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Fossil plants as palaeoenvironmental proxies – some remarks on selected approaches

DIETER UHL

Palaeoecology, Institute of Environmental Biology, Faculty of Science, Utrecht University,
Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD Utrecht, The Netherlands;
e-mail: dieter.uhl@gmx.de

Present address: Villenstraße 13, 67433 Neustadt an der Weinstraße, Germany

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ABSTRACT. All methods and approaches used for the reconstruction of palaeoenvironmental and palaeoclimatic information have inherent shortcomings, limitations, and problems. Consequently there is no optimal, universally applicable and absolutely reliable technique for deriving these from fossil plants. Recent data on the preservation and taphonomic history of fossil plant remains (i.e., permineralized wood and charcoal), the anatomy and morphology of fossil leaves (i.e., cuticular adaptations and leaf physiognomy), as well as the interpretation of Nearest Living Relatives (NLR) are summarised. Although there is undoubtedly information loss through taphonomy, and taphonomical biases must be taken into account, especially when using quantitative methods, the analysis of taphonomic processes also may be used to obtain informations about the palaeoenvironment, whereas preservational modes may allow for the reconstruction of different and, sometimes complementary, palaeoenvironmental information. It is clear that the accuracy of quantitative methods, not only the accuracy of the NLR approach, decreases with an increasing age of a palaeoflora. Consequently, all quantitative methods may be applied most reliably to Cenozoic floras. Based on the results presented here, it is suggested that a combination of different, independent techniques and proxies should be used, not only to overcome the shortcomings, limitations and problems associated with the application of individual methods, but also to combine the advantages of individual methods. Such an integrated analysis of different proxies can lead to more reliable information about palaeoenvironmental conditions and improve our knowledge about the comparability and applicability of these methods.

KEY WORDS: palaeoclimate, palaeoenvironment, Carboniferous, Permian, Tertiary, preservation, taphonomy

INTRODUCTION

As early as the beginning of the 19th century scientists have recognized the potential of fossil plants as “keys” to past climates and environments (Chaloner & Creber 1990, Uhl & Mosbrugger 1999). Since then botanists and palaeobotanists have accumulated an ever increasing understanding of many aspects of the morphology, anatomy, and physiology of modern as well as fossil plant. Today, various methods and approaches are available for the reconstruction of palaeoenvironmental conditions (e.g. Jones & Rowe 1999). However, all these methods and approaches have their inherent shortcomings, limitations, and problems; in fact, there is no optimal, universally applicable and absolutely reliable technique for deriving palaeoenvironmental information from fossil plants (Birks & Birks 1980, Chaloner & Creber 1990, Mosbrugger & Schilling 1992, Mosbrugger & Utescher 1997, Wilf 1997). Hence, a multitude of approaches and techniques and continuous additional research are needed to improve our understanding of the various ways in which fossil plants can be used as palaeoenvironmental proxies.

Four types of proxies are used with fossil plants for the reconstruction of paleoenvironmental conditions. Each provide different, and sometimes complementary, information including:

– the taphonomy and preservation of plant remains

– their anatomy and morphology

– comparisons with the Nearest Living Relatives (NLR) of fossil plants, and

– (geo-)chemical data (stable isotopes, organic molecules, and their diagenetic derivatives)

The aim of the present synopsis is to highlight some of the potentials, but also to point out some of the limitations (especially in connection with taphonomic constraints) of selected approaches based on the first three proxy types. The stratigraphical focus of the selected examples is on the late Palaeozoic (the late Carboniferous and Permian) and the Tertiary, because these two intervals are of particular interest for our understanding of the influence of climatic and environmental changes on vegetation, particularly with regard to possible, anthropogenically influenced climate change (Steffen et al. 2004).

