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Reflections on the relationship between phytogeography, climate and evolution

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Abstract

Eurasian broad-leaved deciduous forests and their extinct analogues have shown three alternative geographical patterns (1) west of the longitudinal boundary along the Urals (Quaternary to Recent), (2) east of this boundary (Late Palaeozoic, Eocene, etc.), and (3) sublatitudinal (Devonian, late Mesozoic). Of these, (1) and (2) correlate with Arctic and Antarctic (Gondwanaland) glaciations, respectively, while (3) corresponds to a non-glacial climate with insignificant atmospheric circulation disturbances. This scheme accounts for the rapid shifts of the forest formations. Non-arboreal survivors of the major deforestation events have experienced bursts of phylogenesis while involved in the next afforestation wave.

1. Introduction

About 2000 BC, nomadic herders from Mesopotamia led by Abraham invaded the land of Canaan which was reconquered by their descendants under Moses in 1200 BC. Europe was repeatedly invaded by Asiatic hordes in about 1300–1200 BC (Arians), 400 BC (Scythians), 400 AD (Huns) and 1240 AD (Tatars). The basis for these history-making events was the expansion of grasslands at the expense of deciduous forests, fostering population growth and migration of cattle-breeding nomads. Major migration waves seem to have occurred every 800 years with minor pulses inbetween (incidentally, the next 800-year period since Batu invasion should commence in the 21st century).

Cenozoic mammalian evolution was governed by the alternate advances of boreal forests vs. open

vegetation of grasslands, savannas or tundras. The dominant extratropical faunistic assemblages, such as the *Hipparrion* or mammoth faunas, have appeared with expansion of their respective biomes—steppes and shrub tundras—and perished with their drastic reduction at the Pliocene/Pleistocene and Pleistocene/Holocene boundaries.

For humans and other terrestrial vertebrates, the carrying capacities of the forested and open environments are very different. Because non-arboreal vegetation is more resilient and provides more accessible phytomass it can support larger populations of the larger consumers. Therefore, the periodic afforestation/deforestation waves have played a significant role in animal and human evolution. Notably, the dinosaur extinction seems to correlate with a major afforestation event at the Cretaceous/Tertiary boundary (Krassilov, 1981).

The least understood part of the story is the

significance of the arboreal–non-arboreal biome interactions for the plants themselves. What made them change their ranges and/or their habits and how have these changes affected phylogenesis?

2. Forest phytogeography

The forest limit is defined either physiognomically as a contour of an extensively forested (ca 75%) area (Larsen, 1989), or physiologically as a boundary beyond which trees are stunted or forest regeneration is hampered by edaphic conditions, fire, pests and other factors. By the latter definition, large forest islands might occur beyond the forest boundary at locally favourable sites (Spear, 1993). Of all the controlling factors soil moisture seems critical in turn depending on the seasonal distribution of precipitation. For a considerable extent the present-day forest boundaries in Eurasia coincide with a precipitation limit of 200 mm per summer season. Major deviations from this limit are caused by human impact in the west and by the permafrost influence in the east. These factors excluded, the correspondence would perhaps be more exact. While the precipitation patterns in middle latitudes are influenced by monsoons, cyclonic activity, circulation blocking and orographic effects, the forest boundaries could be longitudinal as well as latitudinal. Well defined longitudinal boundaries occur, e.g. in eastern North America, northeastern Asia and, more locally, with grassland outliers in Europe, Transbaikalia and the Amur Province. Moreover, some distinct forest types have longitudinal boundaries, such as between the European broad-leaved and West Siberian alder–birch forests along the southern Urals or between the dark evergreen and light deciduous taigas along the Yenisey River in Siberia. Despite some overrepresentation of deciduous leaves or conifer pollen, such boundaries are readily recognizable in the fossil record by major changes of dominant plant components.

A number of phytogeographical units have been defined by palaeobotanists as “floras” or “geofloras”, such as the Archaeopteridean (Devonian), Glossopteridean or Gondwanian (Permian–Triassic), Callipteridean (Permian),

