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Latest Cretaceous (Maastrichtian) climate of the Koryak Upland of North-East Russia based on a quantitative analysis of a palaeo-polar flora

Anastasia A. Zolina[a,*], Lina B. Golovneva[a], Robert A. Spicer[b,c]

[a] Komarov Botanical Institute, Russian Academy of Sciences, 197376, prof. Popov str. 2, St. Petersburg, Russia
[b] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Xishuangbanna, Yunnan 666303, PR China
[c] School of Environment, Earth and Ecosystem Sciences, The Open University, MK7 6AA, UK

A R T I C L E   I N F O

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A B S T R A C T

We describe fossil plant assemblages from the late Maastrichtian Kakanaut Formation of the Koryak Upland, North-East of Russia, which represent a high (75°N) palaeolatitude flora. The flora contains about 40 species, including liverworts, horsetails, ferns, cycadophytes, ginkgos, conifers and angiosperms. Angiosperms and conifers predominate and, unusually, the flora contains typical Cretaceous taxa admixed with elements that are more characteristic of the Paleocene. Reconstruction of the palaeoclimate in the Kakanaut area was made using the Climate Leaf Analysis Multivariate Program (CLAMP) employing a recently developed calibration that yields 23 different climate variables. Analysis was made based on 21 morphotypes of woody dicotyledonous plants from the Kakanaut flora. The analysis indicated a mean annual temperature of 12.2 ± 2.0 °C, a warmest month mean temperature of 20.6 ± 2.5 °C, a coldest month mean temperature of 4.8 ± 3.2 °C. The growing season lasted approximately 7 months, during which there was almost 1 m of precipitation. This and other indicators (relative humidity, vapour pressure deficit and potential evapotranspiration) all suggest a year-round humid regime. The winter temperatures suggest occasional mild frosts in this near sea level setting, so that at higher elevations freezing conditions would have been more persistent. These results throw new light on the living and breeding conditions of diverse latest Cretaceous Arctic dinosaur populations as represented by numerous skeletal and egg remains associated with the plants.

1. Introduction

The Late Cretaceous climate of the Arctic was significantly warmer and wetter than today (Herman, 2004; Spicer et al., 2016; Spicer et al., 2019). During this time, ecosystems with thermophilic plants and dinosaurs existed in the high Arctic at palaeolatitudes up to 80°N (Fig. 1). The most diverse faunas containing many polar dinosaurs have been found in the Maastrichtian deposits of Alaska (USA) in the Prince Creek and the Lower Cantwell Formations (Tomsich et al., 2010; Fiorillo et al., 2014), and the Koryak Upland (the North-East of Russia) where they occur in the Kakanaut Formation (Nessov and Golovneva, 1990; Godefroit et al., 2009). Despite a great number of studies, the habitat conditions supporting these exceptional latest Cretaceous polar megafaunas remain unclear (Spicer and Parrish, 1987; Herman, 2004; Fiorillo et al., 2014; Spicer et al., 2016).

The dinosaur fauna from the Kakanaut River includes Hadrosauridae, Ankylosauridae, Ceratopsidae, Hypsilophodontidae, Troodontidae, Dromaeosauridae, and Tyrannosauridae (Godefroit et al., 2009). Eggshell fragments belonging to hadrosaurids and theropods have also been found, providing evidence for near-polar dinosaur reproduction (Godefroit et al., 2009). Unlike other Arctic dinosaur localities, the Kakanaut Formation contains numerous plant fossils that can be used to derive quantitative palaeoclimatic data.

The Kakanaut palaeoflora contains both angiosperms and gymnosperms, the climate tolerances of which are purely conjectural. However, the angiosperms provide a way of deriving quantitative climate estimates, which then inform our understanding of the environmental conditions tolerated by the extinct gymnosperm taxa. We estimated the principal climatic parameters for the Kakanaut locality using Climate Leaf Analysis Multivariate Program (CLAMP) (e. g. Wolfe, 1993; Spicer et al., 2009; Herman and Spicer, 1996; Spicer and Herman, 2010; Yang et al., 2015). This method exploits the correlation between the morphological characteristics of leaves of woody dicots and the prevailing climate; a relationship that seems to have existed since the early Late Cretaceous.

* Corresponding author.
E-mail addresses: azolina@binran.ru (A.A. Zolina), golovneva@binran.ru (L.B. Golovneva), r.a.spicer@open.ac.uk (R.A. Spicer).

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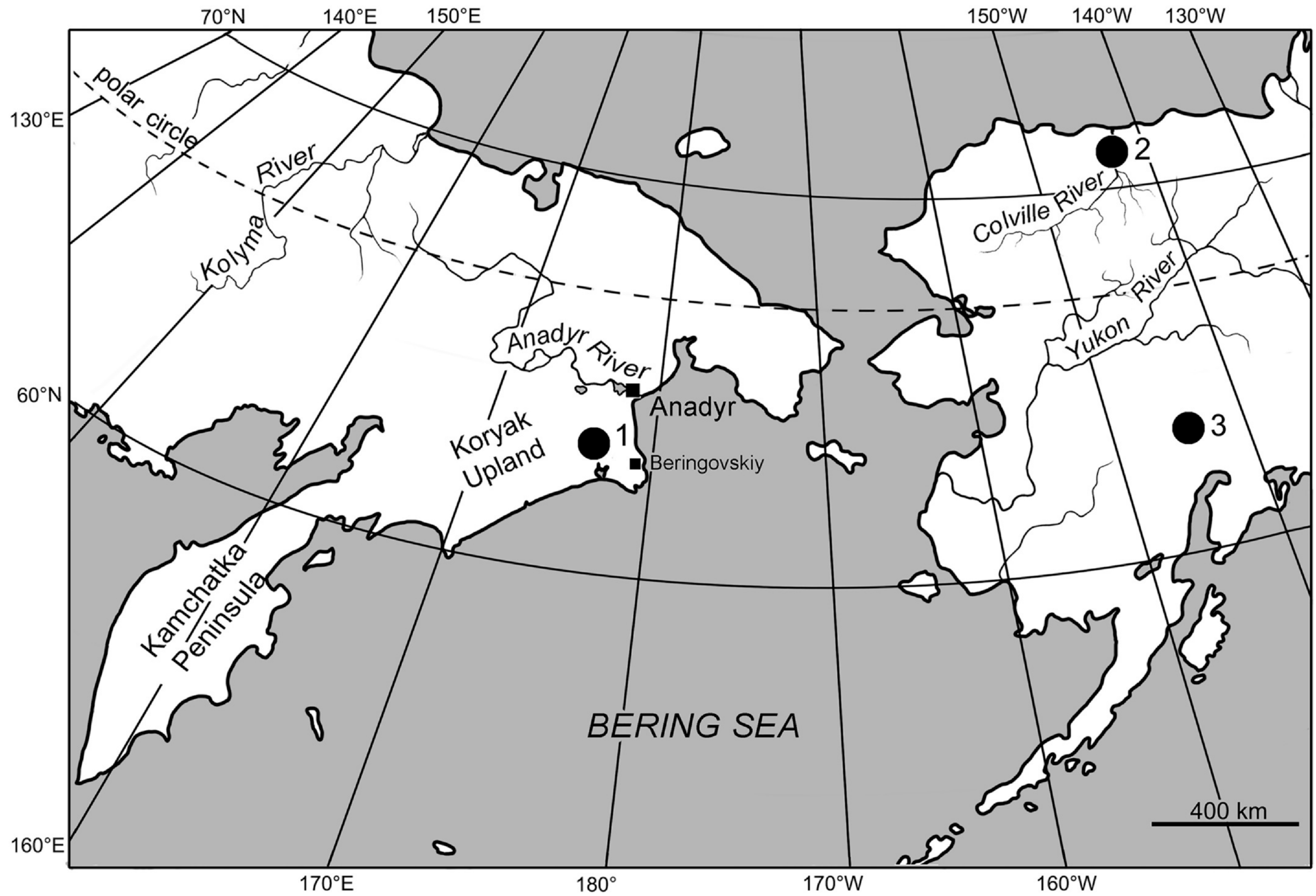

Fig. 1. The Maastrichtian localities of polar dinosaurs: 1 – the Kakanaut River Basin, hosting the Kakanaut Formation, 2 – the Colville River Basin, hosting the Prince Creek Formation, USA, (Brouwers et al., 1987; Fiorillo and Gangloff, 2000; Fiorillo et al., 2009; Fiorillo et al., 2015; Spicer and Parrish, 1987); 3 – Denali National Park, hosting the lower Cantwell Formation, USA (Fiorillo et al., 2014; Tomsich et al., 2010).

