seasonal precipitation from early Eocene megafloras from
1056 Ellesmere Island, Nunavut. *Earth and Planetary Science Letters*, **427**, 18–30.

1057 WOLFE, J.A. 1993. A method of obtaining climatic parameters from leaf assemblages: United
1058 States Geological Survey Bulletin. *United States Geological Survey Bulletin*, **2040**, 1–
1059 73.

1060 WOLFE, J.A. & SPICER, R.A. 1999. *Fossil Leaf Character States: Multivariate Analysis*.
1061 Geological Society, London, 233–239.

1062 YANG, J., SPICER, R.A., SPICER, T.E.V., ARENS, N.C., JACQUES, F.M.B., SU, T., KENNEDY,
1063 E.M., HERMAN, A.B., *et al.* 2015. Leaf form–climate relationships on the global stage:
1064 an ensemble of characters. *Global Ecology and Biogeography*, **24**, 1113–1125.

Formatted: Small caps

Formatted: Font: Italic

Deleted: ¶

Formatted: Font: Bold

Deleted: -

Formatted: Small caps

Formatted: Normal

Deleted: -

Deleted: -

1069 YANG, J., SPICER, R.A., SPICER, T.E.V. & LI, C.-S. 2011. 'CLAMP Online': a new web-based
1070 palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North
1071 America. *Palaeobiodiversity and Palaeoenvironments*, **91**, 163–183.

1072 YOUTCHEFF, J.S.J., RAO, P.D. & SMITH, J.E. 1987. Variability in two northwest Alaska coal
1073 deposits. *In*: Tailleux, I. & Weimer, P. (eds) *Alaskan North Slope Geology*. Society of
1074 Economic Paleontologists and Mineralogists, Pacific Section, Bakersfield, California,
1075 **1**, 225–232.

1076 ZAKHAROV, Y.D., BORISKINA, N.G., IGNATYEV, A.V., TANABE, K., SHIGETA, Y., POPOV,
1077 A.M., AFANANSYEVA, T.B. & MAEDA, H. 1999. Palaeotemperature curve for the Late
1078 Cretaceous of the northwestern circum-Pacific. *Cretaceous Research*, **20**, 685–697.

1079 ZAKHAROV, Y.D., SHIGETA, Y., POPOV, A.M., VELIVETSKAYA, T.A. & AFANANSYEVA, T.B.
1080 2011. Cretaceous climatic oscillations in the Bering area (Alaska and Koryak Upland):
1081 isotopic and palaeontological evidence. *Sedimentary Geology*, **235**, 122–131.

1082

1083

1084

Deleted: -

Deleted: -

1087
1088 Figure Legends

1089
1090 Figure 1. Map of the modern North Pacific Region (NPR) showing the locations of the fossil
1091 assemblages investigated here. Vilui – Cenomanian, Arman River- Coniacian, Novaya Sibir
1092 – Turonian, Kaivayam - Coniacian, Penzhina - Turonian, Grebenka – Cenomanian,
1093 Tylopegyrgynai - Coniacian, North Slope – Coniacian. Details of the stratigraphy and
1094 sedimentary successions at each site are given in <http://arcticfossils.nssi.org.cn>.

Figure 2. North polar projection of Turonian palaeogeography based on Getech Plc. reconstructions. Positions of fossil localities indicated by the following symbols: Square - Vilui River; Diagonal cross - Arman River; Triangle - Novaya Sibir (New Siberia Island); Inverted triangle - Grebenka River; Diamond - Penzhina; Star (partly hidden by the diamond)- Kaivayam; Circle - Tylpergyrgynai; Horizontal cross - North Slope.

Formatted: Indent: Left: 1 cm

Figure 3. Light, thermal and humidity regime for fossil assemblages at palaeolatitude ~80 °N.

Deleted: 2

Figure 4. Light, thermal and humidity regime for fossil assemblages at palaeolatitude ~75 °N.

Deleted: 3

Formatted: Indent: First line: 0 cm

Figure 5. Light, thermal and humidity regime for fossil assemblages at palaeolatitude ~70 °N.

Deleted: 4

1111

1112 Figure 6. CLAMP regression models for the WorldClim2 3brc modern vegetation calibration

1113 sites (open black circles) and predicted climate variables for eight early Late Cretaceous

Deleted: 5

Deleted: a

Deleted: Worldclim2

1117 fossil sites (coloured circles as in the Key shown in Fig. 5a B). Bars indicate ± 1 sd. MAT -
1118 mean annual temperature, WMMT – warm month mean temperature, CMMT- cold month
1119 mean temperature, LGS – length of the growing season (temp. >10 °C), GSP – growing
1120 season precipitation, MMGSP – mean monthly growing season precipitation.

