

The integrated plant record (IPR) to reconstruct Neogene vegetation: the IPR-vegetation analysis

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ABSTRACT. A recently developed semi-quantitative methodology for assessing Neogene zonal vegetation evolution is applied to 19 Miocene/Pliocene plant localities/levels with at least two different organ assemblages. The results obtained from the different organ assemblages at each site are compared in order to test the validity of the applied method. The zonal vegetation formations derived from the foliage and fruit record coincide in all sites analysed. Pollen assemblages tend to point towards more intermediate (warmer and/or more humid) conditions than the leaf and fruit records. Discrepancies underline the necessity of jointly evaluating all available plant records at one site in order to obtain a balanced reconstruction of vegetation formations. On that basis the palaeoclimatic signals derived from the zonal vegetation formations allow the climatic trends and gradients during the Neogene to be followed all over Europe.

KEY WORDS: foliage, fruits, pollen, semi-quantitative method, vegetation reconstruction, IPR-vegetation analysis, Neogene

INTRODUCTION

Today, global terrestrial biomes are defined based on major vegetation features. Applying the actualistic principle, similar interrelations may be expected for terrestrial environments during the Cenozoic.

The Western Eurasian Neogene plant record is by far the richest worldwide. Moreover, the stratigraphic resolution in this part of the world has been the subject of intensive research for many decades, and the dating and correlations of the basin fills (including the plant-bearing sediments) are therefore more precise than elsewhere.

This situation clearly provides an optimal opportunity to evaluate the fossil plant record in terms of vegetation and its evolution in space and time.

Contrary to the traditional methods applied in modern geobotany, the palaeobotanical approach is often limited by widely separated fossil plant sites. This is because plant-bearing sediments are restricted to depositional environments.

The working group on vegetation history and climate reconstruction of the EEDEN (Environments and Ecosystem Dynamics of the Eurasian Neogene) programme (2000–2005) of the European Science Foundation put intensive effort into developing a suitable method to jointly evaluate the fruit, leaf, and pollen record in terms of vegetation. The ultimate goal is to map the zonal vegetation, i.e. the vegetation of the hinterland across Europe during particular Neogene time intervals. We focused on zonal

Table 1. Localities/levels, numbers assigned to the individual organ assemblages derived from the database PANFLEURAS (Paleogene/Neogene floras of Eurasia), stratigraphic position, type of organ assemblage (**F** – fruits, **L** – leaves, **P** – pollen), and references. Numbers correspond with those in Figure 1 (boldface) and Table 3

No.	Locality	Country	Age/stratigraphy	Biozone	Organ	References
Late early Miocene/early middle Miocene						
154	Weingraben	Austria	Mid. Badenian	Sandschaler-Zone	L	Jechorek & Kovar-Eder 2004b
986	Weingraben	Austria	Mid. Badenian	Sandschaler-Zone	F	Jechorek & Kovar-Eder 2004b
786	Weingraben	Austria	Mid. Badenian	Sandschaler-Zone	P	Draxler & Zetter 1991
342	Randeck Maar	Germany	late Orleanian	MN 5	F, L	Rüffe 1963
433	Randeck Maar	Germany	late Orleanian	MN 5	F	Gregor 1982; Günther & Gregor 1998
822	Randeck Maar	Germany	late Orleanian	MN 5	P	Kottik 2002
535	Teiritzberg near Korneuburg	Austria	Karpatian	MN 5	F	Meller 1998
788	Teiritzberg near Korneuburg	Austria	Karpatian	MN 5	P	Hofmann et al. 2002
685	Lipnica Mała	Poland	Karpatian, Badenian		F	Lesiak 1994
976	Lipnica Mała	Poland	Karpatian, Badenian		P	Oszast & Stuchlik 1977
793	Děvinska Nová Ves	Slovak Rep.	late Badenian	Bolivino-Bulimina Foraminifera zone	L	Berger 1951
977	Děvinska Nová Ves	Slovak Rep.	late Badenian		P	Sitar & Kovačová-Slamková 1999
917	Berzdorf, Oberlausitz	Germany	early Miocene	Wiesa floral complex	F	Czaja 2003
948	Berzdorf, Oberlausitz	Germany	early Miocene	Wiesa floral complex	L	Jechorek in prep.
918	Berzdorf, Oberlausitz	Germany	early Miocene	Kleinleipisch floral complex	F	Czaja 2003
951	Berzdorf, Oberlausitz	Germany	early Miocene	Kleinleipisch floral complex	L	Jechorek in prep.
Early late Miocene						
108	Bełchatów	Poland	late Miocene	above fauna of MN 8/9	L	Stuchlik et al. 1990, Lesiak 1998
857	Bełchatów	Poland	late mid.- early late Miocene		F	Worobiec 1998, Lesiak 1998, Worobiec & Lesiak 1998
854	Bełchatów	Poland	Pannonian		L	Worobiec 2003
856	Bełchatów	Poland	Pannonian		P	Worobiec 2003
132	Achldorf near Vilsbiburg	Germany	Miocene	MN 8, MN 9	F, L	Knobloch 1986
823	Achldorf near Vilsbiburg	Germany	Miocene	MN 8, MN 9	F	Gregor 1982
2	Großenreith	Austria	Pannonian		L	Kovar-Eder 1988
5	Lohnsburg	Austria	Pannonian		L	Kovar-Eder 1988
160	Lohnsburg	Austria	Pannonian		P	Kovar-Eder 1988
801	Hinterschlagen	Austria	Pannonian		L	Kovar-Eder & Wójcicki 2001
344	Aubenham	Germany	Miocene	MN 8, MN 9	L	Knobloch 1988
824	Aubenham	Germany	Miocene	MN 8, MN 9	F	Gregor 1982
803	Hambach	Germany	Tortonian	Inden Fmt. 7B	L	Van Stroe 1996, Schäfer et al. 2004
971	Hambach, core SNQ1	Germany	Tortonian	Inden Fmt 7B	P	Ashraf & Mosbrugger 1996, Schäfer et al. 2004
796	Hambach	Germany	Tortonian	Inden Fmt. 7F	L	Belz & Mosbrugger 1994, Schäfer et al. 2004
975	Hambach, core SNQ1	Germany	Tortonian	Inden Fmt 7F	P	Ashraf & Mosbrugger 1996, Schäfer et al. 2004
807	Vilella, La Cerdanya	Spain	Vallesian		L	Barron 1999
808	Vilella, La Cerdanya	Spain	Vallesian		P	Barron 1999
828	Mataschen near Fehring	Austria	Pannonian	B	L	Kovar-Eder 2004, Kovar-Eder & Hably 2006