2. Materials

The Kakanaut Formation is exposed in the Kakanaut River Basin, near Peculney Lake, in the south-eastern part of the Koryak Upland, Russia (Fig. 2). The Kakanaut area is now located at 63°N, but at the end of the Late Cretaceous its palaeolatitude has been estimated to have been approximately 75°N (Torsvik et al., 2012).

The volcanic-terrigenous Kakanaut Formation (Fig. 2) consists of tuffaceous sandstones, siltstones, tuffs, and basalts (Volobueva and Terekhova, 1974; Golovneva and Shczepetov, 2010). These deposits accumulated in a coastal lowland setting (Volobueva and Krasniy, 1979).

The Kakanaut Formation overlies marine deposits in that the lower part contain an early Maastrichtian fauna (Golovneva and Shczepetov, 2010; Fig. 2). The upper marine unit hosts a bivalve *Schachmaticeramus kusiroensis*, demonstrating a late Maastrichtian age (Zonova and Yazykova, 1994; Yazykova, 2004). Moreover, the Vtoroy Creek (62°95′50″N, 177°11′12″E) locality has also yielded the remains of *Schachmaticeramus kusiroensis* overlying plants of the Kakanaut flora.

The Kakanaut Formation is overlain by marine sediments of the Kokuy Unit, that contain a poorly preserved plant fossils and a latest Maastrichtian invertebrate fauna (Golovneva and Shczepetov, 2010). The sediments of the Kokuy Unit are covered by early Paleogene volcanogenic deposits (Fig. 2).

A palynological assemblage from the Kakanaut Formation has been referred to the late Maastrichtian *Wodehouseia spinata— Aquilapollenites subtilis* Palynozone (Markevich and Bugdaeva, 1997). Thus, the age of the Kakanaut Formation is constrained to be early late Maastrichtian (Golovneva and Shczepetov, 2010; Golovneva and Gnilovskaya, 2015).

Plant fossils were found in 43 sites in the Two Bears (62°90′52″N, 177°11′65″E), Perevalniy (62°99′10″N, 177°13′91″E), Dikiy (62°96′56″N, 177°15′49″E), Vtoroy (62°95′50″N, 177°11′12″E), Kustarnichkoviy (62°89′33″N, 177°10′01″E), and Cirkovoy (62°91′18″N, 177°18′19″E) creeks (Fig. 2), and were recovered from the lower part of the Kakanaut Formation. These deposits represented alluvial and lacustrine facies raging from coarse-grained sandstones to fine-grained mudstones. By aggregating the assemblages from within a restricted stratigraphic interval we reduce facies-specific taphonomic biases that may otherwise have distorted the climate estimates. The remains of dinosaurs were found only at the Two Bears Creek (62°90′70″N, 177°10′60″N) and are confined to the transition layers between the plant-bearing volcanic-sedimentary and effusive-pyroclastic parts of the formation (Fig. 2).

Plant fossils from the deposits of the Kakanaut Formation were collected in 1988 and again in 2007–2009 by expeditions from the Komarov Botanical Institute lead by L. Golovneva.

The combined collection of plants from the Kakanaut Formation contains more than 1000 specimens and is stored at the Komarov Botanical Institute, Saint Petersburg, Russia (BIN 1200, 1590). For the most part the fossils display well-preserved macromorphological details and the leaves of woody angiosperms have sufficient features preserved for a CLAMP analysis.

The Kakanaut flora contains more than 40 species (Golovneva, 1994; Gnilovskaya and Golovneva, 2016; Gnilovskaya and Golovneva, 2018). Liverworts, horsetails, and ferns are each represented by one or two species (Fig. 3B). Cycadophytes include two species of Cycadales

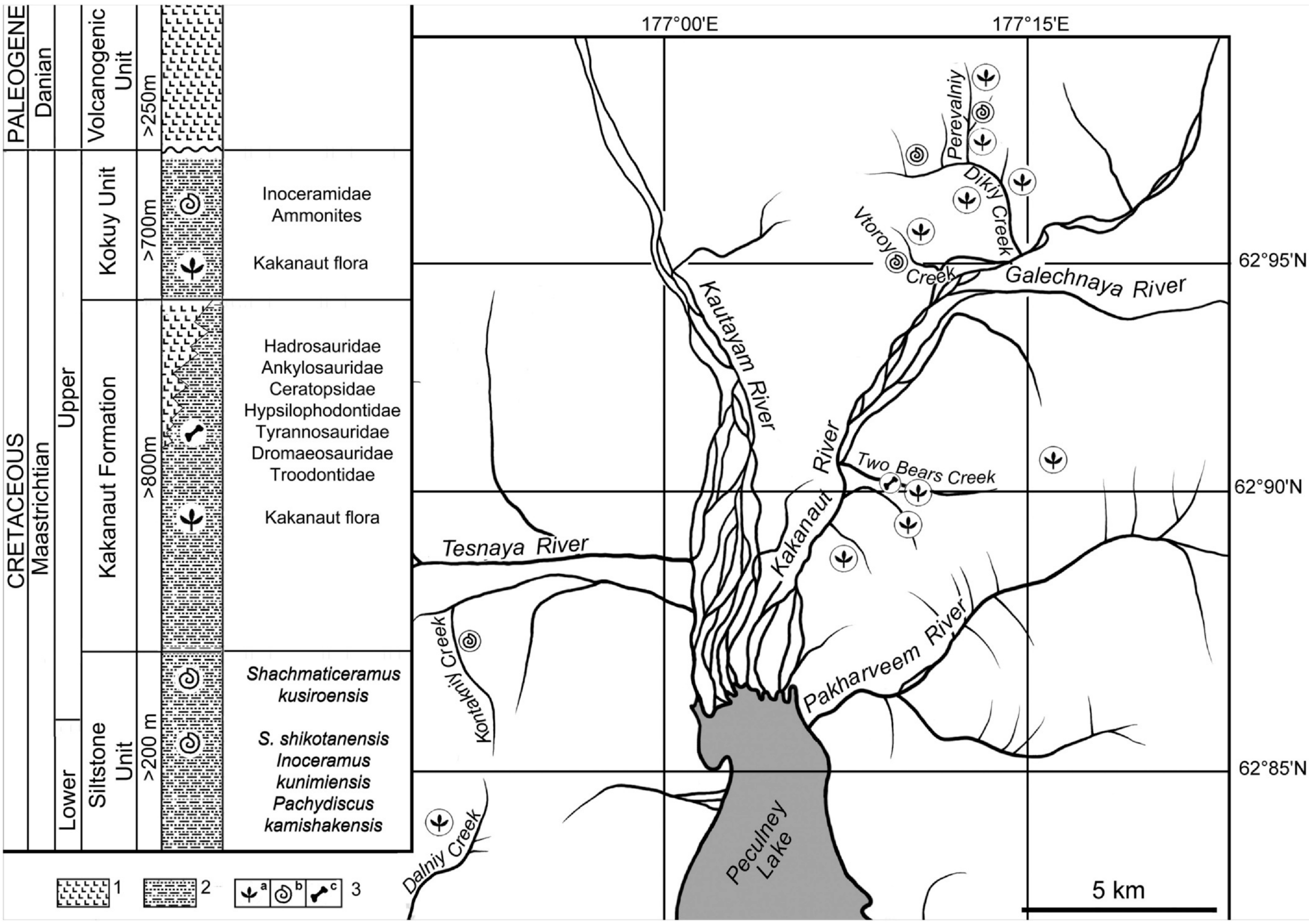

Fig. 2. Generalized stratigraphic section of the Kakanaut River basin (after Golovneva and Shczepetov, 2010) and map showing the main floral and vertebrate localities. Coordinates of main localities are given in the Chapter 2.
1–effusive–pyroclastic deposits, 2 – mainly volcanic-sedimentary deposits; a – remains of plants, b – remains of mollusks, c – remains of dinosaurs (Godefroit et al., 2009).

