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Tertiary vegetation of Europe and its dynamics and climatic signal–new approaches in botany of the past

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ABSTRACT

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Using new methodologies for assessment of vegetation patterns and climatic proxies from the fossil plant record, considerable progress has been made in reconstructing paleoclimatic development at certain time intervals of the Neogene of Europe. Geobotanical mapping has employed new classification of zonal vegetation based on Integrated Plant Record (IPR) and developed a new technology to follow vegetation (and palaeoclimate) dynamics over large areas at a particular time slice. Improved paleoclimatic methodologies of the Co-existence Approach (CA) and the Climate Leaf Analysis Multivariate Program based on dicot leaf physiognomy (CLAMP) produced climatic proxies that provided additional information on the Neogene climate over Europe. The stomatal density studies proved to be another useful tool for palaeoclimatology. New reconstructions of CO_2 concentrations based on several Lauraceae and *Ginkgo* from the mid-Tertiary of Europe showed a positive correlation between higher levels of atmospheric CO_2 (pCO_2) and warming trends, expressed particularly in the Lower-Middle Miocene ("Miocene Climatic Optimum").

Key-words—Vegetation, Climate, CA, CLAMP, Stomatal density, Europe, Neogene.

यूरोप की तृतीयक (टरशियरी) वनस्पति एवं इसका गतिविज्ञान तथा जलवायवी संकेत-विगत वनस्पतिविज्ञान में नवीन पहल

ज़्लेटको क्वसैक

सारांश

पादपाश्म अभिलेख से वनस्पति प्रतिरुपों एवं जलवायी प्रतिपत्रियों के मूल्यांकन हेतु नवीन क्रिया-पद्धतियों का प्रयोग करते हुए यूरोप के नियोजीन के निश्चित समय अंतराल पर पुराजलवायवी विकास पुनर्संरचित करने में महत्वपूर्ण प्रगति हुई है। भू-वानस्पतिक मानचित्रण ने समेकित पौधा अभिलेख (आई पी आर) के आधार पर मंडलीय वनस्पति के नवीन वर्गीकरण प्रयुक्त किए हैं तथा विशेष काल स्तरीखंड में विशाल क्षेत्रों पर वनस्पति (और पुराजलवायु) गतिविज्ञान का पालन करने के लिए नवीन प्रौद्योगिकी विकसित की। द्विबीजपत्री रुप (सी.एल.ए.एम.पी.) पर आधारित सह-अस्तित्व पहल (सी.ए.) एवं जलवायु पत्ता विश्लेषण बहुचर कार्यक्रम की उन्नत पुराजलवायु विधियों ने जलवायवी प्रतिपत्रियां पेश कीं। जिसने यूरोप की नियोजीन जलवायु पर अतिरिक्त जानकारी दी। पुराजलवायुविज्ञान हेतु रंध्र धनत्व अध्ययन और लाभदायक सूत्र साबित हुए। यूरोप के मध्य-तृतीयक से प्राप्त विविध लॉरेसी एवं *गिंकगो* के आधार पर CO_2 सांद्रता की नवीन पुनर्संरचनाओं ने वायुमंडलीय CO_2 (pCO_2) एवं कोष्ण प्रवृत्तियों के उच्च स्तरों में विशेषतः निम्न-मध्य मध्यनूतन ("मध्यनूतन जलवायवी अनुकूलतम") में सुस्पष्ट धनात्मक (सकारात्मक) सहसंबंध दर्शाए।

मुख्य शब्द—वनस्पति, जलवायु, सी.ए., सी.एल.ए.एम.पी., रंध्र घनत्व, यूरोप, नियोजीन।

Changing Scenario in Palaeobotany and Allied Subjects
Editor : J.S. Guleria

INTRODUCTION

THIS article summarizes recent advances in methodology of palaeobotany and palaeoclimatology based on studies of the European Tertiary. The presented data and development of new methodologies have been achieved by the joint efforts of Johanna Eder-Kovar, Stuttgart; Michal Kováè, Bratislava; Wolfram Kuerschner, Utrecht; Vasilis Teodoridis, Prague; Dieter Uhl, Neustadt an der Weinstrasse and many others involved in this research for a couple of years. The sources, where detailed discussions and argumentations can be found, are quoted in all cases whenever the partial results were published.

