The Maastrichtian (Late Cretaceous) climate in the Northern Hemisphere

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Abstract: This investigation of the Maastrichtian climate in the Northern Hemisphere is based on taxonomic and ecological studies of fossil floras, leaf physiognomy and the distribution of dinosaurian faunas. Fossil plant evidence indicates that the climate during Maastrichtian time was warm temperate at high and middle latitudes, and subtropical south of 40°N. Precipitation was relatively high (about 700–800 mm) and evenly distributed over the year. The annual range of temperatures was similar to that of modern maritime climates, but the latitudinal gradient was lower than at present. At high latitudes cold-month mean temperatures were about 3–4°C and probably never dropped below 0°C for extended periods. It seems that these comparatively mild winter temperatures in polar regions were a result of the heating of these areas by warm oceanic upwelling.

The Maastrichtian stage is the youngest stage of the Cretaceous Period, immediately preceding the Cretaceous–Tertiary boundary. At that time there was a great turnover in the Earth's biota and the development of terrestrial ecosystems was significantly affected by changes in climate. Thus, the reconstruction of the Maastrichtian palaeoclimate is of particular importance for the evaluation of climatic change near this boundary. To determine the climate, the taxonomic and ecological characters of fossil land-plant assemblages and dinosaur faunas were analysed.

The conclusions presented in this paper are based largely on the study of 12 fossil floral assemblages from northeastern Asia and the western part of North America from 35°N to 70°N (Fig. 1). These floral assemblages were chosen because they are accurately dated and well described. In Europe there are no rich Maastrichtian macrofloral assemblages that can be used for investigation of palaeoclimates. The floras from northeast Russia and Kazakhstan were studied on the basis of collections in the Komarov Botanical Institute, and other floras were analysed using published data. As a rule, literature-based climatic inferences do not significantly differ from evaluations based on original collections.

The northeastern Asia Maastrichtian floras are known from the Koryak Upland, the island of Sakhalin, Central Asia and Mongolia. In the Koryak Upland, rich floral assemblages come from deposits of the Rarytkin (Late Maastrich-tian) and the Kakanaut (Middle Maastrichtian) Formations (Golovneva 1994, 1995). The Maastrichtian flora of the Avgustovka River from Sakhalin was studied by Krassilov (1979). This assemblage is from the upper part of the Krasnoyarka Formation and includes 16 species. In Kazakhstan, Maastrichtian floras have been found in the lower part of the Severozaysan Formation (Zaysan Depression), at the localities of Zhuvankara and Tajzhusgen (Shilin & Romanova 1978; Akhmetiev & Shevyreva 1989), and at Ulken-Kalkan in the Ili River Basin (Makulbekov 1974). The Ulken-Kalkan flora is rather poor and contains only nine species. It is considered to be of Maastrichtian age; this age is suggested by the presence of dinosaurian bones in the underlying conglomerates although the flora could equally be Early Danian in age. In Mongolia the Maastrichtian flora comes from deposits of the Nemegt Formation, which also contains a rich vertebrate fauna. The Nemegt flora includes about 10 species although it has been studied only in a preliminary way (Krassilov & Makulbekov 1995; Makulbekov 1995). Kogosukruk is the northernmost Maastrichtian locality (70°N) in Alaska (Spicer & Parrish 1987). It is dated to Late Campanian–Early Maastrichtian time by marine fossils and includes only five or six species. Numerous Early and Late Maastrichtian leaf assemblages are known in the Western Interior of North America from the deposits of the Edmonton, Brazeau, Hell Creek, Lance,
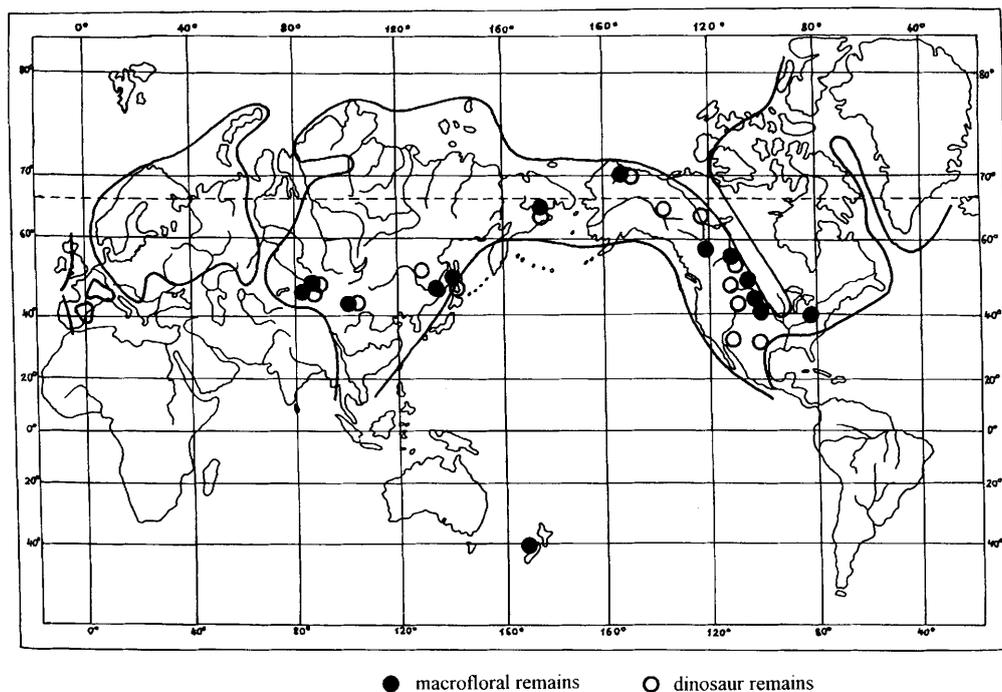
● macrofloral remains   ○ dinosaur remains