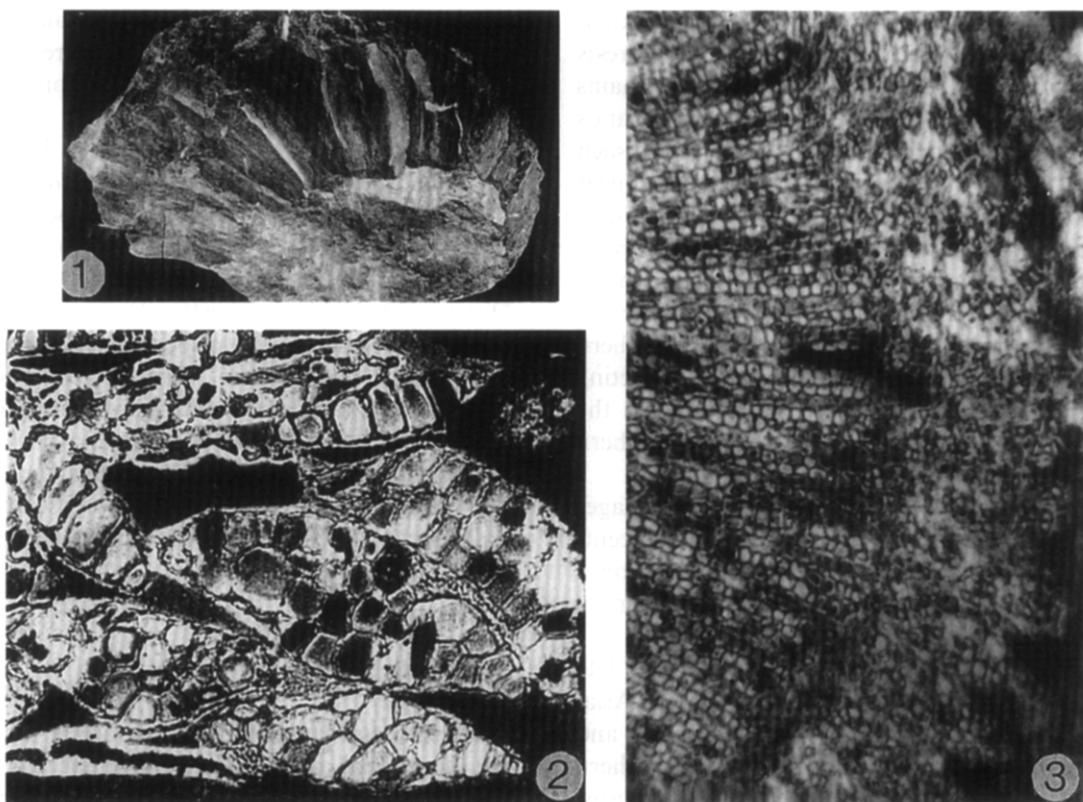
Angarian (Late Palaeozoic), Siberian (Mesozoic), Mastixian (Miocene), etc. They are usually conceived of as vicarious floristically distinct forest provinces. But the notion of uniformly forested primaeval land is a prejudice caused by the mid-Holocene afforestation. I have repeatedly argued that the Siberian Mesozoic “province” of Vakhrameev et al (1978) was primarily an area covered with deciduous forests rather than an endemic flora (e.g. Krassilov, 1987). It was possible to define its boundary more exactly by using such index forms as *Phoenicopsis* (deciduous tuber-like short shoots with ribbon-shaped leaves deposited in huge masses, pendant catkin-like strobili), dominant in Siberia and Arctic islands, and *Cycadeoidea* (short barrel-shaped trunks clothed in petiole armour and ramentum, cauliflorous, never penetrating the Arctomesozoic realm). New finds of *Cycadeoidea* in eastern Asia (Plate I) have substantiated the previously defined boundary as the limit of deciduous mesic forest union (*Phoenicopsion*) bordering on cycadophyte shrublands, scale-leaved conifer forests and fern marshes.

In Europe, open landscapes prevailed for most of its geological history. As for deciduous forest, the following situations seemed to have occurred [the reasons for using modern coordinates rather than palaeolatitudes are given in Krassilov (1987), and elsewhere]

(1) Forests west of the longitudinal boundary along the Urals: Quaternary up to Recent (Fig. 1). The present-day mixed deciduous broadleaved and conifer forests zone cover most of western Europe wedging eastward between the taiga and steppe as far as the Urals, east of which they are replaced by the pine and alder–birch small-leaved formations. Broadleaved forests reappear in moonsonal Far East. In warm interglacials such as the Eemian, they advanced somewhat further south but the general pattern was much like the present.