GEOBOTANICAL MAPPING

Geobotanical maps of any sort arise from a mosaic of vegetation samples - relevé, between which the potential vegetation types are extended. Differences in the scale, methodology and vegetation nomenclature make their lay-out ununiform, particularly in respect of the syntaxonomic units. In palaeobotanical studies we work with fossil plant assemblages as relevé. However, fossil assemblages do not reflect the ancient vegetation directly. They consist of detached organs, leaves, fruits and seeds, and dispersed spores and pollen. Taphonomic processes bias both qualitative and quantitative composition of a given fossil plant assemblage compared with the source vegetation. Another serious problem is the fragmentary nature of the plant record, so that the elements are not always well understood taxonomically.

Nevertheless, fossils are the only direct evidence as to what kind of vegetation was growing at a particular time slice and around a particular spot. Fossil plant assemblages should be in any case understood in terms of vegetation types. It is of particular importance, when palaeoclimatic proxies should be derived from the fossil record. Three kinds of elements usually constitute fossil assemblages: intrazonal, zonal and extrazonal. The intrazonal (or azonal) elements do not reflect well, the climate, because the plants are supplied by ground water or live directly in water. The extrazonal plants deviate strongly from the mean climate of a zone. They may arrive from long distances (mountain areas) or special substrate and strongly distort the palaeoclimatic signal. The source of palaeoclimatic reconstructions should be mainly based on the zonal vegetation. This portion of the fossil plant assemblage is in equilibrium with the standard climatic conditions for the given locality.

The classification of vegetation types is by far not uniform for the Cenozoic. Contrary to the previous models of vegetation units that were intuitively coined on a fossil plant assemblage (e.g. Mai, 1995), our newly developed system for the European Neogene (Kovar-Eder & Kvacek, 2003; Kovar *et al.*, submitted) proposes more objective definitions of vegetation units. It is based on diversity percentages of arboreal components for forest formations and Non Arboreal Pollen (NAP) vs. AP abundance percentages for assessment of open landscape. The components are characterized mainly on leaf physiognomy of zonal vegetation: broad-leaved deciduous (BLD), broad-leaved evergreen (BLE), sclerophyllous (SCL) and- legume-type (LEG). In our attempts of geobotanical mapping we left aside entirely azonal plants that may cover only limited areas in the maps.

Some examples from central Europe may illustrate our concept. Humid temperate Broad-leaved Deciduous Forest is dominated by deciduous woody dicots (at least 80%) and in particular by beech. The warm temperate humid Mixed Mesophytic Forest is still characterized by mainly deciduous taxa, but with additional representation of evergreen components (the BLD component does not reach 80% of all zonal woody angiosperms, the BLE component is below 30% of zonal woody angiosperms, and the SCL + LEG components do not reach 20% of zonal woody angiosperms). The perhumid subtropical Broad-leaved evergreen notophyllous forest (at least 30% BLD, less than 20% SCL + LEG) is a typical forest formation of the Younger Mastixioid Floras *sensu* Mai (1964). Higher representation of subhumid sclerophyllous and legume components (more than 20%) indicates an existence of the subhumid sclerophyllous forest (woodland) with typical sclerophyllous oaks. The vegetation from sites that yielded highly mixed assemblages, like Parschlug from Austria (Kovar-Eder *et al.*, 2004), consists of several zonal vegetation types and must be analysed carefully and reconstructed according to the assumed landscape paleorelief.

On the basis of the new classification and re-evaluation of numerous local assemblages, it was possible to construct maps of percentages of the selected components in larger areas over southern Europe (Kovar-Eder *et al.*, 2006, submitted). The plant assemblages come from a database housed in Stuttgart, which was developed by Johanna Kovar-Eder and contributed by many colleagues. The published two examples show trends of vegetation in the Late Miocene in central and southern Europe (Kovar-Eder *et al.*, 2006, fig. 1). South-north gradients in both BLD and BLE components can be seen in central Europe and the Caucasus area, of which the BLD component dominates over the northern part while the BLE component increases towards the Balkan Peninsula and the Black Sea. No trace of any Messinian xeric phase has been noticed in our study.

In the case of the Central Paratethys area, the palinspastic maps with palaeorelief were obtained (Kvacek *et al.*, 2006) to construction the maps in the following steps:

1. First, constructed a palinspastic map with palaeorelief for a particular time slice.

2. Then placed the circles with the plant assemblages distinguished by colour according to the vegetation types.

3. Finally, filled the space between the circles with raster pattern for different vegetation types among the localities.