(*Nilssonia serotina* Heer, Fig. 3D, *Encephalartopsis vassilevskajae* Krassilov, Golovneva et Nessov, Fig. 3E) and one species of Bennettitales (*Pterophyllum terechoviae* Gnilovskaya, Fig. 3C). *P. terechoviae* is the last representative of the genus *Pterophyllum* and one of the latest Bennettitales in the Northern Hemisphere (Gnilovskaya and Golovneva, 2018). This flora also includes one species of Ginkgoales (*Ginkgo* ex gr. *adiantoides* (Unger) Heer (Fig. 3J)). Leaves of *E. vassilevskajae* and *G.* ex gr. *adiantoides* are very abundant in some layers.

Conifers of the Kakanaut flora are represented by five genera from the family Cupressaceae: *Sequoia* Endlicher (Fig. 3A), *Taxodium* (Fig. 3G), *Mesocyparis* McIver and Basinger (Fig. 3I), *Metasequoia* Miki (Fig. 3F), *Glyptostrobus* Endlicher and two genera of uncertain systematic position: *Elatocladus* Halle (Fig. 3H) and *Cryptomerites* Brongniart. Shoots of *Sequoia* occur more commonly then the remains of other conifers.

Angiosperms form the dominant group in the Kakanaut flora. These comprise more than 20 species including representatives of the families: Cercidiphyllaceae (*Trochodendroides* Berry, Figs. 4A, C, 5A, B, 6A, C), Platanaceae (*Platanus* L., Figs. 4D, 6B), Betulaceae ("*Corylus*" L., Figs. 4E, 5C), Fagaceae (*Fagopsiphyllum* Manchester, Fig. 4F), Rosaceae (*Peculnea* Golovneva Figs. 5F, 6F; *Arctoterum* Golovneva, Fig. 5G), Hamamelidaceae (*Platimelis* Golovneva, Fig. 6D), and Trochodendraceae (*Zizyphoides* Seward et Conway, Fig. 4A, C). The taxonomic affiliation of other genera, such as *Celastrinites* Saporta (Fig. 5H), *Cissites* Debey (Fig. 4B), *Liriophyllum* Lesquereux (Fig. 5E), *Kakanautia* Golovneva (Fig. 5D), *Quereuxia* Kryshtofovich have less certain affinities. Remains of *Celastrinites septentrionales* (Kryshtofovich) Golovneva, "*Corylus*" *ageevii* Golovneva, *Zizyphoides* sp. and *Peculnea lancea* Golovneva are the most abundant.

The Kakanaut flora contains numerous endemic taxa and differs significantly from other Maastrichtian floras of the Northern Hemisphere. The characteristic feature of the Kakanaut flora is a combination of typical Cretaceous genera, such as *Platanus*, *Trochodendroides, Cissites, Celastrinites* and younger elements usually thought of as Paleocene: *Glyptostrobus, Metasequoia, Fagopsiphyllum,* and members of Betulaceae.

3. Methods

The palaeoclimate of the Kakanaut flora was reconstructed using the Climate Leaf Analysis Multivariate Program (CLAMP) (http://clamp.ibcas.ac.cn). CLAMP is a multivariate statistical method that relates leaf characteristics of woody dicots to climate (Wolfe, 1993). Since the technique was introduced it has undergone significant development, the most recent being the introduction of a WorldClim2 (Fick and Hijmans, 2017; http://www.worldclim.org) calibration that returns a wider range of the climate variables (Spicer et al., 2019).

CLAMP is calibrated using the leaf traits of modern vegetation growing under known climate regimes and consists of two datasets. The first dataset, known as a 'Physg' file, is matrix of leaf characters in which leaf form in a range of vegetation types is scored numerically using 31 macromorphological traits encompassing leaf size, lamina

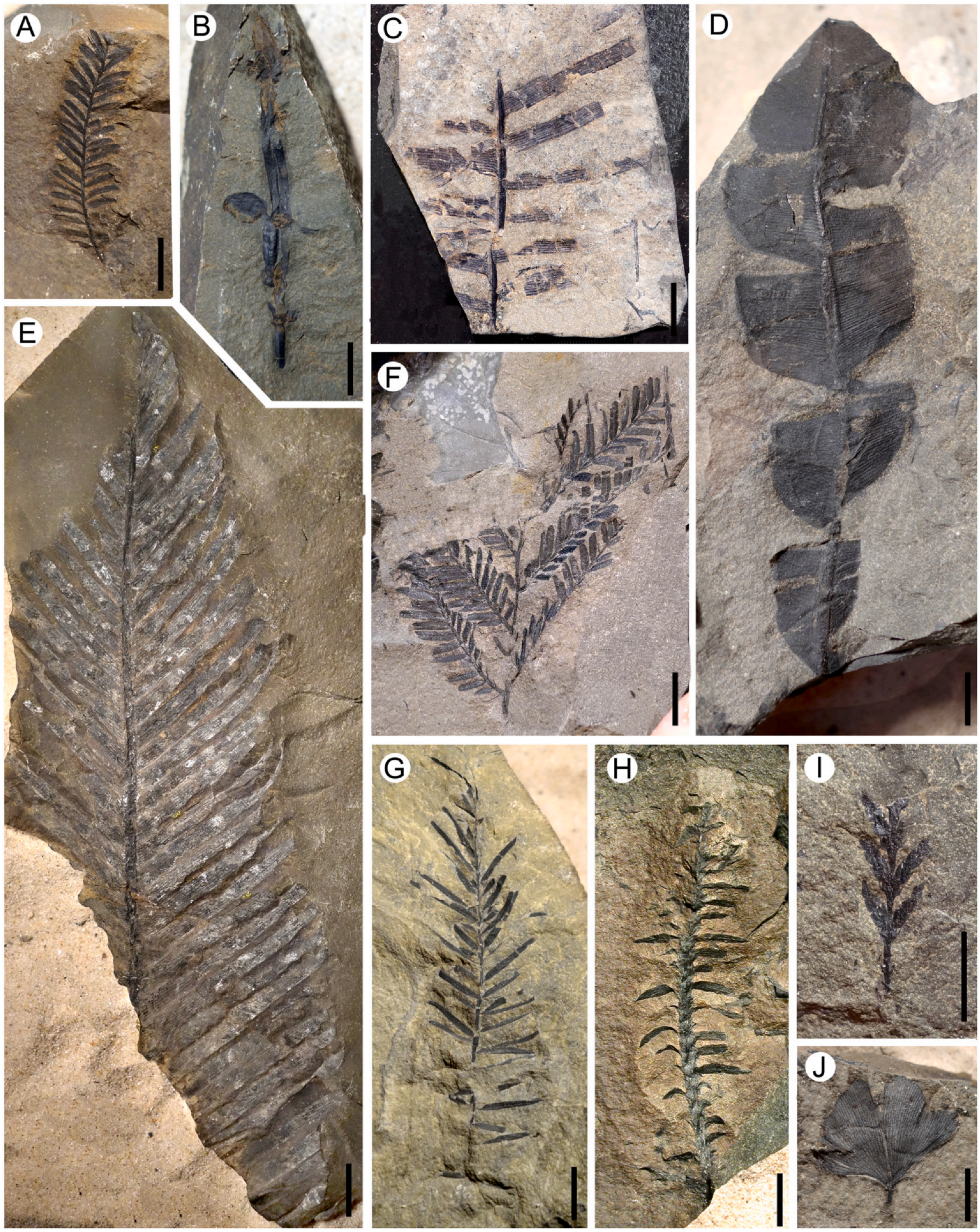

Fig. 3. Horsetails, ferns, cycadophytes, and gymnosperms from the Kakanaut flora:
A – *Sequoia* minuta Sveshnikova, spec. BIN 1200/34; B – *Equisetum arcticum* Heer, spec. BIN 1200/506; C – *Pterophyllum terechoviae* Gnilovskaya, spec. BIN 1590/1, holotype; D – *Nilssonia serotina* Heer, spec. BIN 1200/398; E – *Encephalartopsis vassilevskajae* Krassilov, Golovneva et Nessov, spec. BIN 1200/12, holotype; F – *Metasequoia* sp., spec. BIN 1200/508; G – *Taxodium* sp., spec. BIN 1200/18; H – *Elatocladus smittiana* (Heer) Seward, spec. BIN 1200/500; I– *Mesocyparis beringiana* (Golovneva) McIver et Basinger, spec. BIN 1200/507; J – *Ginkgo* ex gr. *adiantoides* (Unger) Heer, spec. BIN 1200/505. Scale bars: 1 cm.