Fig. 1. Distribution of the Maastrichtian floral and dinosaur remains in the Northern Hemisphere (continuous line indicates the approximate geographical extent of the sea and land masses, after Gorodnitskiy *et al.* (1978).

Medicine Bow, Denver, Raton and Vermejo Formations (Berry 1935; Dorf 1942*a,b*; Bell 1949; Shoemaker 1966; Rouse, 1967; Johnson 1992). Many localities contain rich and well-described floral remains. The flora of the Ripley Formation (Early Maastrichtian) at 35°N is the southeastern-most occurrence considered (Berry 1925).

Several characters of the fossil floras were examined, including their general diversity, the relative abundance of different taxonomic and ecological groups, and the ratio between evergreen and deciduous gymnosperms (Table 1). Palaeoclimatic analysis of the structure of plant assemblages and putative tolerances of living relatives has produced only a generalized interpretation of the Maastrichtian climate. Morphological characters of angiosperm leaves correlate especially well with environmental factors (Richards 1952; Wolfe 1979). Physiognomic analysis of leaves of dicotyledonous woody plants can provide not only general inferences on climate but also rather precise quantitative estimations of climatic factors (Bailey & Sinnot 1915; Dilcher 1973; Wolfe 1979; Wolfe & Upchurch 1987). In this study I applied a recently developed physiognomic analytical procedure called CLAMP (climate leaf analysis multivariate program; Wolfe 1993). This program uses 31 leaf morphological characters to obtain eight climate variables: mean annual temperature, cold-month mean temperature, warm-month mean temperature, mean annual precipitation, mean month growing season precipitation, mean growing season precipitation, precipitation during the three consecutive driest months and length of the growing season. The application of this method has been described in detail elsewhere (Wolfe 1993; Herman & Spicer 1996; Kovach & Spicer 1996). Only floras that included more than 15–20 species of woody dicotyledonous species were scored for CLAMP analysis.

For a more accurate evaluation of the Maastrichtian climate and verification of the CLAMP data, the distribution of the vertebrate fauna, primarily dinosaurs, was analysed and oxygen-isotope data were surveyed. These data were compiled from various publications (e.g. Teis & Nidin 1973; Savin 1977; Yasamanov 1978; Jerzykiewicz & Russell 1991; Weishampel 1991; Nessov 1995). By comparing evidence from independent sources, more precise inferences of the climate can be produced.

