Long time scale Phanerozoic temperature curve inferred from the shifts of phytogeographical boundaries

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Abstract

Long time scale climatic changes are to be inferred from the adequately slow climate-dependent processes such as shifts of the major phytogeographic boundaries. The southern boundary of temperate broad-leaved forests and their extinct equivalents is more or less distinct across the central and eastern Asia since the Late Devonian. This boundary position has shifted longitudinally roughly between 30° and 50° degree north (modern latitudes) indicating three steady states for the "cold", "temperate" and "warm" earth. There were relatively short azonal episodes in the Early Carboniferous, Early Triassic and Late Palaeocene suggestive of extremely high atmospheric CO_2 levels rendering plants less sensitive to precipitation. Transgressions have increased atmospheric CO_2 concentration by reducing terrestrial biomass.

Introduction

Most geological indicators, such as isotope ratios, give momentary estimates of palaeotemperatures then extrapolated on vast intervals of geological time. In consequence, major climatic trends can be blurred by minor fluctuations. Inferences concerning the long-term climatic changes through geological epochs have to be drawn from climatically dependent processes of comparable duration, such as shifts of global vegetational zones.

Global pattern of latitudinal vegetation zones is obviously a function of climatic zonation. Major areas of the present day decidious and evergreen forests occur north of 0°C and south of 8°C January isotherms respectively, with a broad (or sometimes narrow, as in central Asia) ecotone in between (Fig. 1).

Their boundary is, however, influenced also by the seasonal distribution of precipitation which changes from summer-wet to summer-dry within the same ecotone. Precipitation contrasts may cause vegetational boundaries to turn submeridionally, as in the case of the dark evergreen/light deciduous taiga boundary along Yenisey River in Sibiria. Incidentally, the deciduous larch taiga covers the world largest permafrost areas in a comparatively dry climate otherwise unsuitable for conifer forests. Such zonations, however, are related to the in the geological sense transient post-glacial conditions atypical for pre-Quaternary epochs.

Recognition of palaeovegetational zones

The following criteria can be used for recognition of palaeovegetational zones:

(1) Extant analogies, e.g., in the case of the Miocene "Arcto-Tertiary" broad leaved deciduous and "laurophyllous" evergreen zones (Kryshtofovich 1955).

(2) Life form characters, including growth forms of axial organs and subterranean parts, growth increments, shoot homo- or heteromorphy, leaf petiole and blade characters, notably marginal characters, pollination syndrome, diaspore dispersal adaptations, etc.

(3) Synecological criteria, such as life form and taxonomic diversity, life form (e.g. arborial/non-arborial) ratio, dominance, mortmass (plant litter) production, etc.

(4) Taphonomic criteria, such as seasonal plant litter accumulation including leaf mats, shed spur shoots and reproductive organs, frequencies of the bedding plane versus imbedded instantaneous burial, etc.

In practice, however, multiple criteria can be used after (not before) the initial zonation scheme is worked out on the base of a few criteria. Thus, recognition of palaeovegetational zones is a stepwise process following a standard procedure of forwarding and testing phytogeographical hypotheses. A preliminary experimental stage starts with widespread taxa of mutually exclusive (ME) or reciprocal common/rare (RCR) distributions. Incidentally, for the