Table 1. Continued

No.	Locality	Country	Age/stratigraphy	Biozone	Organ	References
931	Mataschen near Fehring	Austria	Pannonian	B	P	Meller & Hofmann 2004
932	Mataschen near Fehring	Austria	Pannonian	B	F	Meller & Hofmann 2004
840	Brjánslaekur	Iceland	Miocene	12 m.a.	L	Denk et al. 2005
841	Brjánslaekur	Iceland	Miocene	12 m.a.	P	Kvaček et al. 2005, Denk et al. 2005
Latest Miocene/early Pliocene						
64	Ruszów	Poland	late Miocene		L	Hummel 1983, 1991
844	Ruszów	Poland	late Miocene		F	Dyjur et al. 1998
864	Ruszów	Poland	late Miocene		P	Dyjur et al. 1998
101	Sośnica	Poland	late Miocene		L	Göppert 1855, Walther & Zastawniak 1991, Zastawniak & Walther 1998, Collinson et al. 2001
107	Sośnica	Poland	late Miocene		F	Göppert 1855; Walther & Zastawniak 1991
873	Sośnica	Poland	late Miocene		P	Stachurska et al. 1973



Fig. 1. Location of the plant sites. Numbers correspond with those in bold in Tables 1 and 3

vegetation because it most precisely reflects the macro-climatic conditions of particular regions (Kovar-Eder & Kvaček 2003, Jechorek & Kovar-Eder 2004a, Kovar-Eder et al. 2006, 2008, Kvaček et al. 2006).

In this paper, we focus on plant sites/levels yielding at least two different organ assemblages, i.e. foliage and fruit, foliage and pollen, fruit and pollen, or foliage, fruit and pollen assemblages, to test the validity of the recently developed method (Fig. 1, Tab. 1).

METHODOLOGY

Geobotanical maps of potential modern vegetation (i.e. vegetation maps excluding human impact) arise from a mosaic of vegetation samples, i.e. relevés, between which the vegetation types are developed. Differences in scale, methodology and vegetation nomenclature cause a heterogeneous layout of vegetation maps. Thus, the detailed geobotanical maps based on the syntaxonomic units

of the Braun-Blanquet school (e.g. Oberdorfer & Lang 1957, Ellenberg 1978) look quite different from maps based on physiognomic features of forest vegetation by Wolfe (1979), who considered only zonal humid and mesic forest vegetation in East Asia. They also differ from that of the East Himalayas vegetation elaborated by Schweinfurth (1957), who also included xeric extrazonal uplands. Recently, the Plant Functional Type approach has been developed to classify plant communities with respect to the function (or adaptation) of the component species (Smith et al. 1997).

In all these cases the vegetation types are very differently characterized and named. None of these methods can be applied directly to the fossil record, but there is a strong demand to map the vegetation of ancient times. Traditional methods fail to use the information potential of the complete fossil plant record (Fauquette et al. 1999).

Every fossil plant assemblage is the basis of a single relevée (*sensu* Braun-Blanquet). In any case, we are dealing with only an incomplete documentation of ancient vegetation biased by different phenomena, e.g. taphonomic factors or different quantities of plant organ production (compare Kovar-Eder et al. 2008). To minimize the effects of different fossilization potentials (e.g. herbs largely lacking in the leaf record; Lauraceae or *Acer* almost absent in the pollen record), it is essential to include all available organ assemblages. A combined evaluation method for different organ assemblages (foliage, fruits and seeds, pollen and spores) will certainly yield the most complete picture of the ancient vegetation. Following this argumentation, the authors put a strong effort into collecting balanced records of the different organ assemblages. A higher number of fruit floras, however, would better balance the representation of the different organ assemblages. The taxonomic resolution of pollen and spore taxa is usually lower than in the leaf and fruit record, and often does not even reach the generic level. Recent efforts have been made to transfer the traditional sporomorph species from the morphological to the botanical system (Ziemińska-Tworzydło et al. 1994 a, b, Stuchlik et al. 2002).

Quantitative analyses of megafossils are often misleading, calling for a greater reliance on the diversity versus the abundance of the elements. Birks (1973) evaluated the spec-

tra of fruit and seed mesofossils obtained by sieving of Minnesota Recent and Quaternary sediments of small lakes in three different vegetation settings: prairie, deciduous forest and coniferous forest. The sub-recent spectra he obtained corresponded well with the vegetation from the surroundings, although the abundance or even presence of aquatic, wetland herbs and woody elements was biased by transport and seed production. Spicer and Wolfe (1987) compared the sieved assemblages from high- versus low-energy stream sediments. They arrived at similar results: the floral spectra are well reflected, but the elements are certainly not quantitatively represented.

In contrast, quantitative or semi-quantitative spectra are typically used in pollen analysis. A wealth of actuopalynological studies are available. Kvavadze and Stuchlik (1990) followed the representation of the NAP and AP (non-arboreal and arboreal pollen) in various modern landscapes in Georgia. They found discrepancies in the representation of arboreal elements due to pollen overproduction, the susceptibility for wind dispersal and fossilisation potential. They documented high NAP values (>40%) in steppe regions and long-distance dispersal of certain arboreal elements, namely Pinaceae, *Alnus* and *Corylus* from closed forest or mountain environments. In the fossil record, such highly allochthonous elements are particularly frequent in marine facies.

Despite quantitative palynological investigations to reconstruct ancient vegetation, the method we pursue below relies solely on the qualitative evaluation of the floristic spectra in the different organ assemblages. The main argument for the purely qualitative versus quantitative analysis is the necessity of obtaining reasonably comparable pictures among the different organ assemblages.