shape, the presence or absence of lobes, leaf margin characters, apex and base shapes and length-width ratios (Table 1). The second dataset is an observed climate matrix for the vegetation sites that make up the Physg file. These two data matrices define what is known as 'physiognomic space' in 31 dimensions, within which a fossil leaf assemblage, in this case representing the Kakanaut flora, scored the same way as the modern leaves, is positioned passively (i.e. it does not distort physiognomic space by its presence). Climate trends through physiognomic space are identified using the climate data, and the position of the fossil assemblage relative to these trends provides the palaeoclimate estimates. Full details of the methodology are given on the CLAMP website (http://clamp.ibcas.ac.cn). CLAMP can tolerate some missing data without losing precision, and to ensure that the data are sufficient the CLAMP trait scoring process calculates a completeness statistic, which varies between 0 (no trait data) to 1 (all trait data present). Only assemblages with completeness statistics greater than 0.66 provide reliable outcomes.

For the Kakanaut area we first analyzed the fossil flora using a global dataset (PhysgGlobal 378) to determine which Physg file was likely to give the most reliable and precise climate prediction. The Kakanaut assemblage was positioned within that part of global physiognomic space occupied by Physg3brcAZ dataset, so this calibration

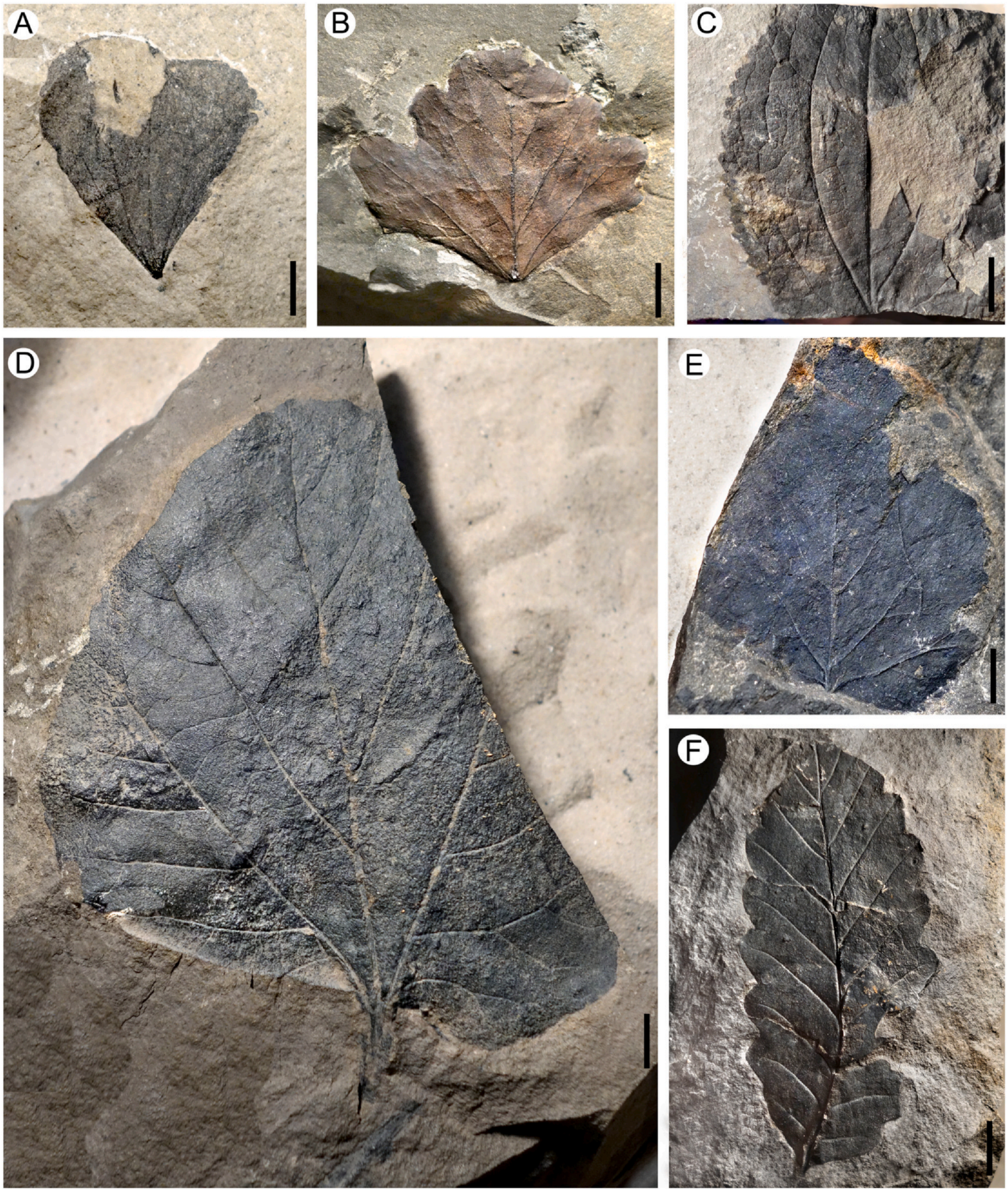

Fig. 4. Angiosperms from the Kakanaut flora. Part 1: A – *Trochodendroides bifida* Golovneva, spec. BIN 1200/69; B – *Cissites kautajamensis* Golovneva, spec. BIN 1200/59, holotype; C – *Trochodendroides deminii* Yudova et Golovneva, spec. BIN 1590/2; D – *Platanus rarinervis* Golovneva, spec. BIN 1200/76; E – *"Corylus" beringiana* (Kryshtofovich) Golovneva, spec. BIN 1200/501; F – *Fagopsiphyllum groenlandicum* (Heer) Manchester, spec. BIN 1200/402. Scale bars: 1 cm.

was selected to obtain a more precise analysis and paired with the matching WorldClim2 data set. The results here were produced using Physg3brcAZ (Table S1) paired with the matching WorldClim2 data set (Table S2).

4. Results

The Kakanaut flora contains 24 species of woody dicotyledonous plants. Three species are represented only by fragments of leaf margin that do not allow us to clearly determine the shapes of leaf apices, bases, overall shape or the size of the complete leaf. These fragments were not used in the CLAMP analysis. After badly fragmented leaves were eliminated, 21 species represented by more complete leaves were selected for the reconstruction of climate parameters (Table S3, Fig. 7). As a consequence, all traits were scored for all morphotypes and the completeness statistic for the analysis was 1.

The majority of woody dicots from the Kakanaut flora (86%) have non-lobed leaves. Lobed leaves are characteristic for only three species: *Arctoterum rubifolium* Golovneva (Fig. 7u), *Cissites kautajamensis* Golovneva (Fig. 7i), and *Liriophyllum aeternum* Golovneva (Fig. 7p). Morphotypes with dentate margins predominate (81%). The majority of morphotypes (76%) have simple teeth. Compound teeth are characterized only for "*Corylus*" (Fig. 7g, h) and *Peculnea* (Fig. 7i, j).