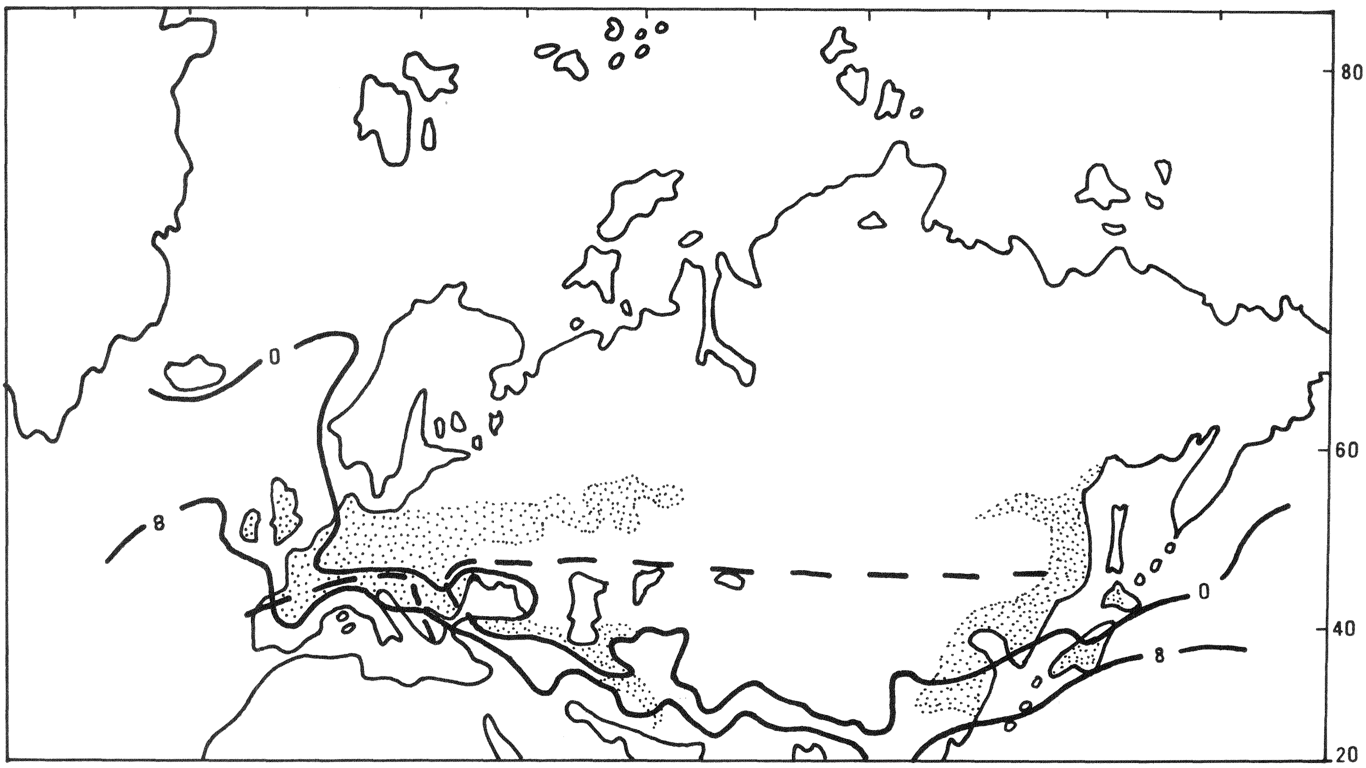


Figure 1
Extant broad-leaved deciduous forest distribution (dotted area) in relation to 0°C and 8°C January isoterms and the boundary between the round year and seasonal precipitation zones (dashed line).

Late Mesozoic epochs *Phoenicopsis* and *Cycadeoidea* are ME throughout their ranges while *Ginkgoites* and *Araucarites* are RCR. Preliminary zonations based on such selected ranges (e.g., Krassilov 1972) are then assessed by their prominance in distribution of other plant groups. Thus, it has been found that the *Phoenicopsis/Cycadeoidea* boundary has divided also the thick/thin horsetail ranges, the ME *Todites/Osmunda* and aphlebial/non-aphlebial *Coniopteris* ranges, at the same time marking the northern limit of the schizaceous ferns, ptilophyllous bennettites, araucariaceous conifers, etc. (Krassilov 1973, 1981, 1987). Accordingly, it is considered a first order division.

Deciduous zone southern boundary

Insofar as deciduousness is reflected in both morphological and taphonomic characters, the boundary of deciduous and evergreen zones should be the most readily recognizable in the fossil records.