To be included in the evaluation described below, the individual organ assemblages should meet the following requirements: They should include less than 33% problematic taxa and at least ten zonal taxa (Kovar-Eder & Kvaček 2003, Jechorek & Kovar-Eder 2004a).

A basically taxonomic/physiognomic grouping, reflecting also essential ecological features, was introduced by Kovar-Eder and Kvaček (2003). As we intended to include foliage, fruit, and pollen to evaluate the fossil record for vegetation reconstruction, this

scheme should also enable reasonably objective comparability between the different organ assemblages.

The components have been described in detail in Kovar-Eder and Kvaček (2003), Jechorek and Kovar-Eder (2004a), and Kovar-Eder et al. (2008), and are therefore merely listed here: zonal components: CONIFER (zonal and extrazonal conifers), BLD (broad-leaved deciduous woody angiosperms), BLE (broad-leaved evergreen woody angiosperms), SCL (sclerophyllous woody angiosperms), LEG (legume-type woody angiosperms), PALM (zonal palms); the ZONAL HERB component is split into herbs characteristic of mesophytic forest undergrowth (MESO HERB component) and of open woodland and grassland (DRY HERB component). Azonal components are: AZONAL WOODY (including all azonal trees and shrubs), AZONAL HERB (wetland herbs, including azonal ferns), and the AQUATIC component.

The FERN component (including zonal and extrazonal ferns) is distinguished but not further evaluated here.

The taxa of every single assemblage (but not their abundances) are assigned to the established groups. This is followed by a quantitative evaluation of the fossil associations. Proportions relevant to decipher zonal vegetation formations are calculated: The proportion of the BLD, BLE, and SCL+LEG components, of zonal woody angiosperms (i.e. of the BLD+BLE+SCL+LEG+PALM components) and the proportion of the ZONAL HERB component of all zonal taxa (i.e. of the CONIF+BLD+BLE+SCL+LEG+PALM+ZONAL HERB components) are calculated (Kovar-Eder et al. 2008). The assignment to the vegetation units described below is based on the respective proportions.

At sites/levels with different organ assemblages treated in this paper, the mean values were calculated for each component from all available organ assemblages. This yielded the final determination of vegetation unit.

VEGETATION FORMATIONS

A summary of vegetation types for Neogene forests and aquatic communities has been introduced by Mai (1981, 1985, 1995). It is extremely detailed, but hard to apply on a more general scale across Europe. Moreover,

it is based on the nearest extant models, but the vegetation types are not clearly defined.

Natural vegetation is in equilibrium with climatic and edaphic factors. It includes zonal (=climax), extrazonal, and azonal (=intrazonal) vegetation formations. Due to human impact, natural vegetation does not exist over large regions today. It is usually reconstructed and then termed potential natural vegetation.

Zonal vegetation: Large-scale vegetation developing under mesic soil conditions (no extremes). It is more distinctly influenced by climatic than by edaphic factors.

Extrazonal vegetation: Due to more extreme climatic conditions at the geographic limits of their natural distribution area, vegetation formations may change their habitat (e.g. from low to higher elevation). One example: moving further south, temperate broad-leaved deciduous forest are restricted to increasingly higher altitudes in their natural distribution area on the northern hemisphere. There, they constitute the extrazonal vegetation where the zonal vegetation (at lower altitudes) is largely broad-leaved evergreen.

Azonal vegetation: The development of plant communities is more strongly influenced by edaphic factors than by climate (e.g. wetland, alluvial vegetation, mangroves).

Previous models of vegetation units were intuitively coined based on a fossil plant assemblage. Our newly developed system for the European Neogene, however, proposes objective definitions of vegetation units based on diversity percentages of BLD, BLE, SCL+LEG components of zonal woody angiosperm taxa for forest formations; for assessing open landscape it proposes using NAP (non-arboreal pollen) versus AP (arboreal pollen) diversity percentages of all zonal taxa (Kovar-Eder et al. 2008).

The current calculations of the zonal woody components exclude the CONIFER component. The argument is that in the pollen record the CONIFER component includes high proportions of extrazonal taxa (high mountain conifers such as *Picea*, *Abies*, *Tsuga*). This hampers the comparison with the CONIFER component in the leaf and fruit records.

For humid zonal forest formations the following types have been defined (Tab. 2):

– zonal temperate to warm-temperate

Table 2. System and characteristics of the zonal vegetation units.

Vegetation formation	Percentage of the BLD component of zonal woody angiosperm taxa	Percentage of the BLE component of zonal woody angiosperm taxa	Percentage of the SCL+LEG components of zonal woody angiosperm taxa	Percentage of the ZONAL HERB (DRY + MESO HERB) component of zonal angiosperm taxa
Broad-leaved deciduous forests	≥ 80%			mostly ≤ 30%
Mixed mesophytic forests	< 80%	< 30%	< 20%	< 30%
Broad-leaved evergreen forests		≥ 30%	(SCL+LEG)<BLE	< 25%
Sub-humid sclerophyllous forests			≥ 20%	< 30%
Open woodlands		mostly < 30%	≥ 20%	30–40%, MESO HERB max. 10% of ZONAL HERB above DRY HERB
Xeric grasslands / steppe				≥ 40%

broad-leaved deciduous forest (broad-leaved deciduous forest);

– zonal warm-temperate to subtropical mixed mesophytic forest (mixed mesophytic forest);

– zonal subtropical broad-leaved evergreen forest (broad-leaved evergreen forest);

For subtropical sub-humid to xeric zonal formations we distinguished (Tab. 2):

– zonal subtropical subhumid sclerophyllous, microphyllous forest (subhumid sclerophyllous forest);

– zonal xeric open woodland (open woodlands);

– zonal xeric grassland / steppe (xeric grassland/steppe).

Modern vegetation is characterized by transitions (ecotones) between the major vegetation types. Consequently, the limits between the different vegetation units in the fossil record are also less sharp than indicated by our mechanistic splitting. We have introduced the above-described 6 zonal vegetation units for practical reasons. Finally, note that the azonal vegetation units are currently omitted. Azonal vegetation will be in the focus of future studies.