Table 1. *Taxonomic and ecological diversity of the Maastrichtian floral assemblages*

Fossil floras	Latitude (°N)	Number of species						Morphological characters of woody angiosperm leaves								Gymnosperm groups		Reference used for calculations
		General	Woody-angiosperms	Aquatic-angiosperms	Conifers	Cycado-phytes	Ferns	Entire-margined leaves		Leaf size (Wolfe, 1993)						Ever-green	Deci-duous	
								n	%	micro1	micro2	micro3	meso1	meso2	meso3			
Kogosukruk	70	10	1	1	1	–	2	–	–	–	100	–	–	–	–	–	1	Spicer & Parrish (1997)
Rarytkin	63	68	30	7	10	–	5	8	30	3	14	24	18	24	16	5	9	Golovneva (1994)
Kakanaut	63	43	23	6	7	2	1	3	15	9	34	37	9	8	3	4	6	Golovneva (1994)
Edmonton	53	35	17	8	5	1	2	5	32	–	24	47	22	5	2	4	3	Bell (1949)
Sakhalin	49	17	5	2	3	3	4	2	40	–	6	36	33	17	6	2	4	Krassilov (1979)
Zaisan	48	22	11	1	8	–	1	2	22	12	38	21	23	11	5	5	3	Shilin & Romanova (1978)
Hell Creek	46	33	30	–	2	–	–	11	31	1	11	28	31	26	3	–	3	Shoemaker (1996)
Ulken-Kalkan	44	9	5	1	1	–	–	–	–	–	–	50	50	–	–	–	1	Makulbekov (1974)
Nemegt	43	7	2	3	2	–	–	–	–	100	–	–	–	1	–	1	2	Makulbekov (1995)
Lance	43	50	29	7	2	–	4	15	53	3	44	36	21	–	–	2	1	Dorf (1942b)
Medicine Bow	40	39	31	2	2	–	3	20	66	–	19	61	13	3	4	2	–	Dorf (1942a)
Ripley	35	54	36	2	6	–	5	22	63	16	36	22	10	3	4	6	–	Berry (1925)

Maastrichtian floral assemblages

The Maastrichtian floras from various parts of the Northern Hemisphere are characterized by widely varying species composition, despite the general similarity of the gymnosperms. The taxonomic composition of the angiosperms differs considerably on both generic and specific levels. During Maastrichtian time, the floras of each area seemed to have developed independently and belonged to different phytogeographical units (Golovneva 1994).

In all floras, except the Alaskan, angiosperm taxa prevail over ferns, conifers and cycadophytes. The relative abundance of ferns is low in comparison with other Mesozoic floras. In many Cretaceous floras ferns amounted to 30% of the total diversity and apparently formed non-forest communities on swampy or poor, disturbed soils. Increased abundance of ferns in floras is usually correlated with epochs of climatic warming (Samylina 1974). During Maastrichtian time the reduced number of fern species and their lower relative abundance (Table 1) were the consequence of the evolutionary replacement of fern communities by angiosperms, rather than a result of climatic cooling. However, the rare occurrence of ferns along with a small number of thin coal layers may indicate an insufficiently moist climate.

The remains of cycadophytes and ginkgos in the Maastrichtian deposits occur only at high latitudes, where they are rather abundant in some localities. These plants had already become extinct by Late Cretaceous time in mid–low latitudes. On the whole, extant cycadophytes are thermophilic plants. Throughout Cretaceous time they were typical elements of tropical and subtropical floras. In the Cretaceous temperate floras an increased ratio of cycadophytes to other taxa has always been considered to indicate climatic warming. Krassilov (1985) proposed a cycadophyte index to evaluate climatic changes during Early and mid-Cretaceous time. By Late Cretaceous time cycadophyte diversity had gradually decreased at all latitudes and, strange as it may seem, northern temperate regions became one of their last refuges. Vakhrameev (1991) ascribed this phenomenon to a milder and more humid climate in these regions. Thus, for Maastrichtian time the latitudinal distribution of cycadophytes cannot be the climatic indicator, but within northern territories their relative abundance can be used to evaluate climates of different Cretaceous ages (Herman & Lebedev 1991; Golovneva 1994).

