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Tracking changes in plant diversity over the last 400 million years

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Convened by:

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ABSTRACTS

Abstracts of presentations and posters

Determining taxonomic diversity trends from late Carboniferous coal-bearing sequences of Europe

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The South Wales Coalfield in the southern UK has an unrivalled record of Late Carboniferous palaeotropical floras that has allowed detailed studies on local-scale and landscape-scale species diversities. Combining species richness studies and polychort analysis has allowed the main diversity changes in the vegetation to be identified through a time interval of c. 9 million years. The swamp appears to have achieved niche saturation within about 1 million years and landscape diversity remained stable at typically between 60 and 80 species. By comparing the results with similar analysis from other basins across Europe and eastern North America, it has been possible to differentiate between diversity changes that were the result of local, mainly landscape changes, and those that were due to more widespread, probably climatic effects. The results provide a benchmark against which other Palaeozoic plant diversity can be compared. The methods used may moreover be applicable to floras of other geological ages.

Investigating plant diversity using Late Quaternary Pollen Databases

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Pollen data provides one of the largest and most accessible sources of information on past plant distribution for the Late Quaternary. Much of the reason for this is thanks to the establishment of regionally distributed pollen databases in the 1990's that have continued to expand and improve. The nature and content of these databases is described, along with their current status and relationship with the new Neotoma (www.neotomadb.org) international paleoecological database. The potential and pitfalls of this data for investigating plant diversity is discussed, together with some examples from a preliminary analysis of data from the Northern Hemisphere extra-tropics over the Holocene period.

The relationship between taxonomy, biostratigraphy and phylogeny

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In addition to the well-known concept of "species", *sensu lato* is the main taxonomic unit of reference in the different fields of palaeobotany (both macrofloral and microfloral): it is extensively used in biostratigraphy, phylogenetic reconstruction and evolution, as well as evaluating palaeodiversity and palaeoecological reconstructions. However, due to the intrinsic nature of each of those fields of study we can observe that the notion of "morphospecies" is not the same. In biostratigraphy the most important is the interval of temporal existence and in this context the species are defined as a function of the needs for defining the range of the biozones, regardless of the biological character implicated. The target in phylogenetic reconstruction is different and, in consequence, the basis of the taxonomic concepts change, being primarily adjusted according to the first emergence of a given biological character. Therefore it is necessary to reflect in what context the taxa have been defined to know the ranges of validity and quality of the data.

Non-pollen palynomorphs as promising additional indicators for human impact on the natural vegetation in submerged archaeological sites: case study from the Varna Lake, northeastern Bulgaria

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The coastal lakes are rich sources of biostratigraphic information that is very useful in palaeoecological reconstructions of climate changes and human impact on the natural vegetation.

This information is of great importance for the archaeological descriptions of submerged pre-historical settlements found in the northern Bulgarian Black sea area. There are four archaeological sites in this area that have been palynologically studied for the last 30 years: the Durankulak Lake, the Shabla-Ezeretz Lake system, the Lake Bolata, as well as the Varna-Beloslav Lake system. Because of the lack of AMS radiocarbon dates for these sites, it was not possible to correlate adequately all palaeoenvironmental results with the available archaeological chronology.

Aimed to receive additional information on the Holocene vegetation dynamics and lake level changes, as well as on the anthropogenic impact during the Late Eneolithic and Early Bronze Age, the high-resolution spore-pollen analysis of AMS dated laminated sediments from a new Core 3 – Varna Lake was combined with analyses of dinoflagellate cysts, acritarchs, and other non-pollen palynomorphs.

The location of the core is close to submerged prehistorical sites and permits the palaeoenvironmental correlations of obtained results with available archaeological and geochronological data. The core is 995 cm long, but its palynologically investigated length is 870 cm. It contains dark grey clay and laminated sediments (varves). Seven samples of sediments were submitted for radiocarbon dating to the National Ocean Sciences Accelerator Mass Spectrometry Facility of Woods Hole Oceanographic Institution. The dates have been calibrated using the program CALIB version 6.1.0 of using the IntCal09 curve. An Age Model for the sedimentation rate was created by the newest version 1.17.16. of the TILIA software.