(2) Forests east of the longitudinal boundary along the Urals: Late Palaeozoic–Triassic, early Eocene and Burdigalian–Langhian warmings in the Tertiary, perhaps also later during the Younger Dryas cooling. Late Palaeozoic vojnovskyalean forests (localities of abundant leaf litter, leaves large ribbon-shaped on massive short shoots, massive bud scales, ovulate organs head-like) have

PLATE I



Recently found *Cycadeoidea* from the Albian of the Bikin River, Far East marking the southern boundary of deciduous forests at about 47°N

- 1 Trunk in petiole armour × 1/3.
- 2 Section through ramenta. × 200.
- 3 Cross-section of a leaf bundle. × 80

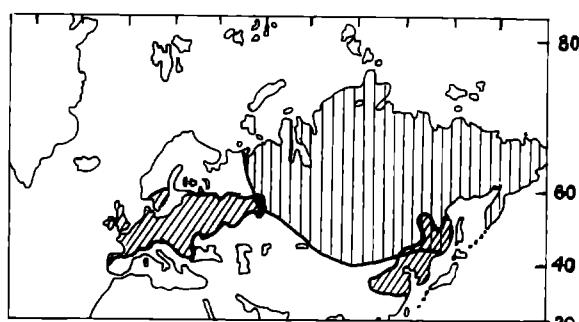


Fig 1 Present-day broad-leaved forests (oblique hatching), and Permian deciduous forests (vertical hatching), the Angarian Province (after Meyen, in Vakhrameev et al., 1978).

been replaced west of the Urals by the peltasperm-conifer shrublands and evergreen forests (some vojnovskyalean leaves resembled the European-American *Cordaites* which represented, however, entirely different life forms).

The Triassic *Phoenicopsion* has evolved in much the same boundaries as the Late Palaeozoic deciduous forests. Numerous localities along the Urals mark its boundary with a peltasperm *Lepidopterietum* assemblage dominating the European floras of the same age. While the temperate Arcto-Tertiary assemblages seem to be the progenitors of the modern boreal and broadleaved forests, the London Clay (Poltavian) and "mastixioid" vegetation of the warmer Tertiary climates

comprised both temperate and subtropical components. However, leaves are typically smaller than in the humid tropical and subtropical forests while fruits and seeds prevail over leaf remains (Kirchheimer, 1957) suggesting open shrublands or savannoid vegetation rather than tall trees such as the extant *Mastixia*. *Taxodium*-*Nyssa* peat bog forests might have bordered on vast open landscapes as in the present-day Gulf region. Subtropical elements are much less prominent in mid-latitude Siberian localities of the same age but patchy "palm horizons" reappear in northern Kamchatka (Budantsev, 1983) perhaps reflecting a mosaic of forested and open landscapes in the area which at present is the largest southern tundra enclave.

The Younger Dryas palynological assemblages west of the Urals are characterised by high percentages of ubiquitous *Artemisia* pollen suggesting a considerable reduction of European forests (Khotinskiy, 1977).

(3) Sublatitudinal boundary across Eurasia: late Mesozoic and Late Devonian (Fig. 2). In Asia, the southern boundary of the Jurassic and Cretaceous *Phoenicopsion* (which is the northern boundary of *Cycadeoidea*, schizaeaceous ferns, *Weichselia*, *Todites*, *Pachypterus*, thick horse-tails, etc., see Krassilov, 1987) had extended along 50°N. In Europe it turned north to 55–57°N then jumping to southern Greenland which may have occupied a more southerly position at the time (this is one of the few cases where phytogeography actually suggests tectonic displacement, i.e. a left-

lateral strike-slip along the Kennedy-Robeson Channels fault system). The boundary maintained its position despite periodic temperature changes shown by fluctuations of thermophilic components in the flora (Krassilov, 1975).

The southern boundary of the late Devonian progymnosperm forests *Archaeopteridion*) across Eurasia, as marked by numerous localities at Minusinsk, Tuva, Kuznetsk (53–54°N), northern Kazakhstan, Uralo-Volgian area, Voronezh District (50–52°N) and western Europe (ca. 50°N) was fairly close to the respective *Phoenicopsion* boundary but more strictly latitudinal. *Archaeopteris*, a tall tree with growth rings, might shed lateral branches as suggested by the regular occurrence of intact branching systems, e.g. in the Don River and other localities (Tscherkova-Zalesskaya, 1957; Ananyev, 1963; Krassilov et al., 1987)

3. Climate

The present-day broad-leaved forests thrive in the monsoonal and pseudo-monsoonal regions of Europe, Far East and North America ("pseudo" means that seasonal precipitation is controlled not so much by the differential heating of land and sea as in the classical monsoon as by cyclonic whirls of maritime air, since the classical concept has changed, all monsoons seem "pseudo", James, 1964)

Forests have advanced in warm humid phases of glacial cycles (e.g. Eemian Interglacial) because the seaborne ice melting excited maritime polar air surges activating mid-latitude cyclogenesis which brought ample precipitation to the European continent