Schematic zonations (Fig. 2a-e) are based on the following pairs of index genera with various amount of supplementary data:

Palaeocene:	*Trochodendroides/Debeya*, RCR (Krassilov 1975);
Late Cretaceous:	*Parataxodium/Sequoia*, *Trochodendroides/Debeya*, RCR (Krassilov 1975);
Early Cretaceous:	*Phoenicopsis/Cycadeoidea*, ME (Krassilov 1972);
Jurassic:	*Phoenicopsis/Cycadeoidea*, ME (Krassilov 1972; Vachrameev et al. 1978);
Late Triassic:	*Phoenicopsis/Scytophyllum* RCR (Krassilov & Shorokhova 1975; Dobruskina 1994);
Late Palaeozoic:	*Rufloria* (Vojnovskiales)/*Gigantopteris*, ME (Vachrameev et al. 1978; Meyen 1987);
Late Devonian:	*Archaeopteris/Cyclostigma* RCR (Krassilov 1994a).

While most of the data are published in the above cited work, few comments are necessary for each of the schemes. *Archaeopteris* and related genera (*Svalbardia*, *Tanaitis*) are reconstructed as seasonally shedding lateral branch systems (leaf analogues), forming leaf mats (e.g., Krassilov et al. 1987). They are dominant in northern Eurasia, but less abundant in the marginal localities of Belgium, Bohemia, Donetsk Basin and Minusinsk. Recently discovered South African localities (H. Anderson, pers. comm.) suggest bipolar distribution. Although these plants might not yet have true leaves they nevertheless might form a tree cover ecologically equivalent to the later appearing broad-leaved deciduous forests. *Cyclostigma* is provisionally chosen as a RCR genus though further range analysis is necessary.

The Late Carboniferous and Permian traditional "floristic" divisions are essentially vegetational. The Angarian localities are dominated by the *Rufloria* ("*Cordaites*") - *Zamiopteris* leaf mats and their associated *Vojnovskya* - *Gaussia* ovulate heads. This mono- to oligodominant high plant litter accumulation rate assemblages reflect temperate deciduous vegetation. The Euramerican, or Trans-Atlantic, flora is often depicted as equatorial and analogous to the modern tropical rain forests. It is, however, different from the latter in typically consisting of oligodominant rather than polydominant assemblages, having a much larger proportion of microphyllous trees and producing a far larger dead mass as a source of thick coals. Similar arguments have been used by Potonié (1951) in his interpretation of the Carboniferous European flora as extratropical semideciduous, perhaps most closely comparable to the present day swamp cypress forests. The Cathaysian gigantopterid flora now extendable to Asia Minor and sharing dominant elements with the Late Pennsylvanian - Éarly Permian flora of southern North America (Read & Mamay 1964) may be best pictured as the most thermophilous Palaeozoic global evergreen zone in which an entire leaf morphotype with several order areolate venation might have been formed convergently in several lineages of seed plants (Asama 1959).

Even in the framework of modern latitudes extended back to Palaeozoic plant geography would suggest certain changes of the relative position of continental blocks, India with glossoptrid and later pentoxylid floras being a familiar example. However a plate tectonic model of India rafted across the Indian Ocean is not the only and perhaps even the least geophysically feasible one. A right-lateral strike-slip translation along the system of Himalayan faults from a more southeasterly Palaeozoic to Early Mesozoic position would seem to fully account for this phytogeographical anomaly.

At least some of the Mesozoic floristic classifications based on quantitative distinctions rather than endemism (e.g., Vachrameev et al. 1978; Dobruskina 1994) may reflect vegetational as well as floristic differences. *Phoenicopsis* maintains as a deciduous zone dominant from mid-Triassic to mid-Cretaceous occasionally occurring also in the early Late Cretaceous when it was subplanted with deciduous conifer *Parataxodium* ("*Cephalotaxopsis*") as a major dominant. Deciduous hamamelid angiosperms, *Trochodendroides* and platanophylls might form understory of these forests but close to the Cretaceous/Tertiary boundary they emerged as dominants of what can be conceived of as progenitorial Arcto-Tertiary vegetation rapidly extending as far south as South Mongolia in early - middle Palaeocene times, but then pushed back during the Late Palaeocene-Early Eocene warm-dry phase (Krassilov 1976; Makulbekov 1988).