Thirty-five samples for spore-pollen analysis were processed according to the standard acetolysis laboratory method, slightly modified to remove the mineral components with sodium pyrophosphate and hydrofluoric acid. Up to 400 pollen grains of terrestrial plants were counted per sample. One-hundred-and-seventeen taxa have been determined. The dinoflagellate cysts and other NPP were counted in the samples prepared for routine spore-pollen analysis. The percentage values of the pollen taxa were calculated on the basis of AP + NAP pollen sum (arboreal plus non-arboreal plants excluding spores, aquatics, dinoflagellate cysts and other algae, acritarchs, and other NPP) and a spore-pollen diagram has been constructed. The frequency of the dinoflagellate cysts and NPP is also presented in percentages based on this pollen sum. The spore-pollen percentage diagram of Core-3-Varna Lake is divided into three local pollen assemblage zones and five subzones to facilitate description and understanding of vegetation succession. TGVIEW version 2.0.1. software was used for all percentage pollen calculations. Cluster analysis program CONISS was applied for more precise zonation as well. Blytt-Sernanders' northerneuropean climatostratigraphic subdivision of the Holocene, the regional archaeological chronology, and the regional palynostratigraphy were used for the correlations of pollen assemblages.

The established Age Model and the high percentage values of marine dinoflagellates *Lingulodinium machaerophorum* and *Spiniferites belearius*, as well as acritarchs *Cymatiosphaera globulosa* shows that the accumulation of lake sediments started after 7870 cal. BP and is connected with a rise of the Black Sea level during the First Phase of the Vityazevyan Transgression. Most probably, the Provadiyska River valley was submerged and turned into firth, connected with the sea. The vegetation palaeosuccession after 7870 cal. BP could be correlated to the Early Atlantic chronozone of the Holocene. Mixed oak forests were widespread and reached their maximal distribution. The extremely high values of arboreal pollen suggests dense forests dominated by *Quercus* with abundant other temperate species such as *Ulmus*, *Corylus*, *Tilia*, *Carpinus betulus*, *Fraxinus excelsior* and *Fagus*. The presence of indicator species such as *Hedera* suggests high humidity and temperature. Single pollen grains of *Juglans* found in this subzone confirm that the walnut was preserved along the Bulgarian Black Sea coast during the Late Glacial.

One-hundred-ninety-cm-long molluscan shell hash layer of *Mytilus galloprovincialis* covers the interval from 7776 to 6183 cal. BP and coincides with the Second Phase of the Vityazevyan Transgression. The mixed oak and hornbeam forests dominated the vegetation cover during the Middle and Late Atlantic, Subboreal and Subatlantic chronozones of the Holocene. An important change in the forest composition occurred at ca 5598 cal. BP, when *Carpinus betulus* increased its spreading due to climatic changes.

The high-resolution reconstruction of palaeovegetation also reveals the extent of anthropogenic influence in Varna Lake area. Two periods of significant presence of pollen from cultivated cereals including *Cerealia*-type and *Triticum*, weeds such as *Centaurea cyanus*-type and *Papaver*, and ruderals *Plantago lanceolata*, *Polygonum aviculare*, Cichoriaceae, *Carduus*-type and *Urtica* were identified. According to the available AMS-radiocarbon data, these periods are attributed to the Late Eneolithic and Early Bronze Age. The anthropogenic impact on the natural vegetation has been identified by deforestation and agricultural practice. The appearance of *Carpinus orientalis* and *Fraxinus ornus* is connected with degradation of forests due to a strong anthropogenic influence. The increased values of *Corylus* coincidently with decrease of *Quercus* and *Ulmus* also suggest clearance of forests and enlargement of arable areas. The absence of microcharcoals and fungal spores of *Neurospora* sp. during the intervals of deforestation provide evidence for clearance of oak woodlands by cutting. This is also confirmed by archaeological finds of stone tools such as axes and adzes from the Varna Lake area for the Late Eneolithic. The high anthropogenic influence on palaeoenvironment is also confirmed by dung indicators such as *Podospora*-type, *Cercophora*-type, *Sordaria*-type, and *Chaetomium*. The low percentage values of marine dinoflagellate cysts *Lingulodinium machaerophorum*, the presence of coenobia of *Pediastrum boryanum*, and pollen of aquatic species such as *Myriophyllum spicatum* and *Potamogeton* suggest the brackish-water environment and shallow open relatively eutrophic waters during the Late Eneolithic. The Black Sea level was low and soils around the Varna Lake were humid, rich in humus and suitable for cultivation during this time of inhabitation of the area.