1121

1122 Figure 7. CLAMP regression models for the WorldClim2 3brc modern vegetation calibration

1123 sites (open black circles) and predicted climate variables for eight early Late Cretaceous

Deleted: 5b

Deleted: Worldclim2

1126 fossil sites (coloured circles as in the Key shown in Fig. 5a B). 3WET -precipitation in the
1127 three consecutive wettest months, 3DRY - precipitation in the three consecutive driest
1128 months, RH.ANN – mean annual relative humidity, SH.ANN – mean annual specific
1129 humidity, ENTH – mean annual moist enthalpy, VPD.ANN – mean annual vapour pressure
1130 deficit.

Figure 8. CLAMP regression models for the WorldClim2 3brc modern vegetation calibration sites (open black circles) and predicted climate variables for eight early Late Cretaceous

Deleted: 5c

Deleted: Worldclim2

1136 fossil sites (coloured circles as in the Key shown in Fig. 5a B). VPD.SUM - mean summer
1137 vapour pressure deficit, VPD.WIN - mean winter vapour pressure deficit, VPD.SPR - mean
1138 spring vapour pressure deficit, VPD.AUT – mean autumn vapour pressure deficit.

1139

1140 Figure 9. CLAMP regression models for the WorldClim2 3brc modern vegetation calibration

1141 sites (open black circles) and predicted climate variables for eight early Late Cretaceous

Deleted: 5d

Deleted: Worldclim2

1144 fossil sites (coloured circles as in the Key shown in Fig. 5a B). GDD_0 - growing degree
1145 days when temperatures are above freezing, GDD_5 - growing degree days when
1146 temperatures are above +5°C, SOIL_M - derived soil moisture capacity, PET.WARM -
1147 potential evapotranspiration during the warmest month, PET.COLD - potential
1148 evapotranspiration during the coldest month, MIN_T_W - minimum temperature of the
1149 warmest month.

1150

1151 Figure 10. CLAMP regression models for the WorldClim2 3brc modern vegetation
1152 calibration sites (open black circles) and predicted climate variables for eight early Late
1153 Cretaceous fossil sites (coloured circles as in the Key shown in Fig. 5a B). MAX_T_C -
1154 maximum temperature during the coldest month, M_COUNT - number of months where the
1155 temperature is above +10°C.
1156

Deleted: 5e

Deleted: Worldclim2

1159
1160
1161
1162
1163
1164
1165
1166
1167
1168
1169
1170
1171
1172
1173
1174
1175
1176
1177
1178
1179
1180
1181
1182
1183
1184

Table legends

Table 1. Summary of CLAMP environmental variables, their acronyms, descriptions and units, derived from WorldClim2 gridded data at ~ 1 km spatial resolution.

Table 2. Summary of temperature-related CLAMP-derived metrics for early Late Cretaceous plant assemblages from the North Pacific Region. Values obtained by a CLAMP calibration based on WorldClim2_3br and GRIDMet_3br (in parentheses) gridded climate data. MAT - mean annual temperature, WMMT - warm month mean temperature, CMMT 0- cold month mean temperature, MIN_T_W - minimum temperature of the warmest month, MAX_T_C - maximum temperature of the coldest month, THERM. - compensated thermicity index: sum of mean annual temp., min. temp. of coldest month, max. temp. of the coldest month, x 10, with compensations for better comparability across the globe, GDD_0 - sum of mean monthly temperature for months with mean temperature greater than 0°C multiplied by number of days, GDD_5 - sum of mean monthly temperature for months with mean temperature greater than 5 °C multiplied by number of days, LGS - length of the growing season when mean temperatures are above 10 °C, M_COUNT - count of the number of months with mean temp greater than 10 °C.

Table 3. Summary of precipitation, soil moisture and moist enthalpy CLAMP-derived metrics for early Late Cretaceous plant assemblages from the North Pacific Region. Values obtained by a CLAMP calibration based on WorldClim2 and, in parentheses, GRIDMet_3br gridded climate data. GSP – precipitation during the growing season, MMGSP – mean monthly precipitation during the growing season, 3WET – precipitation during the three consecutive wettest months, 3DRY – precipitation during the three consecutive driest months, SOIL_M -