Climatic interpretation

With plant geography strongly controlled by global climate palaeophytogeographical classification may be seen as a testing ground for climatic models. The model to be tested here can be briefly described as follows:

(1) In glacial time longitudinal atmospheric heat transport is barred by strong polar fronts thereby halting more heat in low latitudes which, would, in effect, be wormer than in non-glacial time. Moreover, with the heat transport mainly by subtropical front outbreakes the glacial time latitudinal zonation would be less regular (e.g., patchy distribution of broad-leaved deciduous forests) than in non-glacial time;

(2) Due to a steeper altitudinal glacial time temperature gradient the ascending tropical air would cool down rapidly causing equatorial rains. Its less rapid cooling and consequently a longer distance longitudinal transfer of moisture would result in less humid equatorial zone as well as less pronounced low latitude arid zones;

(3) Sea level fluctuations contribute to global temperature fluctuations through their related albedo and atmospheric CO_2 changes. Transgression reduce the area of terrestrial biota (for as much as 40% globally in the Late Cretaceous) by expanding the area of marine biota. Since productivity of the latter is negligible in comparison with the former, the overall biotic production - a major sink of atmospheric CO_2 - decreases. In effect, atmospheric CO_2 concentration increases with transgression. Inasmuch as terrestrial biotic productivity is directly correlated with atmospheric CO_2 concentration there should be a direct correlation with transgression as well.

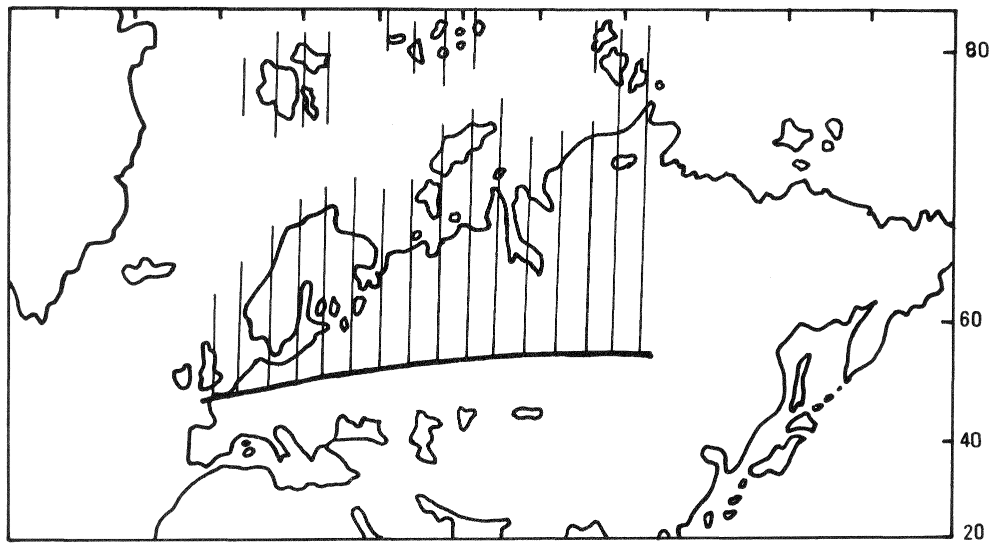


Figure 2
Temperate deciduous vegetational zone (shaded) in Eurasia

Figure 2a
Archaeopterion, Late Devonian.