Conifers in the high-latitude Maastrichtian floras of the Northern Hemisphere are usually represented by both evergreen and deciduous taxa. The number of conifer species generally decreases from north to south. This is accompanied by an increased percentage of evergreen conifers. In the northern regions deciduous Taxodiaceae dominated the conifers. In north-eastern Asia they prevailed in floras up to approximately 45°N, including those at the Zaysan and Ulken-Kalkan localities in eastern Central Asia. Evergreen Araucariaceae appeared only in southern Gobi (Nemegt Fm.). In North America the distribution of deciduous Taxodiaceae extended as far south as Wyoming. In more southern areas conifers were not abundant and were represented mainly by evergreen Taxodiaceae, Cupressaceae and Araucariaceae. The distribution of conifers in the Northern Hemisphere can, therefore, be interpreted as an indicator of a rise in temperature and a decrease in rainfall from north to south.

Most Maastrichtian angiosperms are represented by extinct taxa. This impedes use of nearest living relatives for climatic determinations. Leaves of angiosperms in the Maastrichtian floras of the Northern Hemisphere are on average of moderate size and gradually became smaller southwards. This may be related to more favourable moist conditions at high–mid-latitudes. At the taxonomic level this reduction is reflected by the slow disappearance of platanoids and trochodendroids. The range of leaf sizes and scarcity of drip-tips indicate relatively moderate precipitation (Wolfe 1990). In northern regions leaves of angiosperms are characterized mainly by their dentate margins and thin texture. Lobed and simple pinnately veined leaves with entire margins and thick texture become more abundant to the south. These data indicate warmer and drier climates in southern areas by comparison with more northern ones (Wolfe 1979; Wolfe & Upchurch 1987). The percentage of entire-margined species varies from 15% at 63°N to 65% at 40°N. Accordingly, leaf margin analysis (Wolfe 1979) allows us to conclude that the latitudinal range of mean annual temperatures ranged from 5°C to 20°C.

Thus, the Maastrichtian climate can be evaluated as generally warm temperate in northern regions and subtropical at mid–low latitudes, with moderate humidity decreasing slightly southwards.

CLAMP palaeoclimatic inferences

The results of the CLAMP analysis are in accordance with evidence derived from the general analysis of fossil floral assemblages (Table 2). CLAMP predictions suggest that the

Table 2. Climate data for Maastrichtian time obtained from CLAMP analyses

Fossil floras	Latitue (°N)	Mean annual temperature (°C)	Cold-month mean temperature (°C)	Warm month mean temperature (°C)	Mean annual precipitation (mm)	Mean monthly growing season precipitation (mm)	Mean growing season precipation (mm)	Three consecutive driest months precipitation (mm)	Length of the growing season (months)
Rarytkin	63	11	4	19	1722	129	1410	305	6.9
Kakanaut	63	10	3	19	1414	98	948	181	6.3
Edmonton	53	12	5	19	1804	141	1586	335	7.1
Sakhalin	49	14	8	20	1892	136	1214	293	8
Zaisan	48	11	4	19	1515	106	1065	230	7
Hell Creek	46	12	6	19	1899	131	1094	302	7
Lance	43	14	8	21	1574	119	1216	242	8
Medicine Bow	40	17	13	23	1933	172	1946	348	9.7
Ripley	35	17	11	23	1498	115	1126	204	9.2
SD		1.8	3.3	3.1	430	23	280	70	1.1