The decrease of pollen of cereals and other anthropogenic species such as *Plantago lanceolata*, *Polygonum aviculare*, Cichoriaceae, *Carduus*-type and *Urtica* and the gap in human activities confirm a cultural hiatus of ca. 319 yrs between the Late Eneolithic and Early Bronze Age. The maximum values of cysts of euryhaline marine dinoflagellates *Lingulodinium machaerophorum* and *Spiniferites belerius*, acritarchs *Cymatiosphaera globulosa* and *Michrystidium* cf. *ariakense*, as well as *Foraminifera* at 5598 cal. BP suggest influx of marine waters and increase of salinity in the brackish-water lake. Most probably, the sea level became higher and influenced the Varna Lake area during the First Phase of the Kalamitian Black Sea Transgression. This supports the assumption that settlements near the Varna Lake were abandoned for about three centuries.

Estimating diversity, richness and evenness from late Quaternary pollen diagrams

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Palynology provides the opportunity to make inferences on changes in diversity of terrestrial vegetation over long time scales. The often coarse taxonomic level achievable in pollen analysis, differences in pollen production and dispersal, and the lack of pollen source boundaries hamper the application of diversity indices to palynology. Palynological richness, the number of pollen types at a constant pollen count, is the most robust and widely used diversity indicator for pollen data. However, this index is also influenced by the abundance distribution of pollen types in sediments and estimates of the number of taxa based on different count size have different meaning similar to the series of Hill numbers. In a case study with surface samples from northeast Germany rarefaction estimates based on a low count are highly correlating to the Shannon diversity index calculated from the same samples. In following Hill's arguments sample evenness may be obtained by dividing the rarefaction estimate of the number of taxa for a high count by that for a low count. I will also explore information that can be extracted from the accumulation of taxa over consecutive samples. The log-transformed taxa accumulation curve can be broken up into linear sections with different slope and intersect parameters, describing the accumulation of new taxa within the section. The breaking points may indicate changes in the species pool or in the abundance of high versus low pollen producers. The linear regressions over consecutive

samples can be used to inter- and extrapolate to low or extremely high pollen counts and the slope of the regression contains information on evenness of the sampled system.

Plant diversity in early Mesozoic times

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The diversity of plants in the past has been generally widely discussed due to the fact that only a very small part of plant actually preserve as fossils. It is even more of a task to understand the biodiversity of the flora and fauna after a mass extinction event and/or under difficult taphonomic conditions. Our understanding of the Triassic flora is affected by both of these issues. It grew after one of the largest mass extinctions in Earth history (the end-Permian mass extinction); and the Early Triassic at least is characterized in Europe (and not only there) by difficult taphonomic conditions which have been interpreted as an effect of the mass extinction (slow biotic recovery) and/or due to climatic changes. Thus, most Early Triassic deposits seem barren of plant life in Europe and a rich flora has been described only from the Anisian (early Middle Triassic) at least in terms of the macroflora. An additional aspect to the poorly understood biodiversity of the early part of the Triassic is that Europe was divided into the Alpine and the Germanic Basin, both historically to have been considered colonized by different floras. However, recent studies have not only shown that both basins were closer related from the point of view of their flora than previously considered, but also the biodiversity of the flora of the Early-Middle Triassic was much higher than that proposed in the older textbooks. Even more if we take in consideration both micro- and macrofloras.

Change in plant diversity throughout the Quaternary in Europe

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The Quaternary of Europe is characterised by extinctions of plants, especially trees of tropical humid environments. The usual way to measure diversity is rarefaction analysis of pollen data. However it has serious limitations: no continuous records for the Quaternary, counts made by different palynologists, low level of taxonomic precision, and finally differential pollen productivity and dispersal. The species that were lost are still present in N. America and/or in China, for example *Carya*, *Taxodium*, *Liquidambar* and *Nyssa*. Some others, lost more recently, are found in Anatolia (*Zelkova*) and in the Hyrcanian region (*Parrotia*). It is not clear if extinctions were progressive or stepwise. It has been suggested that in Italy a major period of extinctions of the last subtropical humid taxa was at around 1.2 Ma, when the Milankovitch periodicity changed from obliquity to eccentricity. Using both modern phylogenetic and climate modelling it is possible to infer where refugia of trees occurred in Europe: mostly in the three southern peninsulas and the Balkans. It becomes clear that the study of refugia important for Europe must include the Caucasus and the Hyrcanian region (Elburz Mts). The refugia distribution and the modern hot spots map bear remarkable similarities. Finally it is examined when hominin penetrated into Europe in the Early Pleistocene, and it is hypothesised that it was several times and at the glacial–interglacial transitions when diversity was the highest.