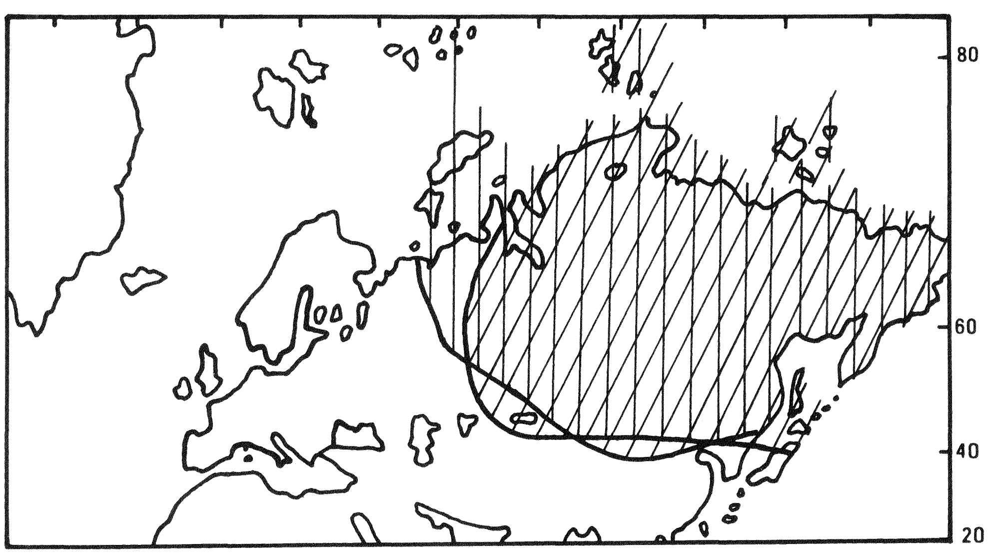


Figure 2b
Vojnovskion, mid-Permian (vertical shading, after Vakhrameev et al., 1978 and Meyen 1987) and Late Triassic (oblique shading, after Krassilov & Shorokhova 1975).

Figure 2c
Phoenicopsion, mid-Jurassic (oblique shading, after Vakhrameev et al. 1978) and Early Cretaceous (vertical shading, after Krassilov 1973).

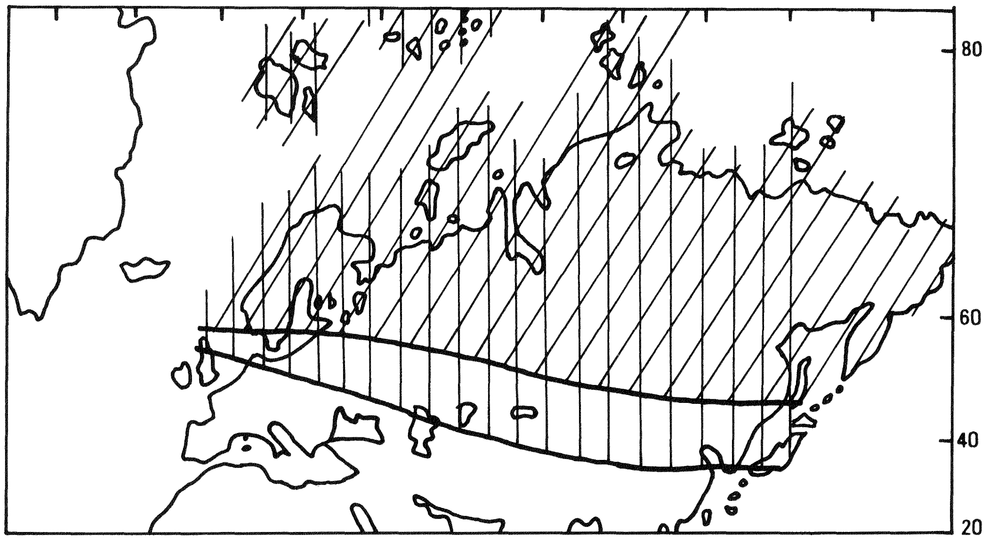


Figure 2d
Late Cretaceous, Parataxodion (vertical shading, after Krassilov 1975) and early Palaeocene, Trochodendrion (oblique shading).