Leaf lengths within the different morphotypes varied from 2 to 40 cm. Medium-sized leaves predominate. Microphyll III and Mesophyll I comprise 35% and 25% of all morphotypes respectively. The smallest leaves (2–3 cm in length) are those of *Trochodendroides* sp. (Fig. 7a). The largest leaves (from 20 to 40 cm long) are those of *Platanus*, *Arctoterum*, and *Liriophyllum.*

The Kakanaut flora includes angiosperms with elliptical, ovate and obovate leaf laminae. Morphotypes with elliptical shapes predominate (64%). Thirty six percent of morphotypes have ovate laminae. An

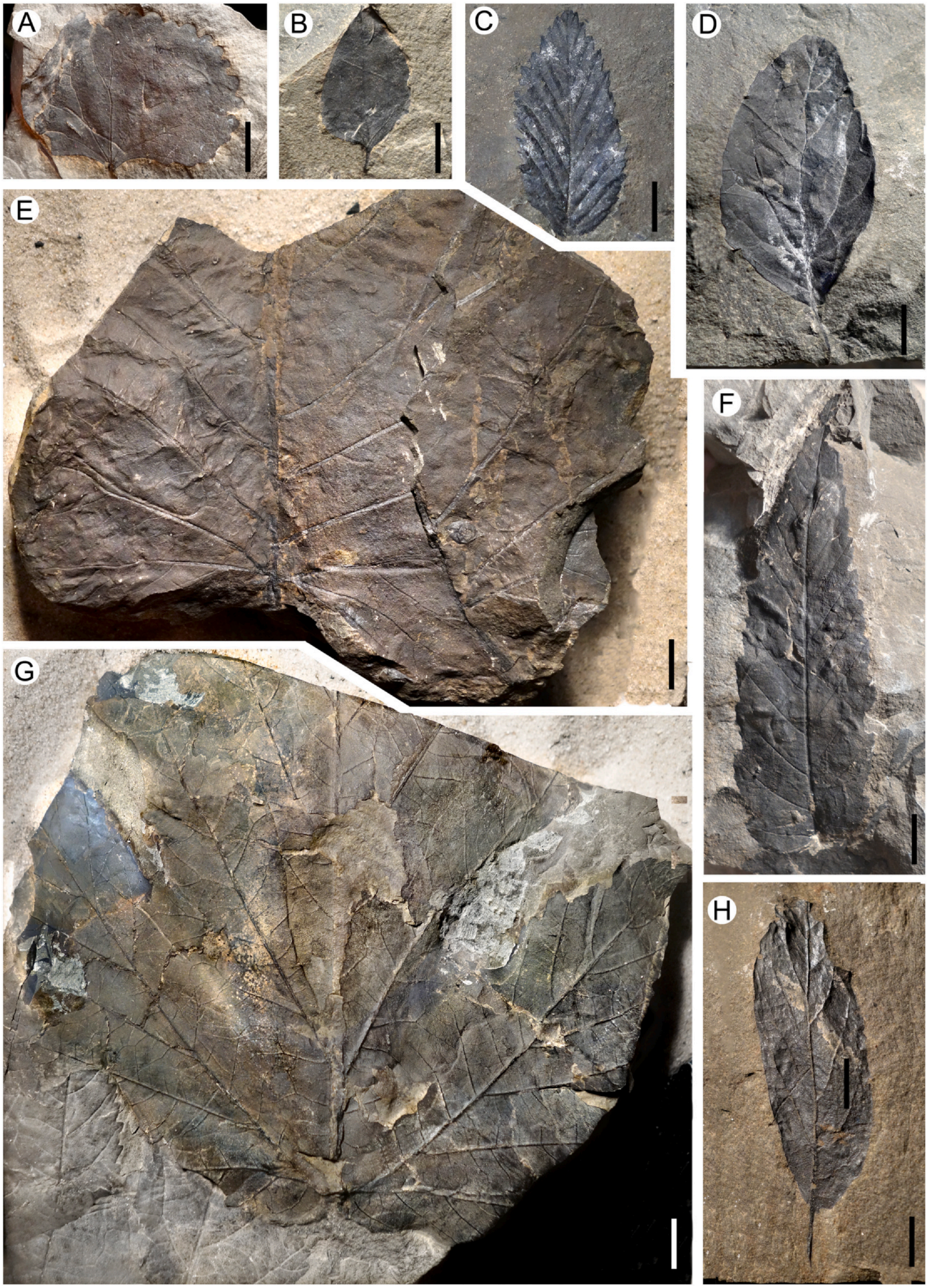

Fig. 5. Angiosperms from the Kakanaut flora. Part 2: A – *Zizyphoides* sp., spec. BIN 1590/3; B – *Trochodendroides* sp. 1, spec. BIN 1200/509; C – *"Corylus" ageevii* Golovneva, spec. BIN 1200/397; D – *Kakanautia repanda* Golovneva, spec. BIN 1200/55, holotype; E – *Liriophyllum aeternum* Golovneva, spec. BIN 1200/502; F – *Peculnea lancea* Golovneva, spec. BIN 1200/141, holotype; G – *Arctoterum rubifolium* Golovneva, spec. BIN 1200/503; H – *Celastrinites septentrionalis* (Kryshtofovich) Golovneva, spec. BIN 1200/504. Scale bars: 1 cm.

obovate lamina is present only in some leaves of *Zizyphoides* sp. (Fig. 7c). The majority of morphotypes have an acute apex (74%), while rounded apices occur less often (14%). An emarginate apex is typical for *Liriophyllum aeternum* and some leaves of *Trochodendroides bifida* Golovneva (Fig. 7e). Leaf bases of most morphotypes (61%) are acute. Morphotypes with rounded bases occur less often (30%). Only *Liriophyllum aeternum*, *Peculnea pinnatiloba* Golovneva and *Platimelis* sp. have cordate leaf bases.

The results of the CLAMP analysis are shown in Table 1. The analysis gave a mean annual temperature for the Kakanaut area of 12 ± 2°C, a mean temperature of the coldest month of 4.8 ± 3.2°C, and a maximum temperature of coldest month of 7 ± 3.2 °C. All uncertainties represent ± 1 sigma. Statistically, this suggests mild frosts were likely to have occurred from time to time. The mean temperature