PRESERVATION OF FOSSIL PLANTS

The influence of taphonomy on palaeoenvironmental reconstructions has been studied and summarised repeatedly by various authors (Ferguson 1985, 1995, Spicer 1989, 1991, Gastaldo et al. 1995, 1996, Martín-Closas & Gomez 2004). Although there is undoubtedly information loss through taphonomy, an analysis of taphonomic processes also may lead to new insights in specific palaeoenvironmental conditions under which the plant material was preserved. One aspect, which is of special interest for the interpretation of palaeoenvironmental conditions, is the mode in which plant remains are preserved. Different preservational modes may contain different and, sometimes, complementary anatomical and morphological information which may help to improve not only taxonomic knowledge of individual taxa, but also knowledge of palaeoenvironmental conditions (Brown et al. 1994, Uhl & Kerp 2002a).

When fossil plants are examined from a distinct area and/or a distinct period, they are preserved in more than one mode. An example is the well studied Zechstein (Upper Permian) flora of Central Europe. The diversity of preservational modes has been documented recently, including some modes previously not known from the Central European Zechstein (Uhl & Kerp 2002a). Plants from this period have been preserved as pyritic and calcitic permineralizations, various forms of compressions (including „mummified“ leaves) and impressions, charcoal (fusain sensu Scott 1989, 2000), and authigenic cementations (Uhl & Kerp 2002a). Some of these preservational modes, which are not only known from the Zechstein but also from other periods of Earth’s history, as well as their potential for the reconstruction of palaeoenviromental conditions are treated in the following sections.

PERMINERALIZED WOOD REMAINS

The secondary wood produced by (pro-)gymnosperm and angiosperm trees is an important source for information about palaeoenvironmental and palaeoclimatic conditions, as far back as the late Devonian (Creber 1977, Creber & Francis 1999, Schweingruber 2001). The taphonomic history of permineralized wood remains record the conditions that occurred prior to, or even during, the process of permineralization (Noll et al. 2003, Uhl 2004b).

Permineralized wood remains long have been used for the reconstruction of selected palaeoenvironmental information (Creber & Chaloner 1985, Chaloner & Creber 1990, Creber & Francis 1999). A well known example is the presence or absence of growth interruptions (i.e. growth rings, Fig. 1A), which provide information about seasonally changing environmental conditions (Schweitzer 1962, Falcon-Lang 1999, 2003, Francis & Poole 2002) or even individual, short-term events like fire-scars as evidence of wildfires (Lageard et al. 2000, Swetnam & Baisan 2003) or non-seasonal changes of environmental conditions, like occassional droughts (Creber & Francis 1999, Falcon-Lang 2003). However, not only the occurrence of growth rings, but also detailed intra-ring analyses of radial cell diameters, can provide information about palaeoenvironmental conditions (Creber & Chaloner 1985, Creber & Francis 1999, Falcon-Lang 2000).

Apart from information about palaeoenvironmental conditions during growth, permineralized wood also can store information about processes and palaeoenvironmental conditions that may have influenced the early taphonomy prior to permineralization (Jones 1993, Brown et al. 1994, Barthel & Rößler 1997, Noll et al.