climate in Maastrichtian time was warm tempe-rate (*sensu* Wolfe 1979, mean annual tempera-ture (MAT) about 10–14°C) at high and mid-latitudes and subtropical south of about 40°N (MAT about 15–17°C). At high and mid-latitudes cold-month mean temperatures were apparently about 3–8°C, and warm-month mean temperatures about 19–20°C. To the south of 40°N, winter temperatures increased to 10–13°C and summer temperatures to 20–23°C. The estimated annual range of temperatures is about 12–16°C and, therefore, similar to that of modern maritime climates. This is consistent with the proximity of many of the fossil localities to sea coasts during Maastrichtian time, although today they are situated in the con-tinental interior (Fig. 1). Predicted precipitation is relatively high in all observed areas. It averaged about 1500–1700 mm and was fairly evenly distributed over the year. Periods of drought are not detectable by CLAMP, but the three driest months were slightly less moist than the mean monthly precipitation. It seems that the drier period corresponded to winter, because the mean monthly precipitation of the growing season was higher than that of the drier period. On the whole, the Maastrichtian climate of northern latitudes was characterized by low seasonal variation in precipitation and moderate seasonality in temperature. Above the Arctic Circle, the light regime was an additional seasonal factor that controlled the structure of vegetation. However, the influence of this factor is uncertain. According to the relationship between temperature and precipitation, the Maastrichtian climate is close to the modern warm temperate and subtropical climates of the eastern coast of North America from Maryland to northern Florida.

Discussion

Temperature

CLAMP temperature predictions are in good agreement with general climate inferences and data based on leaf margin percentages. The evaluation of temperatures in polar areas is of particular importance because the Maastrichtian climate of these regions differed significantly from modern conditions. Palaeobotanical evi-dence suggests that the winters were mild. Sometimes temperatures could drop to 0°C at mid-latitudes and even below 0°C at high latitudes, but the magnitude of minimum winter temperatures and duration of frost periods are uncertain.

The most northerly known Maastrichtian macrofloral localities are Kakanaut from the Koryak Upland and Kogosukruk in Alaska. The Maastrichtian position of the North Pole is assumed to be significantly nearer the Pacific Ocean than it is today, and not far from the coast of northeastern Siberia (Smith & Briden 1978; Howarth 1981). Accordingly, these local-ities were farther north during Maastrichtian time and well within the Arctic Circle. It follows from different continental reconstructions that Kakanaut was at about 75–80°N and Kogosuk-ruk at about 75–85°N. Of these two floras the Kakanaut flora is more diverse, and includes more than 40 species. This number of species is sufficient for valid estimation of climate by CLAMP. Mean annual temperature is determined as 10°C and cold-month mean temperature about 3°C. The Kogosukruk locality contains a poorer floral assemblage, which is character-ized by strong dominance of deciduous conifers and rare occurrence of angiosperms, represented only by 3–4 species. The depauperation of this flora by comparison with other Cretaceous Alaskan floras was previously interpreted as a dramatic drop in diversity during Maastrichtian time. The mean annual temperature for this area was estimated to be about 5°C (Parrish *et al.* 1987; Spicer & Parrish 1987), implying a frequent occurrence of winter temperatures below 0°C. However, pollen assemblages from the North Slope of Alaska (Frederiksen 1991) and from other localities in Alaska and Arctic Canada (Tabbert 1967; Rouse & Srivastava 1972; Felix & Burbridge 1973) usually involve more than 30 species of angiosperms, repre-sented by approximately 15 genera. In taxo-nomic composition and diversity these assemblages are very similar to pollen assem-blages from localities further south, in Alberta and Saskatchewan, and also to assemblages of the Koryak Upland and Yenisei depression in northern Siberia (Samoylovich 1977). Palyno-floras of these regions are characterized by the dominance of *Aquilapollenites* pollen and by the presence of other characteristic genera from the *Triprojectacites* group (Samoylovich 1977; Bat-ten 1984). Close resemblance of spore and pollen assemblages implies that macrofloras were also similar in composition and diversity. Hence, the depauperation of the Maastrichtian Kogosuk-ruk flora may not reflect a change in climate. Perhaps, it could be attributable to a tapho-nomic factor instead. This leads to the conclu-sion that the climate in polar areas during Maastrichtian time was similar to that indicated by the flora of the Kakanaut locality, i.e. cold-month mean temperatures were not lower than 3–4°C. This assumption is confirmed by the

Table 3. *Diversity of vertebrate faunas of the North Pacific region during Maastrichtian time (on the basis of data from Spicer & Parrish (1987), Nessov & Golovneva (1990), Wheishampel (1991) and Nessov (1997)*