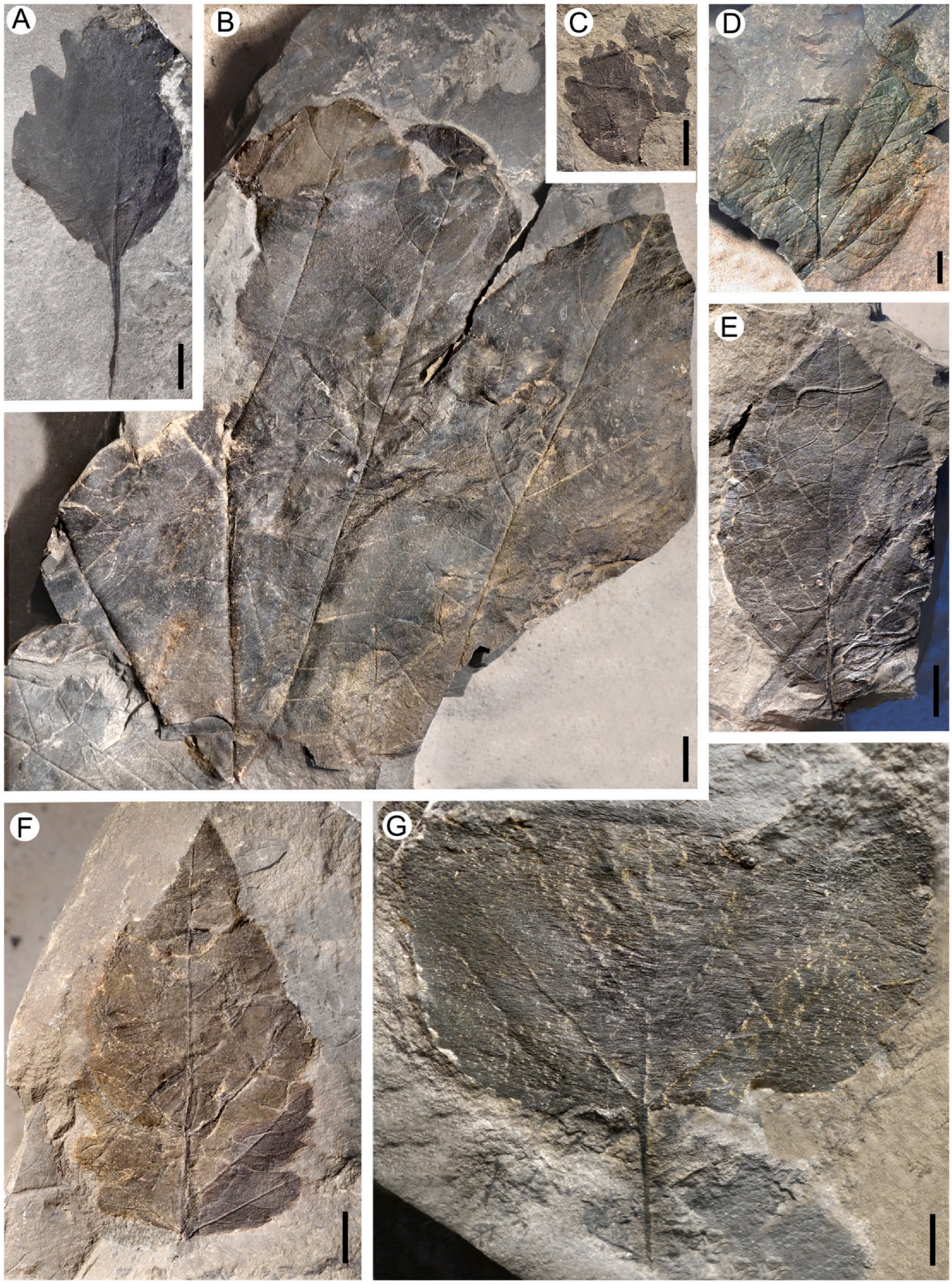

Fig. 6. Angiosperms from the Kakanaut flora. Part 3: A – *Trochodendroides grossidentata* Golovneva, spec. BIN 1200/68, holotype; B – *Platanus* sp. 1, spec. BIN 1200/510; C – *Trochodendroides* sp. 1, spec. BIN 1200/511; D – *Platimelis* sp., spec. BIN 1200/512; E – *Dicotylophyllum* sp. 2, spec. BIN 1590/9; F – *Peculnea pinnatiloba* Golovneva, spec. BIN 1200/135; G – *Dicotylophyllum* sp. 1, spec. BIN 1200/88. Scale bars: 1 cm.

of the warmest month was 20.6 ± 2.5 °C and the minimum temperature of warmest month was 17.6 ± 2.5 °C. Thus, the growing season (the length of time measured in months when temperatures exceeded 10 °C) in the Kakanaut area continued for 7 ± 1.1 months.

Precipitation during this period was estimated to be 934 ± 297 mm. Precipitation during the three consecutive wettest and three consecutive driest months was estimated as 640 ± 230 mm and 222 ± 68 mm respectively. With an approximately 7-month growing season and large uncertainties these precipitation parameters do not provide a reliable insight into the mean annual precipitation, but there is no evidence arising from the CLAMP that there was pronounced drought during the growing season, although some seasonal drying did occur. This agrees with interpretations of palaeobotanical, sedimentological and geochemical data from the Maastrichtian of northern Alaska (Flaig et al., 2013; Suarez et al., 2016) that suggested similar seasonal variations in precipitation under a vigorous hydrological cycle, but no drought conditions. Vapour pressure deficit (VPD) provides more insight into the palaeohydrological regime of the Kakanaut area during

Table 1
Estimated climate variables for the Kakanaut area in the Maastrichtian.

Parameter	Value	± σ
mean annual temperature (°C)	12.2	1.98
warmest month mean temperature (°C)	20.6	2.49
coldest month mean temperature (°C)	4.8	3.24
length of the growing season (months)	7.0	1.05
growing season precipitation (mm)	933.6	296.50
mean monthly growing season precipitation (mm)	139.5	38.67
precipitation during 3 consecutive wettest months (mm)	639.6	230.49
precipitation during 3 consecutive driest months (mm)	214.5	67.69
relative humidity (%)	81.1	9.30
specific humidity (g/kg)	9.7	1.65
enthalpy (kJ/kg)	32.3	0.77
mean annual vapour pressure deficit (hPa)	1.8	1.93
mean summer vapour pressure deficit (hPa)	2.6	3.52
mean winter vapour pressure deficit (hPa)	2.0	1.11
mean spring vapour pressure deficit (hPa)	2.0	1.93
mean autumn vapour pressure deficit (hPa)	2.0	1.98
compensated thermicity index (°C)	241.4	68.48
min. temperature of warmest month (°C)	17.6	2.51
max. temperature of coldest month (°C)	7.0	3.18
annual mean growing degree days above 0 °C	4220	1051
annual mean growing degree days above 5 °C	4870	919
potential evapotranspiration (mm)	1086	578
mean monthly potential evapotranspiration of the warmest quarter (mm)	105.4	24.48
mean monthly potential evapotranspiration of the coldest quarter (mm)	40.8	12.71

the early late Maastrichtian. VPD is the pressure exerted by moisture in a parcel of air relative to what it would be if that parcel was saturated with water, and as such indicates the ease by which transpiration can take place (Huffaker, 1942). The higher the VPD the drier the air is, and the more readily water can be lost from the plant. VPD is also strongly correlated with stomatal conductance and carbon isotope fractionation (Oren et al., 1999; Bowling et al., 2002; Katul et al., 2009). The mean annual VPD is low at 1.8 ± 1.9 hPa, which means the air is humid and this high humidity is more or less constant during the spring, summer, and autumn. Although there are large uncertainties associated with winter VPD values they are estimated to have been 2.6 ± 3.5 hPa, and this points to a slightly drier winter regime. However, many plants were likely dormant at this time due to reduced temperatures a low light conditions, and so may not record winter VPD very reliably. Dormancy, for many taxa, is suggested by thin chartaceous leaves often occurring in dense concentrations on bedding planes (leaf mats), and petioles with expanded points of attachment to the parent plant indicative of a specialized dehiscence mechanism. Such features suggest synchronous seasonal leaf shedding and thus dormancy.

Like VPD, potential evapotranspiration (PET) is a measure of how easily a plant can lose water to the atmosphere, but instead of being based on only the absolute water content of the air it incorporates convective removal of moisture from an evaporating surface. It assumes an unlimited water supply, which seems to apply here based on the precipitation estimates returned by CLAMP and conditions in nearby Alaska at this time (Suarez et al., 2014). Like annual VPD, the Kakanaut annual PET estimate lies the wettest third of all annual humidity regimes experienced by modern vegetation within the CLAMP global dataset, and both the Kakanaut VPD and PET values are similar to those returned by other Cretaceous floras from northeastern Russia and Alaska (Spicer et al., 2019). Unsurprisingly the PET in the summer is much higher than during the winter due to warmer temperatures.

5. Discussion

At a palaeolatitude of ~75°N the Kakanaut localities must have experienced an extended period of winter darkness, with the sun not rising above the horizon for approximately 3 months (e. g. Spicer and Herman, 2010). Nevertheless, prior work has shown Arctic temperatures remained relatively warm despite the lack of direct insolation (Spicer et al., 2019 and references therein). Palaeoclimate parameters for the Kakanaut River area were previously calculated using an earlier version of CLAMP (Golovneva, 2000, Table 2) with climate calibration data based on observations made between 1961 and 1990. The present reconstruction has been produced using a similar physiognomic dataset 'Physg3brcAZ', but is now paired with WorldClim2 climate data which represents observations made between 1970 and 2000 interpolated onto an approximately 1 km^2 spatial grid (Spicer et al., 2009; Spicer et al., 2019). Moreover, the analysis here is based on extended census of woody dicots from the Kakanaut flora including four more species than in previous analyses (Golovneva et al., 2011; Gnilovskaya and Golovneva, 2016).

Inevitably these changes introduce some differences in the palaeoclimate predictions, but as can be seen from Table 2 showing temperature estimates these differences are very small and are indistinguishable from the earlier results when uncertainties are taken into consideration. Previous analysis (Golovneva, 2000) gave a mean annual temperature of 10°C, a mean temperature of coldest month of 3°C, and a mean temperature of the warmest month of 19 °C. Those values are slightly lower than the new estimations. According to the earlier analysis, the growing season in the Kakanaut area was about 6.3 months, a little shorter than given in the present study. However, this is within the earlier uncertainties. Growing season precipitation was 948 mm, which is very close to the values we determine here.