The same mechanism might cause the (1) phytogeographical pattern (see above) during Quaternary glaciation while patterns (2) and (3) correspond to the Antarctic (Gondwanaland) glaciation and non- (or insignificant) glaciation, respectively

In the Northern Hemisphere an Antarctic glaciation would have a stronger climatic impact in the Pacific sector open to Antarctic waters—hence extensive Asiatic humid forests—than in the North

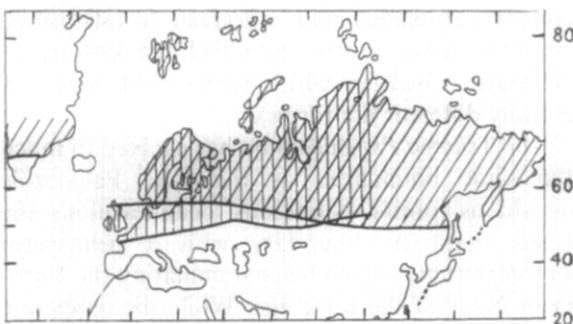


Fig. 2 Late Mesozoic *Phoenicopsion* (oblique hatching) and Late Devonian *Archaeopteridion* (vertical hatching) deciduous forests of Eurasia

Atlantic which was barred by the Walvis–Rio Grande threshold. In the non-glacial climate, precipitation was controlled by a regular atmospheric circulation system rather than circulation disturbances (i.e. outbursts of polar or tropical air masses which are a characteristic if not a dominant feature of glacial climate), hence the latitudinal phytogeographical patterns.

4. Plant evolution

The above considerations suggest rapid restructurings of phytogeographical patterns in response to climatic changes. Forest boundaries have shifted not only latitudinally but also, and to an even greater extent, longitudinally, in extreme cases leaving whole continents open. For instance, the Vojnovskian Asiatic forests, evolutionary static for about 80 Myr, perished at the end of the Permian. Two major surviving groups, peltasperms and voltzians, have dominated an open non-arboREAL or evergreen arboreal vegetation west of the deciduous forest longitudinal boundary along the Urals. After the boundary was swept by climate changes related to the Late Permian–Triassic deglaciation, both groups had phylogenetic outbursts and an entirely new forest union, *Phoenicopsis*, was born.

Meyen (1984, 1987) has linked Mesozoic ginkgophytes with Permian peltasperms. In addition, a peltasperm fructification, *Autunia*, a lax strobilus with semi-peltate biovulate seed-scales bearing platyspermic ovules (see Kerp, 1986) might serve as the prototype for the catkin-like strobili of both the nilssonialean *Beania* (of the same structure but with the more distinctly peltate seed-scales) and the czeckanowskialean *Leptostrobus* in which biovulate cupules were formed of marginally fused peltae (Krassilov, 1989). Thus, half of the *Phoenicopsis* dominants, the czeckanowskialean, ginkgoalean and nilssonialean trees, seem derivable from peltasperms while voltzians might give rise to the other half, the pinaceous and taxodiaceous conifers to which they seemed linked via *Schizolepis* and *Elatides*, respectively.

More than 100 Myr elapsed before the next comparable burst produced angiosperm-dominated forest formations. Early small-leaved

angiosperms seemed to appear in the extensive Neocomian cycadophyte (gnetophyte)–conifer shrub communities (Krassilov, 1973). As a result of the mid-Cretaceous cooling, these communities lost most of their thermophilic bennettite components and their conifer components evolved into forest trees, whereas angiosperms emerged as new marsh and shrubland dominants. They also entered the newly formed conifer forests as their understory members. A subsequent afforestation wave in the early Palaeocene brought them to dominance as deciduous canopy trees (the widely popularized impact hypothesis suggests a worldwide decimation of Cretaceous forest at the Cretaceous/Tertiary boundary; far from that, both North American and Asiatic boundary sections record an advance of mixed deciduous and conifer forests as well as peat bogs).

With time the floristically poor primeval broad-leaved forests formed by hamamelioid, trochodendroid, betuloid, ulmoid and a few other genera became enriched, notably, by salicoid, rosoid and legume components derived from the London Clay–Poltavian subtropical vegetation. In this enrichment process the Tertiary climatic pulses might have served as a pump drawing subtropical angiosperms to higher latitudes where their modified progeny became involved in subsequent afforestation waves as new elements of the Arcto-Tertiary floristic diversity. Certainly this is by no means the only conceivable scheme of macro-evolution–phytogeography–climate interaction which seems to deserve further study.

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