AUTECOLOGICAL ASSIGNMENT OF THE FOSSIL PLANT ELEMENTS (APPENDICES 1–7)

As stated above, the classification of fossil vegetation formations is based on growth form, physiognomy, and ecological requirements of the individual taxa (Kovar-Eder & Kvaček 2003, Jechorek & Kovar-Eder 2004a, Kovar-Eder et al. 2008). Autecology (i.e. ecological properties of individual taxa) can be inferred

in several ways for Neogene plants. Some characters may be unambiguously derived from nearest living relatives, but other properties or even rough estimates of ecological tolerance for fossil plant taxa (precise temperature regime, seasonality, soil quality, etc.) may be equivocal. To avoid crucial mistakes, various parameters are taken into account in assigning the respective plant taxon to the components (autecological groups) employed in our classification.

GROWTH FORM

Properties of the nearest living relative are assumed to provide reliable information on growth form: no fossil alder is herbaceous, nor is a fossil *Salvinia* a xerophyte. In some cases, however, a genus (e.g. *Hypericum*) or a family (e.g. Scrophulariaceae) may today include representatives with different growth forms, both woody and herbaceous. The same may apply for differentiating zonal versus azonal, or evergreen versus deciduous plants. Our system therefore assigns ambiguous taxa to more than one component by splitting the value 1 for a respective taxon (e.g. 0.5/0.5, or 0.25/0.5/0.25). The assigned proportions are attributed according to our experience in the fossil record and to modern botany.

HABITAT

Palaeobotanical research has revealed examples where living relatives may have changed their autecology compared to their fossil ancestors (Kvaček 2005). All available evidence must be considered in determining the correct autecology of the fossil plant ele-

ments. The sedimentary setting may provide information about the preferred environment of fossil plants. For instance, occurrences in lignite facies are typical of swampy environments. Accordingly, the fossil representative of *Craigia* most probably tolerated or even preferred these environments, because flowers, pollen, fruits, and foliage often co-occur in lignite clays or even in coal (Kvaček 2005). Hence, in the European Neogene, *Craigia* must have belonged at least partly to azonal plants, although today this relict is a typical upland tree (Kvaček et al. 2006). *Cercidiphyllum crenatum* most probably changed its autecology during the Miocene because, in early Miocene deposits, it is abundant in swampy/fluvial environments (leaves, fruits, brachyblasts; e.g. Oberdorf, Kovar-Eder et al. 1998). For late Miocene occurrences of *C. crenatum*, riparian habitats are more typical, as for *C. japonicum* today. The autecology of fossil elements lacking a direct living relative can be inferred in a similar manner. An extinct conifer, *Quasisequoia couttsiae*, which regularly co-occurs with *Glyptostrobus* in coaly deposits, was therefore certainly also an azonal swamp element (Kunzmann 1999). Early occurrences of *Byttneriophyllum tiliifolium* are restricted to single specimens at different sites in fluvial environments (e.g. Turów, Czacott & Skirgiełło 1967). Starting from the Sarmatian and mainly in the late Miocene, it typically occurred in great numbers, often as a monodominant element in assemblages with low species diversity deriving from clay and lignitic facies in the realm of Lake Pannon (Knobloch & Kvaček 1965, Givulescu 1992, Hably & Kovar-Eder 1996). The assignment of single species to particular components therefore varies in this analysis, depending on different taphonomic parameters and age.

Autecology, was often inferred based on the floral element (see Mai 1991), for example the Arctotertiary, i.e. deciduous, or the Palaeotropical, generally evergreen. This criterion is the least reliable and often derived from the associated assemblage, hence representing circular argumentation. Nonetheless, such estimates relying on the repeated co-occurrences of specific taxa are often the only way (besides taphonomy and the sedimentological context) to verify the judgment on autecology. In *Cedrelospermum*, an extinct Ulmaceae, mass occurrence in sub-humid assemblages (high

percentages of the SCL and LEG components) supports our judgment to classify this element partly in the SCL and BLD components. Its foliage is tiny, with dense venation, but its texture is not coriaceous. The same applies to other sub-humid plants such as *Ziziphus ziziphoides*, which is assigned to the SCL component. The views vary among palaeobotanists and palynologists as to the role of particular elements in ancient vegetation, with individual experience and attitude playing a role.

PHYSIOGNOMY

The physiognomic properties of foliage, such as coriaceous texture and thick cuticle, may help to decipher whether the element was evergreen, sclerophyllous or deciduous, even in plants with dubious affinities (*Dicotylophyllum* spp.). Cuticle thickness, of course, may be misleading. It is very thin in sclerophyllous oaks because the epidermal-hypodermal tissue is festooned by cellulose sclerenchyma with a thin cuticle cover (Kvaček et al. 2002). On the other hand, thick cuticles of *Ginkgo* or *Platanus neptuni* do not mean that these plants were evergreen. The opposite is true judging from the living relative of *Ginkgo* and, in the case of *Platanus neptuni*, from the buds covered by the base of the petiole (Kvaček & Manchester 2004). The overall size and shape, leaf margin, and venation density of a leaf fossil indicate whether the plant belongs to the LEG or SCL component. One and the same taxon may have been attributed differently. A case in point is *Magnolia* sp.. In the leaf record it may be evergreen or deciduous depending on the leaf texture; this type of information is not available from the fruit and pollen records, and the value 1 for *Magnolia* sp. will be split into different components in the percentage calculations.

The physiognomy of fruits/seeds and pollen/spores provides less straightforward information, independent of the systematic position of the mother plant. Compared to the leaf and fruit/seed record, the taxonomic resolution of pollen/spores is lower. Therefore, the whole plant approach should be employed whenever palaeobotanical/palynological evidence is available. Joint research has always yielded positive results. A whole plant of *Podocarpium podocarpum* and *Tricolporopollenites wackersdorfensis* presents a good example (Liu et al. 2001). Both the examination of pollen *in*

situ and more detailed SEM studies of various types of dispersed pollen made profound contributions (e.g. Zetter 1998, Zetter & Ferguson 2002). Palynologists are still in the early phase of such efforts, and many sporomorphs are difficult to evaluate with respect to the taxonomic affinity and autecology of their mother plants (Ziemińska-Tworzydło et al. 1994a, b, Stuchlik et al. 2002).