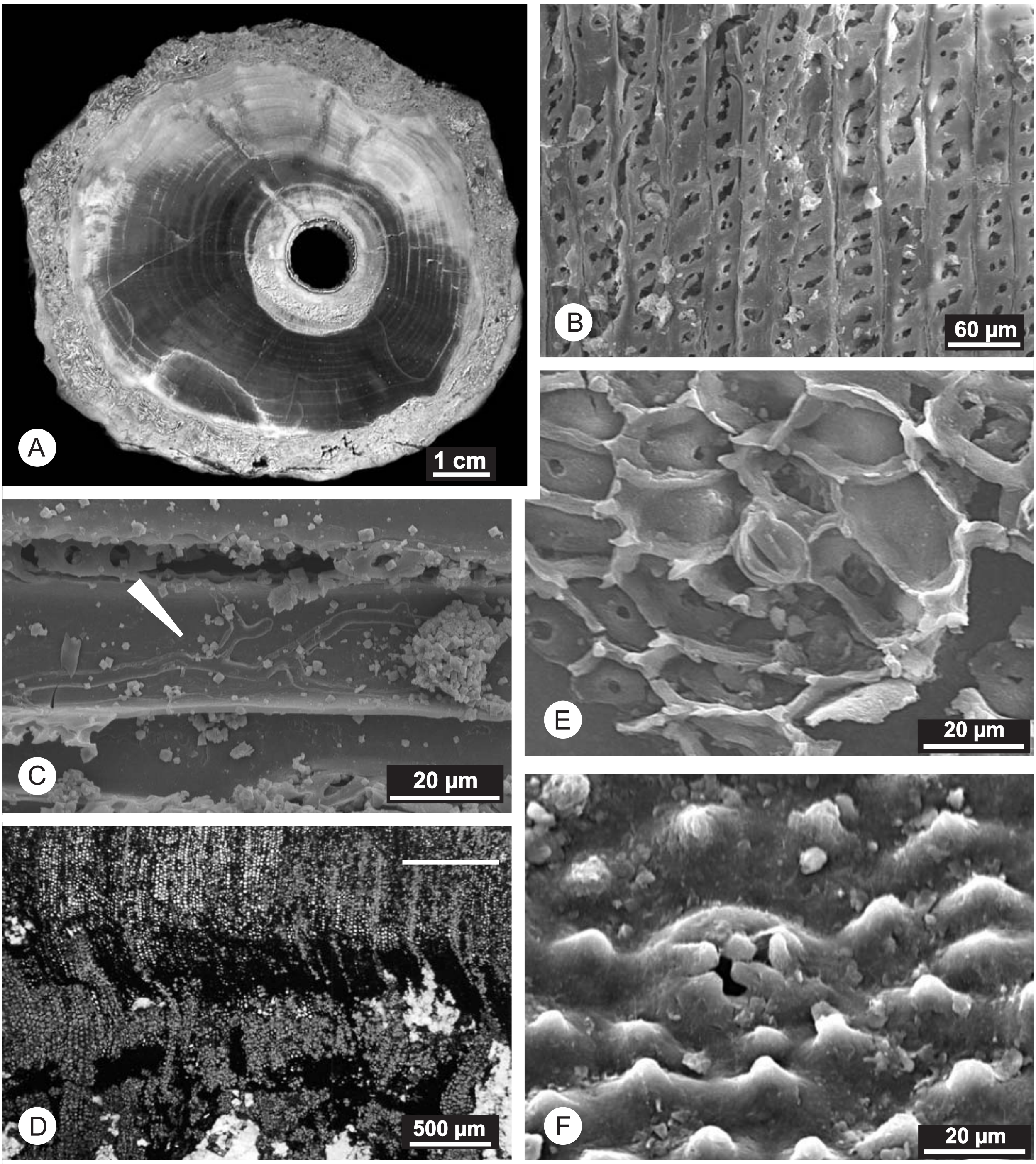

Fig. 1. **A**) Transverse section of silicified gymnosperm wood from the Rotliegend (Lower Permian) of Chemnitz-Hilbersdorf (Saxony, Germany), exhibiting prominent growth rings; **B**) SEM-image of charcoal from the Zechstein (Upper Permian) of Frankenberg/Geismar (NW-Hesse,Germany) exhibiting checked cell walls as a result of dessiccation prior to burial; **C**) SEM-image of charcoal with charred fungal hyphae (arrow) from the Upper Permian of Jordan; **D**) transverse section of pyritized wood from the Zechstein (Upper Permian) of Frankenberg/Geismar (NW-Hesse,Germany) showing pyritized and non-pyritized areas; **E**) SEM-image of a stomatal complex of the inner surface of a cuticle of *Peltaspermum martinsii* from the Zechstein (Upper Permian) of Frankenberg/Geismar (NW-Hesse, Germany), showing remains of the deeply sunken guard cells of a stoma; **F**) SEM-image of the outer surface with overarching papillae of *Peltaspermum martinsii* from the Zechstein (Upper Permian) of Frankenberg/Geismar (NW-Hesse, Germany)

2003, Uhl 2004b). Examples include insect galls or borings, the latter sometimes with in situ coprolites (Rößler 2001, Labandeira & Phillips 2002), the occurrence of fungal remains (Fig. 1C, Wilkinson 2003), anatomical alterations caused by dessiccation (Fig. 1B, Jones 1993, Uhl 2004b) or microbial decay (Kim & Singh 2000), as well as the occurrence of permineralized (i.e., silicified) charcoal as evidence of wildfires (Brown et al. 1994, Barthel & Rößler 1997, Noll et al. 2003, Uhl et al. 2004).