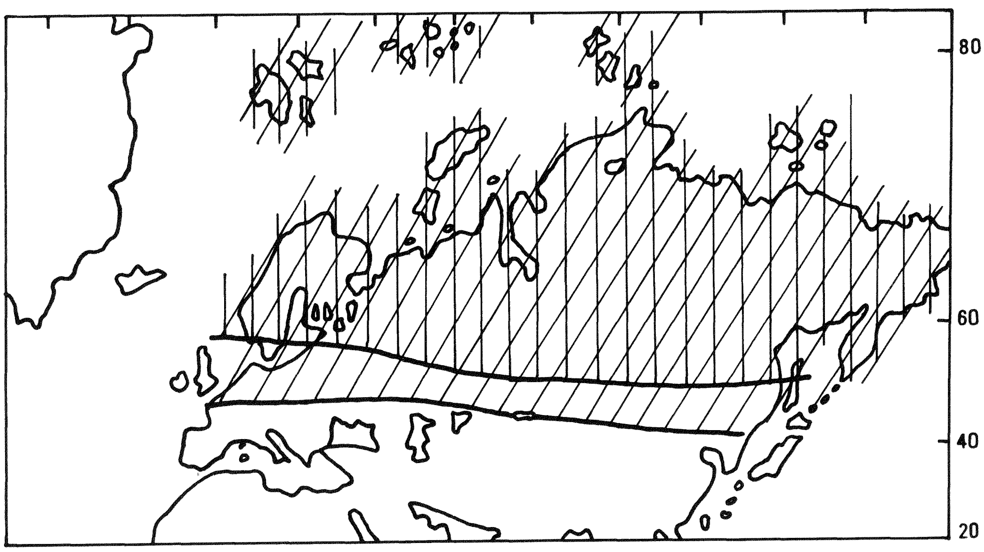
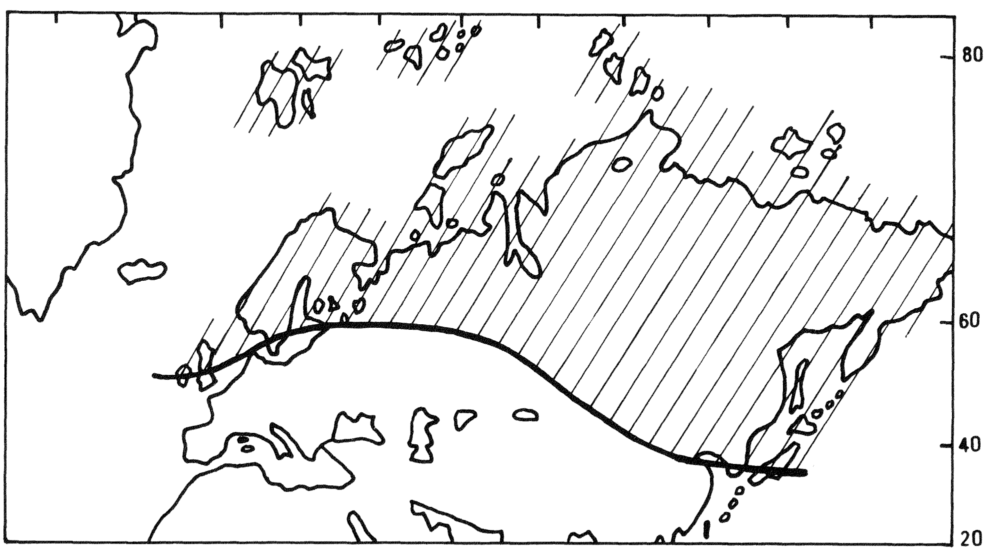


Figure 2e
Miocene, Turgayan (after Kryshtofovich 1955).