AMBIGUOUS TAXA

Many poorly understood enigmatic sporomorphs as well as macrofossils cannot be presently classified and have been excluded from our analyses. Unreliably documented taxa have also been excluded and are summarized under “counted but excluded” (Tab. 3). This is essential because we restrict our analyses to floras with less than one third ambiguous taxa. In some cases the number of ambiguous taxa in single floras were reduced by inspection and revision of the original material/palynological slides.

The CONIFER and FERN components partly encompass extrazonal plants due to long-distance transport, e.g. high-mountain Pinaceae such as *Tsuga*, *Cedrus* etc.. They have often been used to reconstruct the landscape relief (e.g. Kvaček et al. 2006). The CONIFER component has been used only in calculating the ZONAL HERB component (Kovar-Eder et al. 2008). Another problem in evaluating palynospectra involves allotting precise numbers (diversity) and autecology of NAP, such as for the Asteraceae or Chenopodiaceae, i.e. taxa with low taxonomic resolution. This approach usually underestimates the diversity percentages of herbaceous plants. Parallel, routine, quantitative percentage estimates of AP vs. NAP may offer corrections. In this regard, actuopalynological studies determining shifting AP/NAP proportions in various landscape types (forest vs. open vegetation) are very important (Kvavadze & Stuchlik 1990, 1993, Stuchlik & Kvavadze 1987, 1993, 1995).

Appendices 1–7 compile lists for foliage, fruit, and pollen taxa documented at the localities analysed in this paper along with the autecological values we have elaborated. This transparency is crucial for scientific rigor: the reproducibility of our results is a premise for broad acceptance by the scientific community. Moreover, our method can easily be applied to any other Cenozoic flora. The complete

lists for all sites evaluated in our previous papers (Kovar-Eder et al. 2006, Jechorek & Kovar-Eder 2004a, Kovar-Eder et al. 2008) are already much longer, and the taxon lists will continue to grow as progress is made in evaluating the Neogene and Palaeogene plant record. Future progress in taxonomy and systematic affinities will certainly improve our assignments.

These lists do not include taxa of unknown systematic affinity (e.g. *Dicotylophyllum*). However, such taxa have been included in the evaluation if they could be assigned to a particular component based on their leaf physiognomy. Non-vascular plants such as algae, bryophytes, and semiparasitic taxa (Loranthaceae) are excluded.

DATA

In Kovar-Eder et al. (2008) we evaluated 198 plant organ assemblages (foliage, fruit, pollen) from 173 Miocene sites/levels. Priority in selecting the sites/levels was given to reasonable dating, preferably by means other than mere palaeobotanical ones. In this paper, we focus exclusively on plant sites that yielded more than one thoroughly investigated organ assemblage, i.e. either leaves and fruits, or leaves and pollen, fruits and pollen, or leaves, fruits, and pollen (Fig. 1, Tabs 1, 3). These sites deserve special attention because they offer an opportunity to validate our method: the better the analyses of the individual organ assemblages of one site match (i.e. coinciding assignment to the vegetation formations), the greater the validity of our approach. Such a comparison may also reveal incomplete, taphonomically biased floristic spectra of one or another organ assemblage if great discrepancies occur in one site.

Nineteen sites/levels that meet the above-described requirements were available. Six of them derive from the late early Miocene/early middle Miocene, one from the late Badenian (middle Miocene), ten from the early late Miocene, and two from the latest Miocene/early Pliocene. From five sites/levels, all three types of organ assemblages are available. Fourteen sites/levels yielded two different organ assemblages. In sum, 17 foliage-, 12 fruit-, and 14 pollen assemblages were evaluated and compared (Tabs 1, 3).

If a leaf assemblage includes fruit taxa, but their number is below the threshold of 10 zonal

taxa, the fruit taxa were generally included in the leaf assemblage to prevent loss of available information. For this study we made one exception: the fruit taxa for Weingraben, Teiritzberg, and Bełchatów below GTPN unconformity (for explanation see Worobiec 2003) – containing only 8 zonal taxa each – were evaluated separately. This better balanced the representation of the fruit record. The numbers of the organ assemblages in Figure 1 and Tables 1, 3 are derived from the database PANFLEURAS – Paleogene/Neogene floras of Eurasia, used in all our vegetation studies.

RESULTS

Of the 19 investigated sites/levels, 9 yielded both fruit and leaf assemblages. All of them (Weingraben, Randeck Maar, Berzdorf-Wiesa, Berzdorf-Kleinleipisch, Bełchatów below GTPN unconformity, Achldorf, Aubenham, Mataschen, Ruszów and Sośnica) provided a consistent assignment to the defined vegetation units (Tab. 3). Leaf and pollen assemblages were evaluated from 11 sites/levels. In only two cases (Hausruck/Kobernaussen and Inden Formation 7B) were the results obtained from the leaf and the pollen identical. Comparing fruit and pollen assemblages, our evaluation arrived at the identical vegetation formation in only one of 6 sites (Teiritzberg). The pollen assemblages clearly tended to point towards more intermediate (warmer and/or more humid) conditions than the leaf and fruit records (mixed mesophytic forest, broad-leaved evergreen forest). For example mixed mesophytic forest is deduced from the pollen record, while broad-leaved deciduous forest are inferred from the fruit or leaf record in Lipnica Mała, Bełchatów/KRAM 217, Sośnica, and Ruszów. Another example is mixed mesophytic forest (indicated by pollen) versus broad-leaved evergreen forest (leaf and fruit record) in Mataschen. In Weingraben, leaves and fruits indicated subhumid sclerophyllous forest, whereas pollen pointed to broad-leaved evergreen forest. The pollen record clearly often includes the far-distance influence. Additionally, low taxonomic resolution (to the family or generic level only) yielded less precise discrimination of the autecology in the pollen record (e.g. Berberidaceae, *Ligustrum*, *Lonicera*). The leaf assemblage from the

Inden Formation 7 F indicated broad-leaved deciduous forest, but the pollen pointed to broad-leaved evergreen forest. Only at Vilella (Spain) and Brjánslaekur (Iceland) did the pollen record indicate subhumid sclerophyllous forest. In the former case, the leaf record pointed to mixed mesophytic forest. A major discrepancy was evident between the leaf and pollen records in Brjánslaekur: leaves indicated broad-leaved deciduous forest (Denk et al. 2005), pollen subhumid sclerophyllous forest.