The previous version of CLAMP also allowed for the estimation of mean annual precipitation (Wolfe, 1993; Herman and Spicer, 1996). This parameter for the Kakanaut area was estimated at 1414 mm (Golovneva, 2000). However, dormant plants are not greatly constrained by winter precipitation (Wolfe, 1993), and in order to be preserved as fossils the leaves must have been from plants that grew close to water bodies. This in turn means locally high ground water levels and so a degree of independence from reliance on local rainfall for plant survival. Consequently, mean annual precipitation is not now regarded as a useful or reliable climate metric within CLAMP, and the other rainfall parameters should be interpreted with care. The advantage of the new calibration is that it gives much greater insight into the overall hydrological regime by returning VPD and PET estimates, which relate to atmospheric conditions, not the soil water, and show much better correlations with leaf form than precipitation. The precipitation, relative humidity (81%), low VPD (annual and seasonally uniform) all indicate a year-round humid maritime climate. This result is consistent with taphonomic and sedimentological data indicating that deposits of the Kakanaut Formation accumulated on the coastal lowland (Volobueva and Krasniy, 1979).

The temperature parameters and the length of the growing season calculated using the new version of CLAMP are slightly warmer than before, and more compatible with what we assume to be the requirements of the more thermophilic gymnosperms found in the assemblage. During the Maastrichtian the area of the Kakanaut locality was characterized by cool/mild winters and warm summers. The estimated Kakanaut mean annual temperature of +12 °C, corresponds to a temperate climate (Alisov, 1936). The relatively high temperature of the coldest month (+4.8 °C) and the difference between mean temperatures of the coldest and the warmest months (15.8 °C), like the hydrological measures, indicate a maritime climate.

The results of CLAMP-analysis confirm the idea that the climate in the Koryak Upland at the end of the Cretaceous was significantly warmer than today (Table 3). In the Beringovskiy village, situated on the coast of the Bering Sea just north of the Kakanaut locality (Fig. 1), the mean annual temperature today is −5.1 °C, the mean temperature of the coldest month is −17.7 °C, and a mean temperature of the warmest month is +8.9 °C (Scientific and applied reference guide to the climate of the USSR, 1990). The mean annual precipitation in Beringovskiy village is 563 mm, which is almost half that of the growing

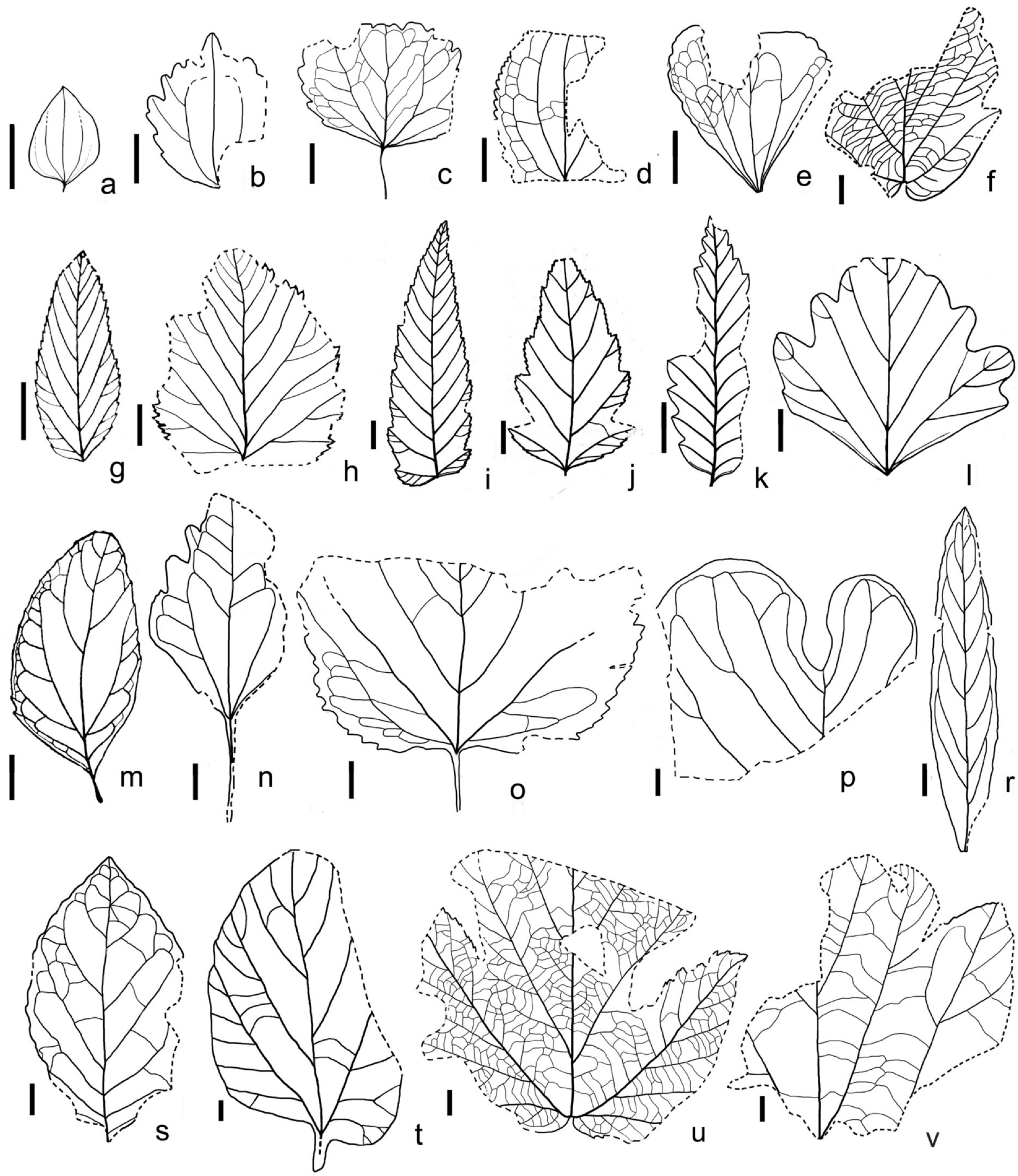

Fig. 7. Morphotypes of woody dicotyledons of the Kakanaut flora: a – *Trochodendroides* sp. 2; b – *Trochodendroides* sp. 1; c– *Zizyphoides* sp.; d – *Trochodendroides deminii* Yudova et Golovneva; e – *Trochodendroides bifida* Golovneva; f – *Platimelis* sp.; g – *"Corylus" ageevii* Golovneva, holotype; h – *"Corylus" beringiana* (Kryshtofovich) Golovneva; i – *Peculnea lancea* Golovneva, holotype; j – *Peculnea pinnatiloba* Golovneva; k – *Fagopsiphyllum groenlandicum* (Heer) Manchester; l – *Cissites kautajamensis* Golovneva, holotype; m – *Kakanautia repanda* Golovneva, holotype; n – *Trochodendroides grossidentata* Golovneva, holotype; o – *Dicotylophyllum* sp. 1; p– *Liriophyllum aeternum* Golovneva; r – *Celastrinites septentrionalis* (Kryshtofovich) Golovneva; s – *Dicotylophyllum* sp. 2; t –*Platanus rarinervis* Golovneva; u – *Arctoterum rubifolium* Golovneva; v – *Platanus* sp. 1. Scale bar is 1 cm.

season precipitation at the Kakanaut area in the Maastrichtian. Today the climate in the vicinity of Beringovskiy village is classified as subarctic maritime.

According to the CLAMP database, the main climate parameters of the Kakanaut locality are most similar to those of the Umedaira area, east coast of Honshu Island, Japan (Table 3). This area is characterized by mild summer, mild winter and high annual precipitation. The vegetation of Umedaira is typifed by broad-leaved deciduous forests with predominance of beech, birch, elm, and sapindaceous members. At the Kakanaut area in the Maastrichtian the forest was rich in *Platanus, Trohodendroides*, and "*Colylus*". These plants are similar in their ecological preferences to those growing now in Umadaira.

5.1. Comparing the paleoclimate of Maastrichtian polar dinosaur localities

Palaeoclimate reconstructions have also been made for two Maastrichtian dinosaur localities in Alaska: in the Denali National Park (Fig. 1, site 3) and along the Colville River (Fig. 1, site 2). We will now

Table 2
The paleolatitude and palaeotemperature parameters for the Maastrichtian localities of polar dinosaurs of the Koryak Upland and Alaska.