The deciduous/evergreen zone boundary as defined above is fairly distinct during glacial times, such as Late Palaeozoic, Middle-Jurassic or Late Cenozoic and less prominent but still definable for most of non-glacial periods. Another distinction evident from the maps (Fig.2) is that in glacial periods deciduous zone can be discontinuous like the present day broad-leaved forests while in non-glacial periods it has a more regular latitudinal configuration. A further distinction is that inland coal accumulation was widespread in glacial periods (e.g., Late Palaeozoic and Jurassic coals of Kuznetsk and other Siberian basins) but was confined to continental margins in non-glacial periods (e.g., Cretaceous coals of the northern Pacific and Arctic coasts). Moreover, the southern evergreen zone was typically drier than the deciduous zone. Incidentally, in the Cretaceous there was no evidence of equatorial humid zone until Maastrichtian (Herngreen & Chlonova 1981; Srivastava 1994) when coal accumulated in the Benue Basin and elsewhere.

For Eurasia the inferred Mesozoic and Tertiary palaeolatitudes are more or less parallel to the present day latitudes, so that the above conclusions holds for these palaeolatitudes as well. However Palaeozoic Eurasia or its constituent plates are placed submeridionally on most reassemblies (e.g., Smith et al. 1973; Scotese & McKerrow 1990). Both Devonian and Late Palaeozoic zonal boundaries run almost perpendicular to the respective palaeolatitudes. The traditional division of the northern hemisphere Late Palaeozoic floras into the Euramerican, Angarian and Cathaysian (Chaloner & Lacey 1973) makes no climatic sense in respect to palaeolatitudes, for they traverse Eurasia submeridionally. Moreover, the Cathaysian and North American floras sharing their dominant elements occur at approximately the same modern latitudes, but at widely descrepant palaeolatitudes. They, thus, can be considered as being in favour of the modern latitudes rather than the reconstructed palaeolatitudes for the Palaeozoic Eurasia and North America.

From the mid-Devonian on the western part of Eurasia was covered with marine transgressions more frequently and to a larger extent than the central and eastern parts. Therefore it is assumed that in these latter areas of relatively stable continental development vegetation was controlled by global climatic changes rather than by local eustatic and related events.

Long-term climatic trends, thereby, seem to me more reliably reflected by the latitudinal zonal boundary shifts in central-eastern Asia than in other areas. Figure 3 shows the southernmost Asiatic extents of the deciduous zone for successive geological periods:

Mandschurian, extant	30°N
Acto-Tertiary, Miocene	35°N
Trochodendrion, Palaeocene	43°N
Parataxodion, Mid-Cretaceous	50°N
Phoenicopsion, Mid-Jurassic	35°N
Phoenicopsion, Late Triassic	42°N
Vojnovskion, Mid-Permian	38°N
Archaeopteridion, Late Devonian	54°N