DISCUSSION

Here, we apply the IPR-vegetation analysis only on selected sites/levels containing different organ assemblages; this study therefore includes only few of the available plant sites from the different time intervals (compare Kovar-Eder et al. 2008). Nonetheless, the results reflect representative fragments of evolution in the Neogene European vegetation. The floral record from Weingraben and Randeck Maar indicates subhumid sclerophyllous forest based on the leaf and the fruit record at both sites, while the pollen indicates broad-leaved evergreen forest. The joint evaluation of the three organ assemblages at Weingraben and Randeck Maar ultimately yields subhumid sclerophyllous forest as the most probable zonal vegetation unit. This result is consistent with that derived from other sites in this part of Europe that yield only one organ assemblage, e.g. Parschlug (Austria), Eger-Tihamér (Hungary), Derching, Goldern (Germany) all late early to early middle Miocene in age. (Kovar-Eder et al. 2008).

In Teiritzberg, the fruit and pollen records indicate mixed mesophytic forest. The leaf record is too poor to be included, yielding few azonal taxa only (Kovar-Eder 1998). The fruit record, which we have included, is composed of more than two thirds azonal taxa; only 8 are zonal (Meller 1998). This may explain the discrepancy with the climate interpretation derived from different organism groups (Harzhauser et al. 2002); they correlated the Teiritzberg ecosystem to the middle Miocene climate optimum, for which broad-leaved evergreen forest or subhumid sclerophyllous forest are more reasonable vegetation formations.

Although floristically distinguishable (Czaja 2003), the fruit assemblages from two different

levels at Berzdorf are both representative of broad-leaved evergreen forest according to our evaluation. They are characteristic Younger Mastixioid floras that thrived in large parts of Europe during the early and early middle Miocene, and are known as far north as Jutland (Friis 1985). The leaf record of Děvinska Nová Ves (late Badenian) has been re-evaluated during this study after reinvestigating the original collection. In contrast to the results presented in Kovar-Eder et al. (2008), where the leaf record pointed to mixed mesophytic forest as the most probable vegetation unit, we now consider broad-leaved evergreen forest to be most probable. Note that the flora is poorly preserved and the number of taxa is rather low. The assignment to broad-leaved evergreen forest based on the leaf record reflects 30% in the BLE component, precisely the decisive threshold for this assignment. Děvinska Nová Ves is the only locality where the leaf record indicates slightly warmer conditions than the pollen record. The joint evaluation of the leaf and pollen assemblages, however, indicates mixed mesophytic forest as the most suitable vegetation formation; this corresponds with the earlier results (Kovar-Eder et al. 2008).

The floras of the early late Miocene and the latest Miocene/early Pliocene included here reflect the general Miocene climatic cooling. This is indicated by the IPR-vegetation analysis, which results in the assignment to mixed mesophytic forest (Achldorf, Inden Formation 7F, Vilella, Bełchatów/KRAM 217, Sońnica) and broad-leaved deciduous forest (Bełchatów below GTPN-unconformity, Hausruck/Kobernaussen, Aubenham, Ruszów). The flora of Mataschen deserves special attention: here, broad-leaved evergreen forest is the most likely vegetation formation (broad-leaved evergreen forest indicated by foliage and fruits, MMF by pollen, joint evaluation broad-leaved evergreen forest). The floristic spectrum and sociological aspects indicate a close relationship to the broad-leaved evergreen forest of SE Asia today. Thus, this flora is unique among the rich late Miocene plant record of Central Europe. Mataschen may offer insight into a climatically favourable niche and/or a favourable climatic fluctuation (Kovar-Eder & Hably 2006).

The flora from the Lower Rhine embayment is long known and reflects a climatically favourable refuge. This is documented by

a longer persistence of broad-leaved evergreen subtropical taxa than in more continental parts of Europe. The floral record from the Inden Formation is extremely rich but only for the levels Inden 7B and 7F it was possible to correlate different organ assemblages (Tab. 3). These levels, however, document this phenomenon quite well (broad-leaved evergreen forest derived from one leaf and two pollen assemblages). When, however, the leaf record is rather poor and includes a high percentage of azonal taxa (at Inden 7F, 10 of 24 taxa, i.e. almost 50%), then the IPR-vegetation analysis may be less reliable. The result is a “cooler” vegetation unit, in this case broad-leaved deciduous forest. For comparison, in the level Inden 7 B, the relation of zonal/azonal leaf taxa is 18.5/7.5 (71% zonal taxa). The pollen record from the Inden Formations A and C-E evaluated in Kovar-Eder et al. (2008) all indicate broad-leaved evergreen forest as most probable vegetation formation; there, the proportion of the BLE component varies between 30 and 37%. It is lowest in Inden Formation C (30%) and highest in level D (37%).

The interesting discrepancy between vegetation formations derived from the leaf (broad-leaved deciduous forest) and the pollen (subhumid sclerophyllous forest) assemblages from Brjánslaekur is certainly caused by the incompletely documented pollen assemblage (extremely low diversity of zonal pollen – 14 taxa only) and low taxonomic resolution (Akhmetiev et al. 1978). For the late Miocene of Iceland (today's latitude 65° N, similar in the Miocene) the zonal vegetation unit subhumid sclerophyllous forest is far from being realistic. Discrepancies have also been recognized when comparing this macro-record with pollen data from deep-sea drillings (Denk et al. 2005, Mudie & Helgason 1983).