Diversity of middle Moscovian wetland floras; case study from the Radnice Member

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The Radnice Member (early Bolsovian) in central and western Czech Republic contains numerous volcanoclastic bands. Those associated with coals often preserve *in situ* and partly even in growth position buried T0 plant assemblages not further biased by sedimentary processes. Among such plant-bearing volcanoclastics belongs the Bělka tuff bed in the roof of locally mined the Lower Radnice Coal which both are irregularly distributed over a distance of about 80 km. This tuff bed provides a unique

opportunity to study composition and structure of peat swamp vegetation in various scales. Plant fossil collections from individual coal mines allow for estimation of diversity of peat forming assemblages in a scale of hectares to few square kilometres whereas composition and structure of peat-forming vegetation has been recently studied in detail in several excavations situated at two different localities: Ovčín and Štílec. At the Ovčín locality nearly 200 m² large excavated area situated at the edge of abandoned opencast mine provided record of lepidodendrid-cordaitalean forest structured into well-developed stories. The canopy story of this vegetation was dominated by *Lepidodendron* (*Paralycopodites*) *simile*, *L. lycopodioides*, *Lepidophloios acerosus* and *Cordaites borassifolius*. They formed a relatively dense canopy, locally interrupted with significant gaps allowing development of a rich groundcover that together with liana-like plants represents the most diverse part of the forest. A less diverse understory composed of calamites, medullosan pteridosperms and *Psaronius* tree ferns displays a patchy distribution pattern presumably related to density of the canopy. Important and most diverse part of the forest consist herbaceous ground cover and climbers represented by ferns, sphenophylls and lyginopterid pteridosperms which together makes about 19 species of 30 whole plant taxa found in the excavated area. This number is very close to 33 plant species found in the Bělka in 10 hectares of adjacent opencast mine. It suggests that 200 m² can be considered as the minimal area that sufficiently represents the pattern of this coal forest phytocoenosis although lower stories are well represented even within much smaller areas of about 60 m². At the Štílec locality a low-diversity plant assemblage dominated by small ferns and calamites with subdominant lycopsids not taller than about 1–1.5 m covered (not continuously excavated) area exceeding 900 m². This unique herbaceous assemblage comprises four fern species (*Kidstonia heracleensis*, *Dendraena pinnatilobata*, *Desmopteris alethopteroides* and *Sphenopteris cirrhifolia*), *Calamites* sp. and the small lycopsid *Spencerites leismanii*. Each species bears mature fertile organs with spores that indicate them to represent small but fully mature plants and not juvenile arborescent taxa. This plant assemblage is interpreted as a pioneer phytocoenosis that colonised a shallowed pond or lake, and that developed in the Lower Radnice Coal peat swamp after flooding. Revision of the „Bělka“ peat-forming floras collected from particular coal mines allowed for comparison of diversities of vegetation from different areas each of which occupies several hectares. Number of species varies between 5 and 45 species and the total amount of species found in the Bělka at all the localities approaches 90 biological taxa. This is relatively high diversity comparing to coal-ball data which suggest that diversity of peat swamp vegetation of major Moscovian coals in paralic basins of Euramerica varies between 30 and 50 species.

The representation of arboreal taxa in pollen trap samples from Snowdonia, North Wales

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This presentation examines the representation of arboreal taxa in surface pollen samples from a woodland in Snowdonia, North Wales. A series of modified Tauber pollen traps were established in ancient deciduous woodland near Capel Curig in 1996 as part of the Pollen Monitoring Programme. Samples from the traps have been collected annually to produce a long record of surface pollen deposition from the woodland. Results from a selection of traps show considerable annual variation and differences between traps in pollen accumulation rates of *Quercus*, *Betula*, *Corylus*, *Pinus* and *Picea*. The results are compared to the local vegetation. For example, for *Corylus* and *Betula*, while two traps from within the woodland produce broadly similar patterns, there are far higher pollen accumulation rates of these two taxa found in the trap from the woodland edge, where *Corylus* and *Betula* are more abundant in the local vegetation. Problems associated with methodology and resolution are considered. An eleven year record is presented but this should be extended to produce more reliable and representative results for comparison with fossil data, to reconstruct past vegetation.