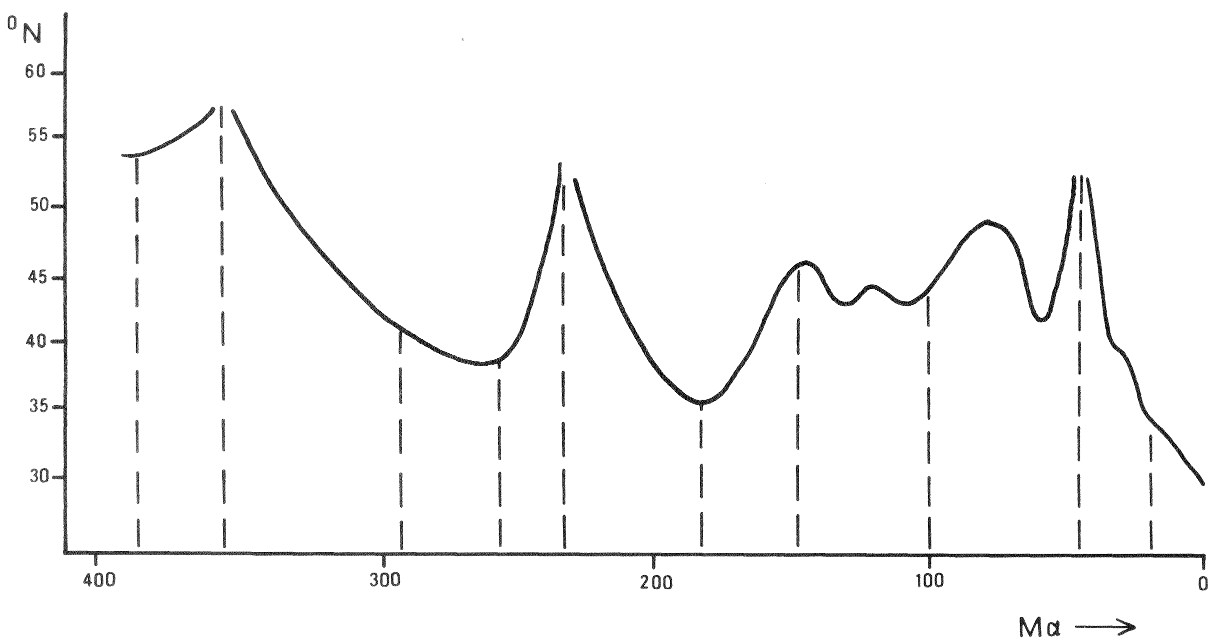


Figure 3

Shift of the temperate deciduous zone southern boundary in central Asia (Fig. 2) indicating long-term temperature changes presented as the southernmost coordinates of the boundary for successive geological periods.

The long-term boundary shifts are sinusoid, mostly within the limits 35-55°N, with an amplitude of about 4.000 km. Notably, the Cretaceous peak is somewhat lower than the Devonian while the mid-Jurassic trough is even lower than the Late Paleozoic one. The latter feature is in accord with glacial Jurassic deposits in northern Asia (Epstein 1978) and the low diversity Bathonian flora (Vachrameev 1991).

Open peaks in Figure 3 correspond to the intervals of obscure zonation in the Early Carboniferous, Early Triassic and early Eocene when arborial lycophytes, *Pleuromeia* and palms have spread over the Arctic Circle (e.g. Krassilov & Zakharov 1975; Budantsev 1983).

Insofar as zonation is caused by precipitation as well as temperate gradients, the periods of obscure zonation may evidence not only equable temperatures but also a more uniform precipitation. Alternatively, plants could have been less sensitive to precipitation difference due to a higher atmospheric CO_2 concentration which typically decrease water uptake.

CO_2 greenhouse effect was and sometimes still is considered as a leading factor of global climatic change. Recently it was shown, however, that CO_2 changes lag behind temperature changes in both short-term El-Nino fluctuations and the longer term glacial-interglacial ice core records (Raynaud et al. 1993; Siegenthaler 1990). Characteristically, the inferred greenhouse episodes coincide with the widespread anoxic events, thus evidencing oceanographic control over CO_2 fluctuations (Krassilov 1994b).

The most conspicuous temperature minima at the Permian/Triassic and Cretaceous/Tertiary boundaries as well as in the early Bathonian coincide with major regressions (see Hallam 1975 for the mid-Jurassic regression) and are immediately followed by sharp peaks conceivably related to a rapid build up of atmospheric CO_2 at the onset of transgression.

Climatic inferrences from the vegetation zonal shifts, schematically outlined above, seem generally compatible with the long-term eustatic and CO_2 curves (Berner 1990). However the climatic curve in Fig. 3 differs from the latter by the Devonian, Early Triassic and Late Cretaceous peaks being of approximately the same magnitude rather than of steeply descending magnitudes and the mid-Jurassic trough being deeper than the Permian rather than much shallower as depicted by Berner. Furthermore, there are rather deep troughs at the Early/Late Cretaceous as well as Cretaceous/Tertiary boundaries while the late Palaeocene - early Eocene peak is much higher than in the Berner's curve. With a more precise zonation the phytogeographical approach may, thus, substantially alter our ideas of the long-term climatic changes and even can potentially be used for more detailed climatic reconstructions.

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