Special attention should be given to the zonal herb component, which is documented in the fruit and pollen records but never in foliage assemblages. Only in Lipnica Mała and Bełchatów below GTPN unconformity (both fruit assemblages) does the ZONAL HERB component of all zonal taxa exceed 30% (32%). Note also that open woodland or xeric grasslands have not been derived for any of the localities investigated here. This corresponds with all the other Central European localities investigated in Kovar-Eder et al. (2008). Records of xeric grasslands are known

only from the Russian Plain, beginning from the early late Miocene. In southern parts of Europe, open woodlands are documented more commonly during the latest Miocene/early Pliocene.

The proportions of the BLD, BLE, and SCL+LEG components of zonal woody angiosperms and the proportion of the ZONAL HERB component of all zonal taxa constitute essential parameters to classify vegetation formations (Kovar-Eder et al. 2008). The IPR-vegetation analysis demonstrates that these components are fairly comparable among the different organ assemblages. It underlines the better agreement between the leaf and fruit record than between the latter two and the pollen record. Clearly, this new semi-quantitative evaluation based on the integration of the different plant organ records more satisfactorily interprets ancient vegetation than strictly quantitative approaches.

CONCLUSIONS

A team of experienced specialists in several disciplines is needed to obtain reliable data for vegetation maps of the Cenozoic. The methodology introduced here (the integrated-plant-record vegetation analysis – IPR-vegetation analysis) requires a well-determined and rich plant record based on all available plant organ assemblages (foliage, fruits, pollen). Older data should not be neglected, but revised and transferred to the state-of-the-art systems if possible.

Both high taxonomic resolution and high diversity of zonal taxa improve the results. These criteria are normally met to different degrees in the different organ assemblages, e.g. higher taxonomic resolution in the leaf and fruit record versus lower one in the pollen record, high diversity in the pollen and fruit record versus lower diversity in the leaf record.

The test of the IPR-vegetation analysis at sites/levels with at least two different plant organ assemblages corroborates the validity of this approach.

The geographical and stratigraphic distribution of recognized vegetation units provides an opportunity to follow climatic trends and gradients over large parts of Europe. Future

research will extend this possibility to other parts of Eurasia.

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APPENDICES

Assignment of the individual taxa to the different components (restricted to taxa documented in the here-investigated plant assemblages). Every taxon has the value 1. It may be assigned to one or more components. In the latter case the value 1 is split.

Appendix 1. Leaf taxa of pteridophytes, gymnosperms, and monocotyledons

Leaf taxa pteridophytes, gymnosperms, monocotyledons	Zonal								Azonal			
	CONIFER component	BLD component	BLE component	SCL component	LEG component	PALM component	DRY HERB component	MESO HERB component	FERN component	AZONAL HERB component	AQUATIC component	AZONAL WOODY component
Pteridophytes												
<i>Adiantum</i> sp.									1.00			
Filices									1.00			
Polypodiaceae									1.00			
<i>Pronephrium stiriacum</i>									1.00			
<i>Pteridium oeningense</i>									1.00			
<i>Salvinia mildeana</i>											1.00	
Gymnosperms												
<i>Abies steenstrupiana</i> , <i>Abies</i> sp.	1.00											
Abietoideae	1.00											
<i>Amentotaxus gladifolia</i>	1.00											
<i>Cephalotaxus pliocenica</i>	1.00											
<i>Cryptomeria anglica</i> , <i>C. rhenana</i>	1.00											
<i>Ginkgo adiantoides</i>		1.00										
<i>Glyptostrobus europaeus</i>												1.00
<i>Juniperus</i> sp.	1.00											
<i>Picea</i> sp.	1.00											
<i>Pinus hepios</i> , <i>P. taedaiformis</i>	1.00											
<i>Pinus</i> sp.	0.50											0.50
<i>Sequoia abietina</i>	0.50											0.50
<i>Taiwania paracryptomerioides</i>	0.50											0.50
<i>Taxodium dubium</i>												1.00
<i>Tetraclinis salicornioides</i>	1.00											
<i>Tsuga moenana</i> , <i>Tsuga</i> sp.	1.00											
Monocotyledons												
<i>Bambusa lugdunensis</i>										1.00		
<i>Limnobiophyllum expansum</i>											1.00	
Monocotyledoneae										1.00		
<i>Phragmites</i> sp.										1.00		
Poaceae indet.							0.33	0.33		0.33		
<i>Rhizocaulon zingiberoides</i>										1.00		
<i>Smilax hastata</i> , <i>S. protolancaefolia</i> , <i>S. sagittifera</i> , <i>S. weberi</i> , <i>Smilax</i> sp.			1.00									
<i>Typha latissima</i>										1.00		