Area or locality	Latitude (°N)	Number of dinosaur genera	Main vertebrate groups
Alaska (Kogosukruk)	70	5	fish, dinosaurs, mammals
Yukon Territory, Canada	66	1	dinosaurs
Northwest Territories, Canada	64	2	dinosaurs
Koryak Upland (Kakanaut)	63	2	sharks, plesiosaurs, dinosaurs
Amur region	49–50	4	dinosaurs, turtles, crocodiles
Kazakhstan (Zaysan)	48	8	dinosaur egg shells
Sakhalin	47	1	dinosaurs
Kazakhstan (Ulken-Kalkan)	44	5	dinosaurs
Southern Gobi (Nemegt)	43	13	crocodiles, turtles, dinosaurs
Southwestern Canada and northwestern USA	40–53	≈ 20	fish, amphibians, turtles, crocodiles, lizards, dinosaurs, mammals
Southern USA	< 40	≈ 26	fish, amphibians, turtles, crocodiles, lizards, dinosaurs, mammals

presence of taxa from the subtropical families Loranthaceae, Nyssaceae, Proteaceae and Olacaceae in pollen assemblages at high latitudes (Samoylovich 1977). The disappearance of subtropical thermophilic elements is observed only in the Khatanga–Lena palynological province in northeastern Siberia. It is not yet clear if this depauperation of palynofloras is associated with proximity to the North Pole or with more severe winters in the Siberian continental interior.

Comparison of the predicted Maastrichtian polar climate with the database developed by Wolfe (1993) shows that climatic characteristics of the Kakanaut locality are closest to those of several sites in Maryland, including Battle Creek Cypress Swamp State Park. Forests consisting of deciduous Taxodiaceae, which were similar to the modern genera *Taxodium* and *Metasequoia*, were very common plant communities of high latitudes in Maastrichtian time, and sometimes they were dominant in the vegetation. Thus, the predicted polar climatic values do not contradict the putative temperature tolerance of the Maastrichtian plants.

However, the discovery of dinosaurian remains in polar regions was not expected, because dinosaurs have been previously regarded as animals adapted to warm climates. In the North Pacific region dinosaurian and other vertebrate faunas are associated with most of the same localities as the floral remains (Table 3). Maastrichtian high-latitude dinosaurs have been reported from the North Slope of Alaska (Spicer & Parrish 1987), the Northwest Territories and

Yukon Territories of Canada (Weishampel 1991), as well as from the Koryak Upland of northeast Russia (Nessov & Golovneva 1990). The diversity of the dinosaur fauna decreases northwards, and is presumed to be linked not only to diminishing temperatures, but also to a decreasing number of localities at high latitudes. However, a drop in diversity to the north of *c.* 55–60°N (from 5–10 genera to 1–3 genera) can be probably related to the former position of the Arctic Circle and long dark polar nights. Taxonomically, only one biogeographical border in the distribution of dinosaurs in North America has been identified. This is marked by the appearance of sauropods south of 35–40°N (Lehman 1987). In Maastrichtian time, sauropods were also distributed in tropical regions of South America, India and southern Europe (Weishampel 1991). This boundary corresponds to that between warm temperate and subtropical climates, which is inferred from floral data, and also corresponds to the boundary between the *Aquilapollenites* and *Normapolles* palynological provinces (Samoylovich 1977; Batten 1981, 1984). The fauna of mid- and high latitudes is taxonomically very similar, but high-latitude assemblages were more depauperate. The decreased diversity reflects, in particular, the absence (or rarity) of amphibians and non-dinosaurian reptiles, which were abundant and taxonomically diverse further south (Clemens & Nelms 1993). Among the large reptiles that lived within the Arctic Circle during Maastrichtian time were plesiosaurs and dinosaurs represented