Assessing plant diversity during Early Jurassic times in SE Europe

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The Early Jurassic floras of SE Europe occurring in Romania, Serbia and Bulgaria occur mainly in the Carpathian-Balkan orogen and their distribution corresponds to lower palaeolatitudes, related to the northern frame of the Tethys realm. Neighbouring floras, such as the Hungarian flora of the Mecsek Mountains, have a northern palaeolatitude during the Early Jurassic times and their composition is slightly different than the Carpathian and the Balkan floras. Southern neighbouring floras, such as the Iranian (Alborz and Kerman basins) and Afghanistan floras have similar compositions, belonging to the same Eurosinian Province during the Early Jurassic times.

Assessing the Early Jurassic plant diversity in SE Europe means accurate data acquisition in the field, precise and extensive collecting of fossils, cuticle analysis, in situ spores and pollen and palaeoecology. Unique research possibilities permitted by extensive and deep underground mining works in fossil *Lagerstätte* localities such as Anina (Romania) unveiled fossil assemblages distributed three dimensionally in the volume of the coal bearing formations. In this way, the palaeofloral associations and their lateral distribution were assessed in terms of diversity, paleoecology and stratigraphy. Open cast mines offered two dimensional research possibilities for the spatial distribution of plant assemblages, while natural outcrops offered punctual data.

The Hettangian-Sinemurian floras of SE Europe are typical compressive, coal floras with various degrees of preservation and diversity, represented by bryophytes, pteridophytes and gymnosperms. The Hettangian is represented by the *Thaumatopteris brauniana* assemblage Zone and the Sinemurian is marked by the *Nilssonia cf. orientalis* acme Zone. These assemblages are well defined in the South Carpathians. Less frequent Hettangian-Sinemurian permineralisations occur in several localities in Romania, they are related to local volcanism which generated well preserved and diverse silicified conifer assemblages in the South Carpathians.

The Pliensbachian-Toarcian floras are clastic floras, usually represented by drifted remains in shallow marine or brackish black shales and marls, associated with ammonites, bivalves and belemnites.

The origin of Neotropical biodiversity: some persisting problems and a potential solution

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This study contends that progress in the understanding of the origin and maintenance of extant Neotropical biodiversity by means of empirical evidence is hampered by the persistence of anachronistic conceptual approaches, notably the adherence to closed paradigms or ruling theories. The topic is discussed from three main perspectives: (1) the tendency to shift from one paradigm to another, (2) the use and abuse of broad generalizations from a single or a few case studies and (3) the use of inadequate phylogenetic dating (usually crown dating alone) for a sound appraisal of diversification timing. The origin of Neotropical biodiversity is a complex subject that requires an open-minded attitude to be fully captured. The solution proposed is fairly easy, somewhat trivial, and rooted in the classical multiple working hypotheses (MWH) approach. The MWH seeks to explore any explanation possible for observed phenomena and develop every testable hypothesis in relation to their possible causes. The MWH approach promotes thoroughness, suggests lines of inquiry that might otherwise be overlooked and develops the habit of parallel and complex thought that, unfortunately, is not fully developed in the empirical study of Neotropical biodiversity.

What does the amber fossil record tell us?

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Ambers are fossilized plant resins, which are generally very rare in the fossil record. However, we can now recognise three distinct occasions of globally significant amber deposits, which are characterized by large amber accumulations at numerous localities worldwide, termed 'amber bursts'. The three amber bursts occur during significant times in plant and earth history: in the Late Triassic, c. 230 million years ago (Mya), Early to mid-Cretaceous, 145-80 Mya and Eocene to Miocene, 55-17 Mya. The causes of amber bursts are currently unknown, but they can provide us with rich windows in to past ecosystems. Amber preserves floral (both micro- and macrofossil), faunal and micro-organismal

remains. The coincidence of these organisms from different kingdoms together as an assemblage is unusual in its self across the fossil record. The states of preservation within ambers can vary from remains that have been totally replaced by minerals like pyrite, to mummified and shrunken remains which can also leave a cast impression in the amber, to fossils with perfect microscopic (and sometimes molecular) fidelity. The specificity of what amber preserves is both its' strength and weakness: it is a limited taphonomic snapshot of organisms that live on or around the amber-producing plants, in particular the bark of the tree trunks and the surrounding forest floor/soil, but the diversity of organisms co-occurring, and the fact that some taxa only have a fossil record from amber means that this unique taphonomic window is potentially very interesting for diversity studies.