Appendix 4. Fruit and seed taxa of monocotyledons

Fruit and seed taxa monocotyledons	Zonal								Azonal			
	CONIFER component	BLD component	BLE component	SCL component	LEG component	PALM component	DRY HERB component	MESO HERB component	FERN component	AZONAL HERB component	AQUATIC component	AZONAL WOODY component
<i>Acorellus distachyoformis</i>										1.00		
<i>Alisma crassicaarpum</i>											1.00	
Alismataceae											1.00	
<i>Aracispermum canaliculatum</i>										1.00		
<i>Butomus umbellatus</i> , <i>Butomus</i> sp.											1.00	
<i>Calamus daemonorops</i>						0.50						0.50
<i>Caldesia proventita</i> , <i>Caldesia</i> sp.											1.00	
<i>Carex acutiformis</i> , <i>C. conescendoidea</i> , <i>C. elongatoides</i> , <i>C. flagellata</i> , <i>C. globosaeformis</i> , <i>C. gracilis</i> , <i>C. hartauensis</i> , <i>C. lasiocarpa</i> , <i>C. limosioides</i> , <i>C. loliacea</i> , <i>C. marii-srodoniowiae</i> , <i>C. plicata</i> , <i>C. pilulifera</i> , <i>C. pseudocyperoides</i> , <i>C. szaferi</i> , <i>C. ungeri</i> , <i>Carex</i> sp.										1.00		
<i>Caricoidea jugata</i>										1.00		
<i>Cladiocarya europaea</i> , <i>C. lusatica</i> , <i>C. trebovensis</i>										1.00		
<i>Cladium oligovascularre</i> , <i>C. palaeomariscus</i> , <i>C. trilobatum</i> , <i>Cladium</i> sp.										1.00		
Cyperaceae										1.00		
<i>Cyperus borealis</i> , <i>C. glomeratus</i> , <i>C. leptodermis</i>										1.00		
<i>Damasonium</i> sp.											1.00	
<i>Dichostylis minor</i> , <i>Dichostylis</i> . sp.										1.00		
<i>Dulichium arundinaceum</i> , <i>D. marginatum</i> , <i>D. spathaceum</i> , <i>D. vespiforme</i>										1.00		
<i>Eichhornia tertiaris</i>											1.00	
<i>Epipremnites ornatus</i> , <i>E. reniculus</i> , <i>Epipremnites</i> sp.								1.00				
<i>Hydrocharis neogenica</i>											1.00	
<i>Juncus</i> sp.										1.00		
<i>Lemna</i> sp.											1.00	
<i>Lemnosperrum pistiforme</i>											1.00	
<i>Limnocarpus eseri</i>										1.00		
<i>Monochoria striatella</i>											1.00	
Monocotyledonae							0.5	0.25		0.25		
<i>Najas flexilis</i>											1.00	
<i>Pistia sibirica</i>											1.00	
<i>Potamogeton dravertii</i> , <i>P. dubnanensis</i> , <i>P. pseudonatans</i> , <i>P. nochtensis</i> , <i>P. piestanensis</i> , <i>P. wiesaensis</i> , <i>Potamogeton</i> sp.											1.00	
<i>Ruppia maritima miocenica</i> , <i>R. palaeomaritima</i>											1.00	
<i>Scirpus lusaticus</i> , <i>S. ragozinii</i> , <i>S. sylvaticus</i> , <i>Scirpus</i> sp.										1.00		
<i>Sparganium bessarabicum</i> , <i>S. camenzianum</i> , <i>S. crassum</i> , <i>S. haentzschelii</i> , <i>S. minimum</i> , <i>S. nanum</i> , <i>S. neglectum</i> , <i>S. noduliferum</i> , <i>S. pulchellum</i> , <i>S. pusilloides</i> , <i>S. ramosum</i> , <i>S. tanaiticum</i> , <i>Sparganium</i> sp.										1.00		
<i>Spirellea germanica</i>											1.00	
<i>Spirematosperrum wetzleri</i>										1.00		
<i>Stratiotes kaltennordheimensis</i> , <i>Stratiotes</i> sp.											1.00	
<i>Typha pliocenica</i> , <i>Typha</i> sp.										1.00		
<i>Urospathites cristatus</i> , <i>U. dalgasii</i> , <i>Urospathites</i> sp.										1.00		
<i>Xyris lusatica</i>										1.00		

Appendix 7. Continued

1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Carya</i> sp.		0.50										0.50	
Caryophyllaceae							0.60	0.20		0.20			
<i>Castanea</i> sp.		1.00											
<i>Castanea vel Castanopsis</i> sp.		0.50	0.50										
<i>Castanopsis</i> sp.			1.00										
<i>Celtis</i> sp.		0.50		0.50									
<i>Cercidiphyllum</i> sp.		0.50										0.50	
Chenopodiaceae							0.50	0.25		0.25			
<i>Cissus</i> sp.		0.33	0.33									0.33	
Cistaceae				0.70			0.30						
Clethraceae		0.33	0.33									0.33	
Compositae							0.33	0.33		0.33			
<i>Convolvulus</i> sp.								0.50		0.50			
Cornaceae		0.50	0.50										
Cornaceae – Araliaceae		0.50	0.50										
<i>Cornus</i> sp.		1.00											
<i>Corylopsis</i> sp.		1.00											
<i>Corylus</i> sp.		0.50										0.50	
<i>Craigia – Intratripolenites insculptus</i>		0.50										0.50	
Cruciferae								1.00					
Cyrtaceae		0.33	0.33									0.33	
<i>Decodon</i> sp.										1.00			
<i>Diervillea</i> sp.		0.50										0.50	
<i>Diospyros</i> sp.		0.50	0.50										
<i>Dipelta</i> sp.		1.00											
<i>Distylium</i> sp.			1.00										
<i>Elaeagnus</i> sp.		0.33	0.33	0.33									
Empetraceae												1.00	
<i>Engelhardia</i> sp.		0.50	0.50										
<i>Erica</i> sp.			0.33	0.33								0.33	
Ericaceae		0.25	0.25	0.25								0.25	
<i>Eucommia</i> sp.		1.00											
Fagaceae		0.40	0.40	0.10								0.10	
<i>Fagus</i> sp.		1.00											
<i>Fraxinus</i> sp.		0.50										0.50	
<i>Geranium</i> sp.								0.50		0.50			
<i>Hedera</i> sp.			0.50									0.50	
<i>Helianthemum</i> sp.				1.00									
<i>Hemiptelea</i> sp.		1.00											
<i>Illex</i> sp.		0.25	0.25	0.25								0.25	
<i>Illexpollenites clavopolatus</i>		0.25	0.25	0.25								0.25	
<i>Illexpollenites iliacus</i>		0.25	0.50	0.25									
<i>Illexpollenites margaritatus</i>		0.50										0.50	
<i>Intratropipollenites instructus</i> – Tiliaceae		1.00											
<i>Itea</i> sp.		0.50	0.50										
Juglandaceae		0.50										0.50	
<i>Juglans</i> sp.		1.00											
Labiatae							0.33	0.33		0.33			
Lamiaceae							0.33	0.33		0.33			
Lauraceae			1.00										
Leguminosae					0.75			0.25					
<i>Ligustrum</i> sp.		0.25	0.25	0.25								0.25	
<i>Liquidambar</i> sp.		0.50										0.50	
<i>Liriodendron</i> sp.		1.00											
<i>Lithocarpus</i> sp.			1.00										
<i>Lonicera</i> sp.		0.25	0.25	0.25								0.25	
Lythraceae		0.10						0.20		0.60		0.10	