Locality	Palaeolatitude	Mean annual temperature (°C)	Coldest month mean temperature (°C)	Warmest month mean temperature (°C)
the Kakanaut River Basin (present paper)	75°N (Torsvik et al., 2012)	12.2 ± 1.98	4.8 ± 3.24	20.6 ± 2.49
the Kakanaut River Basin (Golovneva, 2000)		10 ± 1.2	3 ± 1.9	19 ± 1.6
the Kakanaut River Basin (Amiot et al., 2017)		9 ± 7	–	–
the Colville River Basin (Spicer and Parrish, 1987)	80–85°N (Spicer and Parrish, 1987; Torsvik et al., 2012)	5	–	–
the Denali National Park (Tomsich et al., 2010)	70–75°N (Torsvik et al., 2012; Tomsich et al., 2014)	7.42 ± 1.2	−2.3 ± 1.9	17.1 ± 1.6

re-examine these in the context of our new results from Kakanaut in order to try and understand more generally the conditions polar dinosaurs experienced.

The first locality of the Maastrichtian dinosaurs in Alaska is situated near Mount Denali. Here in the Lower Cantwell Formation traces of theropods, hadrosaurs, ceratopsians, ankylosaurs, and pterosaurs have been found (Fiorillo et al., 2014; Capps et al., 2019). The age of these deposits was determined as early Maastrichtian (~71 Ma) based on isotopic data (Tomsich et al., 2014). The palaeolatitude of this area according to palaeomagnetic analysis was estimated to have been 70–75°N (Tomsich et al., 2014).

The climatic parameters for the Denali National Park locality were calculated using the CLAMP methodology (Tomsich et al., 2010) with the same Physg3brcAZ calibration but older ungridded 1961–1900 climate observations, which did not return estimates of VPD or PET. Twenty three morphotypes were recognized in the plant assemblage from the Lower Cantwell Formation.

CLAMP analysis of the Denali assemblage yielded a mean annual temperature of 7.42 ± 1.2 °C, a mean temperature of the coldest month of −2.3 ± 1.9, and a mean temperature of the warmest month of 17.1 ± 1.6. The CLAMP results indicated a negative mean temperature of the coldest month in the Denali National Park locality. This temperature value is significantly lower than for the territory of the Kakanaut River (Table 2), although both localities were situated at similar palaeolatitudes (Tomsich et al., 2014; Torsvik et al., 2012). The results of the analysis in part likely reflects the more inland location of the Denali fossil assemblage, and this is supported by Denali returning an approximately 4 °C greater mean annual range of that temperature than Kakanaut. The leaves in Denali National Park, as illustrated in the study of Tomsich et al., (2010), were more fragmented than those of Kakanaut and a full systematic analysis has not yet been published.

Along the Colville River, northern Alaska, dinosaur skeletal remains have been found in the predominantly Maastrichtian Prince Creek Formation, although farther upstream footprints have been found from sediments as old as the Cenomanian (Parrish et al., 1987). The main Prince Creek Formation finds are from the Liscomb (Brouwers et al., 1987), Kikak-Tegoseak Quarr quarries, and from sediments of the Kogosukruk Tongue (upper Prince Creek Formation) (Fiorillo et al., 2014). The age of these deposits was determined as early Maastrichtian from isotopic data and spore-pollen analysis (Conrad et al., 1990; Flaig et al., 2011). The Prince Creek faunal complex includes tyrannosaurids, troodontids, dromaeosaurids, ornithomimids, hadrosaurids, ceratopsians, and pachycephalosaurs (Takasaki et al., 2019).

The plant fossils of the Prince Creek Formation come from the Kogosukruk Tongue (Spicer and Parrish, 1987). The palaeolatitude of this locality is estimated to have been 80–85°N (Spicer and Parrish, 1987; Torsvik et al., 2012). The complex of plant fossils from this locality includes only ten species belonging to ferns, ginkgos, conifers, and angiosperms. Angiosperms in this flora are represented by only two species *Quereuxia angulata* Newberry and *Hollickia quercifolia* (Hollick) Krassilov. The authors suggested that the low number of angiosperms represented reality because extensive searching failed to reveal any more angiosperm material, and that deciduous coniferous forests dominated this region (Spicer and Parrish, 1990). This angiosperm diversity is not sufficient for CLAMP analysis, so temperature conditions were estimated approximately using Wolfe's (Wolfe, 1979) nomogram for vegetation dominated by conifers (Spicer and Parrish, 1990), which produced a figure of +5 °C for the annual mean. Subsequently this estimate was modified using latitudinal projections based on CLAMP analyses of more southerly Kakanaut and Cantwell floras (Spicer and Herman, 2010). According to this reconstruction, the mean annual temperature in the Colville River area was about +6.7 ± 2.2 °C (Table 2). It is significantly lower than in the Kakanaut area, but this understandable because it was farther north in the Maastrichtian (~ 82°N) (Spicer and Herman, 2010). Winter temperatures in the area of Kogosukruk locality were below freezing for extended periods (Spicer

Table 3
Temperature parameters estimated with CLAMP-analysis for the Kakanaut locality and modern data for the Beringovskiy village in Chukotka and Umedaira in Japan.

Parameter	Kakanaut locality	Beringovskiy village	Umedaira
mean annual temperature (°C)	12.2 ± 1.98	−5.1	12.71
warmest month mean temperature (°C)	20.6 ± 2.49	8.9	24.56
coldest month mean temperature (°C)	4.8 ± 3.24	−17.7	2.42
length of the growing season (months)	7.0 ± 1.05	4	7.1
mean year precipitation (mm)	–	563	–
growing season precipitation (mm)	933.6 ± 296.50	210	985
mean monthly growing season precipitation (mm)	129.4 ± 26	52.5	139
precipitation during 3 consecutive wettest months (mm)	540.3 ± 145	215	462
precipitation during 3 consecutive driest months (mm)	222 ± 32	82	100
relative humidity (%)	81.4 ± 5.1	82	74.6
mean annual vapour pressure deficit (hPa)	1.8 ± 1.93	1.0	–
mean summer vapour pressure deficit (hPa)	2.6 ± 3.52	2.1	–
mean winter vapour pressure deficit (hPa)	2.0 ± 1.11	0.3	–
mean spring vapour pressure deficit (hPa)	2.0 ± 1.93	0.5	–
mean autumn vapour pressure deficit (hPa)	2.0 ± 1.98	1.1	–

and Parrish, 1990). Recently a loose block that was originally collected by Arnold in 1951 from bank of the Colville River in northern Alaska, has been shown to contain a much richer flora than hitherto realized (Rothwell et al., 2020). Regrettably the provenance of this block is unknown, but it suggests that further careful collecting may yet show a greater floral diversity in near polar (palaeolatitudes > 80°N) forests than is currently documented.

Given this context the Kakanaut flora provides significant new information for both the climate and vegetation that existed in the Arctic at approximately 75°N near the end of the Late Cretaceous, and can be compared with the temperature conditions for the Koryak Upland made by measuring carbon and oxygen isotopes (δ^{18}Op; δ^{13}Cc) in the teeth of the Kakanaut dinosaurs and in the shells of their eggs (Amiot et al., 2017). This approach revealed a mean annual temperature of 9 ± 7 °C (Table 3). This result is close to the estimates obtained from the analysis of plant fossils, but colder. Significantly the study of egg-shells also showed that female dinosaurs drank meltwater during shell formation (Amiot et al., 2017), which would have lowered the mean annual temperature estimate. Presumably this meltwater came in part from more upland regions, and it suggests that regional upland temperatures could fall below zero long enough to accumulate a snow pack and/or large ice volumes.

6. Conclusions

A CLAMP analysis of the Maastrichtian Kakanaut coastal paleoflora, using the Physg3brcAZ and the WorldClim2 calibration data sets, yielded a mean annual temperature of ~12 °C, a warmest month mean temperature of ~21 °C, and a coldest month mean temperature of ~5 °C. Mild frosts are likely to have occurred from time to time near sea level, which suggests that at higher elevations within the Koryak Uplands colder conditions could have resulted in seasonal, or possibly year-round, snow cover. This is evidenced by earlier isotope work. Growing season precipitation was estimated to have been almost 1 m over a period of ~7 months. Overall the climate was temperate maritime and humid year-round.

This climate regime is somewhat similar to modern Umedaira, Honshu, Japan and provides an insight into the climate regime experienced by nesting dinosaurs and extinct gymnosperms associated with the Kakanaut polar angiosperms.

Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2020.109997.

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