The resulting geobotanical maps depict spacial changes in vegetation and palaeoclimate at certain times. An important climatic period after the "Miocene Climatic Optimum" has been illustrated on the map of the Late Badenia (Kvacek *et al.*, 2006, fig. 3). There the southernmost sites in Romania, Serbia and Hungary differ from the remaining spectra by thermophilous, partly sub-humid aspects under subtropical climatic conditions, which continued from the Karpatian-Early Badenian time. A general cooling trend appears in other sites by an increasing role of deciduous (BLD) elements, while thermophilous plants gradually withdrew southwards and only a part of them survived. This is in contrast with the preceding "Wieliczien" (Middle Badenian), when the thermophilous humid mastixioid assemblages continued even in the northern part of the Carphathian Foredeep in Poland. The climatic gradient between the southern and northern part of the Central Paratethys increased after the Lower-Middle Miocene Climatic Optimum. At that time *Fagus* was the major constituent of the forest accompanied by other deciduous Fagaceae. Over most of the Central Paratethys, warm-temperate Mixed Mesophytic Forest thrived, and in the Western Carpathian and the Transcarpathian Ukraine some sites already exhibited characteristics of temperate broad-leaved deciduous forests.

Detailed work on the Palaeogene floras is yet to carried out. Partial evaluations of the floras are available particularly for the Oligocene (see Kvacek & Walther, 2001). A more complete picture of the zonal vegetation for the European Eocene was given by Kvacek (2006).

The coldest assemblages correspond to the Polar Deciduous to Mixed Mesophytic Forest, as exemplified by the Eocene of Spitsbergen and Mull within the Brito-Arctic Igneous Province. This type of vegetation is characterized by the predominant broad-leaved deciduous component, usually with large size of the leaf lamina, *Ginkgo* and mesophytic conifers – *Amentotaxus*, extinct Cupressoideae. Examples of zonal plant elements from Mull include *Amentotaxus*, *Corylites*, *Davidoidea*, *Camptodromites*, *Juglandiphyllites*, *Fagopsiphyllum* (Boulter & Kvacek, 1989). Similar examples from the Spitsbergen assemblages include *Ginkgo*, *Ushia*, *Corylites* and *Aesculus* to name most characteristic plants (Kvacek *et al.*, 1994).

Mid-latitude Notophyllous Evergreen Forest is best documented at Messel and Eckfeld (Middle Eocene), less completely at Lábatlan (Middle Eocene) and Kuèlín (Late Eocene). It is characterized by Lauraceae, Leguminosae, Juglandaceae (common), Ulmaceae (*Cedrelospermum*), Malvaceae *("Ficus" reussii* alias *Byttneria apiculata*), rare conifers (*Tetraclinis*, *Doliostrobus*, *Cephalotaxus*) and various accessory exotic and extinct elements (e.g. *Pungiphyllum*, *Ailanthus*, *Sloanea*, Icacinaceae, Menispermaceae, Vitaceae). Foliage size category range from notophyllous to microphyllous. Messel is by far the most promising site and has provided well preserved material, which has not yet been fully documented by taxonomic studies (Wilde, 1989; Wilde & Frankenhäuser, 1998; Wilde & Manchester, 2003; Wilde *et al.*, 2005).

The Late Eocene diatomite in North Bohemia, Kuèlín, comprises of impressions without cuticles. Recent collections by amateurs brought new records of various exotic and extinct plants, partly in common with Messel. The foliage category is microphyllous or smaller (Kvacek, 2002).

The mid-latitude Quasi-paratropic Rain Forest is best documented in the London Clay flora (Early Eocene), but only a part of this highly allochthonous assemblage can serve for reconstruction of mesophytic vegetation (Collinson, 1983). Probably a similar kind of vegetation is reflected in the Belleu assemblage from near Paris (Early Eocene), which unfortunately is little documented taxonomically. The Quasi-paratropic Rain Forest can be characterized (Collinson, 1983) by polydominating families Anonaceae, Cornaceae, Icacinaceae, Lauraceae, Menispermaceae, Palmae, Rutaceae, Vitaceae, etc. Conifers are rare – *Tetraclinis?*, *Doliostrobus?*, *Quasisequoia?*. Foliage size category does not correspond to the tropical vegetation (hence "quasi-paratropic") as it hardly attains the macrophyllous category. The London Clay flora contains various woody components, documented by fruits and seeds and indicating mostly tropical affinities. Much poorer documentation is available for Belleu at Paris, which only provides evidence on the physiognomy of large-sized foliage.