by the herbivorous hadrosaurs and ceratopsians, as well as by carnivorous carnosaurs and small terapods. This rich fauna of reptiles could not survive long severe winters. Small modern reptiles of the temperate zone can hibernate in shelters during the winter, but large dinosaurs could not do the same because of their size (Parrish *et al.* 1987). Hence, polar dinosaurs were probably active throughout the winter. Most recent reptiles need average winter temperatures to be not less than 10–12°C to sustain the necessary level of activity, although they can endure slight frosts for short periods (McKenna 1980; Hutchison 1982). If dinosaurs were simple ectothermic animals and had temperature tolerances similar to those of other reptiles, we should assume that mean winter temperatures during Maastrichtian time were also about 10–12°C or above. These estimates of cold period temperatures are much higher than the estimations inferred from plant physiognomy. Wolfe (1987) suggested that the deciduousness of high-latitude forests resulted from the polar light regime rather than from lower in temperature. He estimated mean annual temperatures of polar regions to be about 10–15°C. However, the gradual change in abundance of species with entire-margined leaves along a latitudinal gradient, which is not accompanied by an abrupt change close to the former Arctic Circle, and the presence of a relatively large numbers of these species (20–30%) at high latitudes, indicates that deciduousness was determined primarily by seasonality in temperature, rather than by the light regime. It seems that some entire-margined species could have been evergreen and survived the polar winter in a dormant state.

Some investigators have supposed that polar dinosaurs, like caribou today, could have migrated southwards to escape cold winters (Hotton 1980). However, because of the lower thermal gradient in Maastrichtian time by comparison with the present, the dinosaurs would have had to cover a vast distance of 2500–4000 km to reach significantly warmer environments. The predominance of juvenile individuals in dinosaurian assemblages contradicts this concept of southward migration (Nessov & Golovneva 1990; Clemens & Nelms 1993). It is highly improbable that hatchlings and young dinosaurs were involved in such long-distance annual migrations.

These conclusions indicate that dinosaurs were able to remain in polar areas all year round and tolerated a cool, dark winter. It is possible that they differed metabolically from modern reptiles. Smaller turtles and crocodiles did not live so far north, although they had the capacity to hibernate (Clemens & Nelms 1993). In this case the occurrence of dinosaurs cannot be used as a climatic indicator because their temperature tolerance is uncertain. It is most likely that they were not fully endothermic and used some other physiological mechanisms (e.g. gigantothermy) to maintain their body temperature (Paladino & Spotila 1994). In any case, the presence of reptiles with naked skin indicates that winter temperatures in polar regions were generally above freezing and never dropped below 0°C for long periods.

The summarized data obtained from oxygen-isotope analyses indicate that mean annual temperatures were about 18–22°C (Douglas & Savin 1973; Saito & Van Donk 1974) or 20–25°C (Frakes *et al.* 1994) at tropical latitudes; about 11–16°C in mid-latitudes (Teis & Nidin 1973; Yasamanov 1978; Frakes *et al.* 1994); and about 10°C at high latitudes (Teis & Nidin 1973; Boersma 1984; Frakes *et al.* 1994). The Arctic Ocean is generally believed to have lacked a permanent ice cap in Maastrichtian time (Clark 1974).

Evidence coming from oxygen-isotope data for high and mid-latitudes is therefore in good agreement with climate predictions derived from plant physiognomy.