It is always good to know the spatial distribution of palynological taxa – examples from the Late Palaeozoic

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Palynostratigraphy includes not only the knowledge of the distribution of stratigraphic (vertical) ranges of certain miospore taxa and their numerous synonyms. A broader knowledge about where, when and (if possible) why a specific palynological taxon occurs in regions far away from the respective study area is useful as well.

It is shown by examples from the author's field of research how a well-founded expertise and results on the biogeographic distribution of palynological species can contribute to subjects such as

- Patterns of miospore (plant) biogeography
- Improved results in stratigraphy
- Helping in publishing the research results that have been obtained.

Ecological interpretations of lycophytes from Asturian and Cantabrian microspore floras of European and North American

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The distribution and amounts of six genera of lycophyte spores, Lycospora, Densosporites, Crassispora, Cirratiradites, Endosporites and Cadiospora, are compared in coals from the Dobrudzha, Forest of Dean, West Virginia and Tennessee coalfields, the Glace Bay borehole in the Cape Breton coalfield and in clastic sediments from the southern crop of the South Wales Coalfield. Inverse relationships are shown between Lycospora and Densosporites and between Lycospora and Crassispora in the samples from all four coalfields. Ecological interpretations of the lycophyte floras are suggested for the changes in microspore assemblages.

Vegetation changes during the Stephanian/Autunian transition in the Saar-Nahe Basin(SNB) and the possible implication of 'missing taxa'

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New findings of fossil plant remains from the Remigiusberg-Formation (Lower Rotliegend; Glan-Subgroup; Gzhelian? – Asselian?) enlarge our knowledge about the flora of the basal-most part of the lithostratigraphically defined Rotliegend Group within the Saar-Nahe basin in SW-Germany.

The flora consists of the following taxa: Calamites sp., Calamites undulatus, Asterophyllites equisetiformis, Asterophyllites longifolius (?), Scoleopteris sp., Pecopteris cyathea, Pecopteris sp., Autunia conferta, Autunia naumannii, as well as a number of so far unidentified carpological remains and strap-like leaves of unknown taxonomic affinity. In contrast to the palynoflora of the Remigiusberg Formation, which contains a number of „modern“, meso-xerophytic Hinterlandelements, the macroflora is dominated by „archaic“ elements from wet habitats. This discrepancy can probably be explained by taphonomic filters.

Differences between this flora and the macroflora from the unconformably underlying Breitenbach Formation (Stephanian C, Gzhelian) can probably be explained by climatic and/or tectonic changes which also led to considerable changes in the depositional facies of this basin. The onset of the Rotliegend sedimentation included not only a change from predominating meandering rivers to braided rivers, but also the almost total disappearance of coal swamps (the permanently more humid end of plant habitats) in the lower Glan-Subgroup. This probably represents a regional extinction of the most hydrophilous taxa in the basin, as these taxa (as well as their potential descendants) are from this time on missing in the fossil record of the Saar-Nahe basin.

The permanent disappearance of typical Stephanian taxa within the Saar-Nahe basin (in contrast to many other Central European Rotliegend basins) may indicate that some environmental threshold had been crossed, that led to the establishment of conditions within the basin that prevented the re-migration of these taxa into or the re-establishment of certain taxa within the basin. The nature of this threshold is so far unclear; besides climatic changes it is also possible that tectonics may have played a role (e.g. leading to different depositional environments with more unstable sedimentological conditions and/or hydrological changes). Palaeozoological data point to an immigration of new taxa, the so called Remigiusberg invasion (Boy & Schindler 2012, *Schriftenr. Dt. Ges. Geow.* **61**: 143-160). This points to the opening of new (fluvial) passages, a process likely related to tectonic activities in the Variscan mountain chain. As such fluvial corridors could also represent possible migration ways for hydrophilous plants it seems unlikely that the re-migration / re-establishment of these taxa was only hampered by the presence of purely physical barriers.

At the moment it is still not clear how the (permanently) 'missing taxa' should be interpreted in terms of climate change or tectonics etc, but it should also be considered that these 'missing taxa' simply represent a gap in the fossil record of the basin.