If we summarize the distribution of various vegetation types, a rough phytogeographical map may indicate boundaries between (1) polar deciduous, and (2) subtropical evergreen and quasi-paratropical forests. In the former case the boundary runs across Europe from Great Britain northeastwards and in the latter from Great Britain across France southwards. The boundaries were moving during the Eocene and the quasi-paratropic rain forest disappeared soon from Europe.

The classification of the zonal vegetation based on species diversities of the broad-leaved components, as defined by Kovar-Eder and Kvacek (2003), needs to be expanded for the above-mentioned categories of the Palaeogene. It will certainly not be an easy task and will require a team of contributors, like in the case of the Neogene database. The difficulties in such a project is the availability of limited data and an ancient type of plants, in which the autoecology is a problem to assess accurately. In such a situation, the true percentages of component diversity are usually impossible to calculate.

CO-EXISTENCE APPROACH VERSUS CLIMATE LEAF ANALYSIS MULTIVARIATE PROGRAM VERSUS PALAEOATMOSPHERIC CO_2 RECONSTRUCTIONS

Three palaeoclimatic methods have been lately developed to utilize fossil plant assemblages for assessing palaeoclimate independently from understanding of vegetation dynamics. The co-existence approach (CA) developed by Mosbrugger and Utescher (1997) relies on climatic requirements of the Nearest Living Relatives for a local fossil flora. The aim is to find climatic ranges, in which most of them can coexist today. Such climatic parameters are considered the best description of palaeoclimate for a given fossil plant assemblage. The CLAMP analysis developed by late Jack Wolfe and improved by Robert Spicer (Wolfe & Spicer, 1999) employs the well-known correspondence between climate and leaf physiognomy (morphology, margin, size, etc.) of dicots. This computer-aided technique is independent of exact knowledge of taxonomy of elements involved. The CO_2 analysis developed by Beerling and Chaloner (e.g. Beerling & Chaloner, 1993; Beerling, 1994) and followed by others (e.g. van der Burgh *et al.*, 1993) relies on the variation of stomatal index and stomatal density due to changes of carbon dioxide concentration in the atmosphere. This method requires a good preservation of leaf fossils with cuticles.

All three methods have some limitations as we can demonstrate on new results from the Lower Miocene of the Most Basin, North Bohemia. We have tried to select most diversified and up-to-date plant records from well-dated stratigraphical positions.

The CLAMP analysis gave different palaeoclimatic proxies for different environmental settings of the same time slice (Teodoridis & Kvacek, 2006). The site Brešt'any known since Sternberg's time corresponds to the mixed evergreen and deciduous forest vegetation from the basin and its periphery, the site Prívlaky from the same stratigraphical level reflects the riparian mostly deciduous forest. The latter gives colder climatic proxies, obviously due to environmental influence. The CA approach gives similar palaeoclimate proxies for both types of vegetation at the sites studied and is obviously less influenced by environment (Teodoridis *et al.*, 2006). However, climatic characteristics of selected extant relatives for palaeotropical and neotropical European Cenozoic showed discrepancies obtained for their direct ancestors (Kvacek, in press). This may warn us not to lay too much stress on such actualistic data. Methodologies relying on autecology of the nearest living relatives may produce climatic proxies biased in this respect.

The pCO_2 analysis seems to be more promising. The curve of stomatal index and stomatal density of four various lineages of woody plants (*Ginkgo biloba – adiantoides*; *Laurus azorica – nobilis – abchasica*; *Ocotea foetens - hradekensis* and an extinct *Laurophyllum pseudoprinceps*) obtained for the time interval of the Late Oligocene to late Middle Miocene corresponds well in the negative correlation with the oscillations of the mean annual temperature obtained by oxygen isotopic data. It has been possible to corroborate warming peaks towards the end of the Lower Miocene that largely correspond to the Miocene Climatic Optimum (Kuerschner & Kvacek, 2006).

CONCLUSIONS

To achieve further progress in Tertiary paleobotany and climatology based on the terrestrial plant records, the following urgent tasks should be fulfilled:

1. More intense and urgent taxonomic research.
2. Integration of macropalaeobotanical (carpological, foliage and wood anatomical) and palynological data.
3. More objective characteristics and assessment of fossil vegetation units in relation to the present-day conditions.

More data on palaeoclimatic evaluation of individual plant assemblages by statistical methods, both dependent (CA) and less dependent (CLAMP) on accurate understanding of taxonomy of the plant elements that constitute the assemblage.

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