Deleted: ¶

Formatted: Indent: Left: 0.25 cm, First line: 0 cm

Deleted: ¶

Deleted: 1

Deleted: 2

1189 Derived available soil water capacity (volumetric fraction) predicted using the global
1190 compilation of soil ground observations
1191 (ftp://ftp.soilgrids.org/data/recent/AWCh1_M_sl2_250m.tif), ENTH-annual mean moist
1192 enthalpy.
1193
1194 Table 4. Summary of humidity metrics, soil moisture and moist enthalpy CLAMP-derived
1195 metrics for early Late Cretaceous plant assemblages from the North Pacific Region. Values
1196 obtained by a CLAMP calibration based on WorldClim2 and GRIDMet_3br (in parentheses)
1197 gridded climate data. RH.ANNUAL - annual mean relative humidity, SH.ANNUAL - annual
1198 mean specific humidity, VPD.ANN - annual mean vapour pressure deficit, VPD.SUM - mean
1199 VPD for the summer quarter, VPD.WIN - mean VPD for the winter quarter, VPD.SPR -
1200 mean VPD for the spring quarter, VPD-AUT - mean VPD for the autumn quarter, PET.ANN
1201 - annual mean potential evapotranspiration, PET.WARM - mean potential evapotranspiration
1202 for the warmest quarter, PET.COLD - mean potential evapotranspiration for the coldest
1203 quarter.
1204

Deleted: 3

Table 1. CLAMP Climate Variables and Descriptions

Formatted Table

Name	Acronym	Description	Units
Mean annual temperature	MAT	Mean temperature throughout the year	°C
Warm month mean temp.	WMMT	Average temperature of the warmest month	°C
Cold month mean temp.	CMMT	Average temperature of the coldest month	°C
Length of the growing season	LGS	Number of months when temperatures are ≥ 10°C	Number
Growing season precipitation	GSP	Total precipitation during the growing season (temperature ≥ 10°C)	cm
Mean monthly growing season precipitation	MMGSP	Average precipitation per month during the growing season	cm
Precipitation during the three wettest months	3-WET	Average precipitation during the three consecutive wettest months	cm
Precipitation during the three driest months	3-DRY	Average precipitation during the three consecutive driest months	cm
Relative humidity	RH.ANN	Average annual relative humidity	%
Specific humidity	RH.ANN	Average annual specific humidity (the amount of water in a kg of dry air)	g/kg
Enthalpy	ENTH	Average annual moist enthalpy (energy per kilogram of air)	kJ/kg
Minimum temperature of the warmest month	MIN_T_W	Lowest daily temperature during the warmest month	°C
Maximum temperature of the coldest month	MAX_T_C	Warmest daily temperature during the coldest month	°C
Compensated Thermicity Index	THERM	Sum of mean annual temp., min. temp. of coldest month, max. temp. of the coldest month, x 10, with compensations for better global comparability	°C
Growing degree days 0	GDD_0	Sum of mean monthly temperature for months with mean temperature > 0°C multiplied by the number of days this occurs	Number
Growing degree days 5	GDD_5	Sum of mean monthly temperature for months with mean temperature > 5°C multiplied by number of days this occurs	Number
Month count	M_COUNT	Count of the number of months when the temperature > 10°C	Number
Soil Moisture	SOIL_M	Derived available soil water capacity (volumetric fraction) at 7 standard depths predicted using the global compilation of soil ground observations.	%v
Mean annual vapour pressure deficit	VPD.ANN	Average annual vapour pressure deficit	hPa
Mean summer vapour pressure deficit	VPD.SUM	Average vapour pressure deficit during the three summer months	hPa
Mean winter vapour pressure deficit	VPD.WIN	Average vapour pressure deficit during the three winter months	hPa
Mean spring vapour pressure deficit	VPD.SPR	Average vapour pressure deficit during the three spring months	hPa
Mean autumn vapour pressure deficit	VPD.AUT	Average vapour pressure deficit during the three autumn months	hPa
Potential evapotranspiration (PET)	PET.ANN	The ability of the atmosphere to remove water through evapo-transpiration, given unlimited water supply, averaged over the year	mm/month
Mean PET of the warmest month	PET.WARM	PET averaged over the warmest month	mm/month
Mean PET of the coldest month	PET.COLD	PET averaged over the coldest month	mm/month