Precipitation

CLAMP predictions for precipitation in Maastrichtian time are high (about 1500–1700 mm) and indicate an even distribution throughout the year. No latitudinal differences in rainfall were revealed by CLAMP. This amount of precipitation corresponds to a humid climate and closed-canopy forest vegetation. However, general physiognomic analysis of fossil floral assemblages, scarcity of drip-tips and range of leaf size suggest only moderate humidity that decreased slightly southwards. Coal layers are insignificant (usually several centimetres) in the Maastrichtian deposits at high latitudes and almost disappear in the mid-latitudes. The existence of large dinosaurs is consistent with open vegetation and, therefore, semi-arid conditions (Wing & Tiffney 1987). In its turn, disturbance of vegetation by large herbivores must have favoured the formation of open landscapes. It is probable that the precipitation values derived from CLAMP analysis are somewhat overestimated. This overestimation can be caused by taphonomic factors because fossil assemblages are primarily formed by plants from river valleys, lake shores and other lowland environments. In these conditions the magnitude of moisture content is always much greater than for
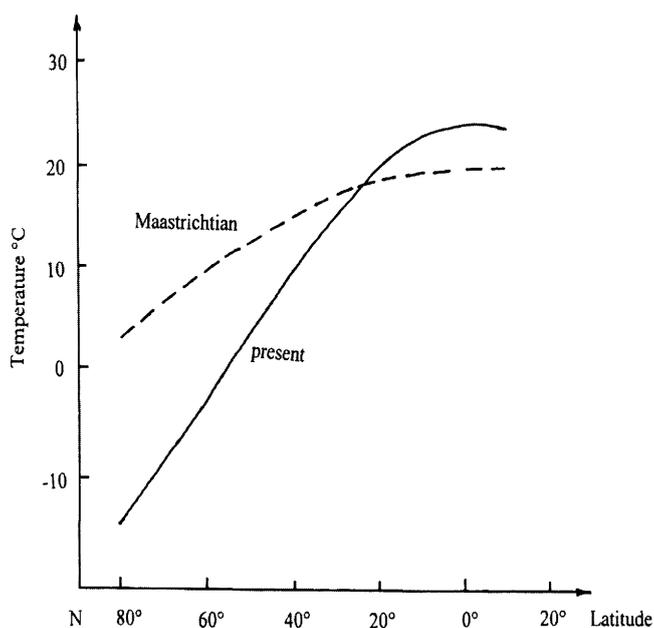
Fig. 2. Temperature gradients for present (continuous line, after Barron (1983)) and the Maastrichtian stage (dotted line).

upland areas. It seems that the vegetation during Maastrichtian time would be a mosaic of open woodland on uplands and closed-canopy forests along river valleys. Wolfe (1990) estimated the mean annual precipitation at mid-latitudes to be about 700–900 mm, deriving this value from the estimated precipitation for the driest months. This approach seems more appropriate for estimating precipitation during Maastrichtian time.

Latitudinal temperature gradient

On the whole, the Maastrichtian climate was characterized by high average temperatures and high equability both in precipitation and seasonal range of temperature. Oxygen-isotopic and palaeobotanical data indicate that temperatures were relatively lower in the tropics and significantly higher at high latitudes by comparison with conditions today. The latitudinal thermal gradient was less pronounced (Fig. 2). The difference between mean annual temperatures of polar and tropical areas during Maastrichtian time was about 10°C. This is 4–5 times less than today.

The greatest differences between the Maastrichtian and modern climates are observed at high latitudes. The much higher Arctic temperatures during Maastrichtian time may have

resulted from heating of polar areas by warm oceanic upwellings (Nessov & Golovneva 1990; Nessov 1997). The temperature of the bulk of deep oceanic waters is now about 2°C. These water masses are formed as the result of the descent of cold, dense water at high latitudes. Later they appear near the western margins of continents at low latitudes as upwellings of cold waters containing a large amount of nutrients. In tropical and subtropical areas only a thin surface layer of water is warmed. Thus, the modern vertical ocean circulation is determined by cold high-latitude downwellings.

However, during Maastrichian time the picture was different. The temperatures of deep ocean waters reached 10–14°C (Boersma 1987). These waters were probably heated at low latitudes in shallow epicontinental seas. As a result of surface evaporation the salinity and density of these waters increased, leading to their descent to the bottom and into the deeper parts of the ocean. These warm downwellings transferred the heat from the sea surface to the depths of the ocean. At present, similar downwellings are observed in the Mediterranean and Red Seas, but the influence of this type of downwelling on the heat balance of the oceans is not great, because the areal extent of these seas is comparatively small. In Cretaceous time, epicontinental seas in subtropical arid regions were

widespread. As a result, vertical oceanic circulation was determined not by cold downwellings at high latitudes, but by warm downwellings at low latitudes. At high latitudes the warm deep waters rose to the surface. During Campanian time, these upwellings are well marked by findings of hesperornidids, because the distribution of these birds in the Cretaceous period was related to the occurrence of water masses of high productivity (Nessov & Yarkov 1993).

Warm upwellings at high latitudes heated both the surface waters and the atmosphere. At that time the ocean could have been an accumulator of heat, storing it at depth for a long time and then redistributing it from the mid-latitudes to the poles. This model could explain the low temperature gradients during Maastrichtian time and the general equability of the climate.

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