1209

Table 2. Temperature-Related Metrics

LOCALITY	AGE	MAT (°C)	WMMT (°C)	CMMT (°C)	MIN_T_W (°C)	MAX_T_C (°C)	THERM. (°C)	GDD_0	GDD_5	LGS (months)	M_COUNT (months)
Vilui "B"	Cenomanian	13.1 (12.8)	21 (21)	6.2 (5.3)	16.9	9.3	260	47124	53955	7.5 (7.4)	7.3
Greibenka	Cenomanian	13.5 (12.9)	21.2 (20.8)	6.8 (5.9)	15.2	11.1	261	49372	56645	7.7 (7.4)	7.4
Tylpergyrg.	Coniacian	8.7 (8.4)	18.4 (18.8)	-0.8 (-1.6)	11.7	3.4	100	25612	34745	5.5 (5.4)	5.3
Novaya Sibir	Turonian	9.8 (9.2)	17.3 (17)	2.4 (1.1)	11.0	5.5	161	30389	38347	5.9 (5.8)	5.6
North Slope	Coniacian	13.9 (13.3)	19.1 (19.1)	9.4 (7.9)	14.2	12.0	320	50590	55643	7.6 (7.6)	7.3
Arman	Cenomanian	8.0 (8.2)	17.8 (18.7)	-1.9 (-2)	11.1	2.2	78	22150	31392	5.2 (5.3)	5.0
Kaivayam	Coniacian	9.9 (9.6)	18.1 (18.3)	1.9 (1.1)	12.2	5.4	158	31201	39311	6.0 (6.0)	5.8
Penzhina	Turonian	7.6 (7.7)	16.9 (17.7)	-2 (-2.4)	10.0	1.8	75	20161	29057	5.0 (4.9)	4.8
Standard Deviation		2.0 (1.1)	2.5 (1.4)	3.2 (1.9)	2.5	3.2	68	10510	9195	1.1 (0.7)	1.1

Deleted: 1

Formatted Table

1210
1211
1212
1213

Table 3. Precipitation, Soil Moisture and Enthalpy Metrics

LOCALITY	AGE	GSP (cm)	MMGSP (cm)	3WET (cm)	3DRY (cm)	SOIL_M (%V)	ENTH (kJ/kg)
Vilui "B"	Cenomanian	98 (105)	13 (13.5)	66 (62)	20 (21)	17.3	323 (324)
Greibenka	Cenomanian	82 (82)	10 (9)	60 (58)	14 (15)	17.1	319 (317)
Tylpergyrg.	Coniacian	50 (48)	9 (9)	53 (49)	12 (13)	18.5	305 (303)
Novaya Sibir	Turonian	47 (54)	8 (8.2)	52 (50)	12 (15)	18.4	313 (310)
North Slope	Coniacian	58 (79)	7 (9)	51 (53)	13 (13)	17.1	328 (326)
Arman	Cenomanian	47 (48)	9 (9)	53 (48)	12 (14)	18.8	303 (304)
Kaivayam	Coniacian	53 (60)	9 (9)	53 (52)	13 (15)	18.2	312 (310)
Penzhina	Turonian	37 (38)	8 (8)	49 (47)	11 (14)	18.9	304 (304)
Standard Deviation		30 (30)	4 (3)	23 (14)	7 (3)	1.6	8 (5)

Deleted: 2

Formatted Table

1214
1215

Table 4. Humidity Metrics

LOCALITY	AGE	RH.ANNUAL (%)	SH.ANNUAL (g/kg)	VPD.ANN (kPa)	VPD.SUM (kPa)	VPD.WIN (kPa)	VPD.SPR (kPa)	VPD.AUT (kPa)	PET.ANN (mm)/10	PET.WARM (mm)	PET.COLD (mm)
Vilui "B"	Cenomanian	78 (80)	9.3 (9.6)	2.8	3.8	2.4	2.7	3.0	97.9	119.9	42.3
Greibenka	Cenomanian	71 (73)	8.3 (8)	4.5	6.5	2.8	4.1	4.7	110.0	140.3	42.8
Tylpergyrg.	Coniacian	71 (71)	5.8 (5.3)	3.4	6.1	1.3	2.6	3.7	90.1	133.7	24.0
Novaya Sibir	Turonian	77 (77)	7.6 (7)	2.0	3.9	1.2	1.4	2.1	90.0	122.9	33.0
North Slope	Coniacian	80 (80)	10.5 (10.1)	2.3	3.3	2.5	2.4	2.2	104.4	117.9	57.6
Arman	Cenomanian	72 (74)	5.6 (5.8)	3.0	5.7	1.0	2.2	3.3	85.9	130.5	21.9
Kaivayam	Coniacian	75 (76)	7.3 (7)	2.5	4.5	1.4	2.0	2.7	91.1	125.0	31.7
Penzhina	Turonian	73 (75)	5.8 (5.8)	2.5	5.1	0.7	1.7	2.7	83.7	126.5	22.8
Standard Deviation		9 (5)	1.6 (1)	1.9	3.5	1.1	1.9	2.0	14.6	24.5	12.7

Deleted: 3

Formatted Table

1216
1217