Besides the potential to store information about palaeoenvironmental conditions during growth and early taphonomic history prior to permineralization, permineralized woods also may store information about the processes and palaeoenvironmental conditions involved in the permineralization processes itself (Dietrich et al. 2000, 2001, Grimes et al. 2001, 2002, Noll et al. 2003, Uhl 2004b). Besides silica and carbonate, pyrite (FeS_2) and its oxidation products frequently are found in fossil remains (Fig. 1D, Kenrick 1999).

In many cases the formation of pyrite can be linked to high levels of bacteriogenic decay (Brown et al. 1994, Poole & Lloyd 2000). To date little work has been done about the actual processes involved in the pyritization of fossil plants, and most studies have dealt with plants from the Devonian (Kenrick & Edwards 1988, Tibbs et al. 2003), and Cenozoic (Allison 1988, Canfield & Raiswell 1991, Grimes et al. 2001, 2002). Experimental studies on the processes involved in the pyritization of extant plants have been carried out by Grimes et al. (2001, 2002).

Knowledge about these processes now can be used to reconstruct parts of the taphonomic history of pyritized plant material, which occurs frequently in the fossil record (Kenrick 1999). Well known examples include abundant pyritized fossils from the Eocene London clay (Allison 1988, Grimes et al. 2002) and the Zechstein deposits of NW-Hesse (cf. Ullmann 1803, Bronn 1828, Göppert 1850, Uhl & Kerp 2002a, Uhl 2004b, Fig. 1D). Although pyritized remains from the latter region have been known for more than 200 years (Waldin 1778), little work has been done to unravel the processes involved in the formation of these remains, the so-called “Frankenberger Kornähren”. Nevertheless, in a first taphonomic study of wood from NW-Hesse, it has been demonstrated that the taphonomic history of pyritized wood included severe dessication, microbial decay, and mechanical stresses – the latter probably during transport and burial of the wood (Uhl 2004b). A combination of all these processes may have played an important role during permineralization of this particular wood, and probably also during permineralization of the abundant pyritized plant remains, which have been found in the Zechstein of NW-Hesse.

Taken all the cited studies together, it now can be stated that there is no doubt, that detailed investigations of pyritized plant remains give us a wealth of information about taxonomically and evolutionary important anatomical details of the plants, as well as information about the processes involved in the formation of pyrite, although this proxy has so far largely been neglected by many authors.

MICRO AND MACRO MORPHOLOGY OF FOSSIL LEAVES

Leaves, are the primary photosynthetic organs of a plant and are optimally adapted to environmental conditions. Thus these organs react most sensitively to short-term environmental changes. The following synopsis focuses on the use of cuticles and leaf physiognomy as palaeoenvironmental proxies.

CUTICLE

The cuticle is a protective layer covering almost all surfaces of higher plants, consisting of the organic polymers cutin and/or cutan and an outer wax layer (Tegelaar et al. 1991, 1993). Cutan, a polymer of assumed diagenetic origin (e.g. Mösle et al. 2002), is highly resistent against (further) physical and (bio-) chemical degradation (Kerp 1990, Tegelaar et al. 1991, 1993). The cuticle displays cellular characteristics of the underlying epidermis in many plant taxa and these epidermal patterns are often specific for individual taxa. Hence, cuticles are important and widely used tools in plant taxonomy and certain cuticular characters also can be interpreted in terms of functional adaptations that can be used to extract palaeoenvironmental informations from fossil cuticles (Kerp 1990, Kerp & Barthel 1993, Kvaček & Walther 1988, Uhl 2004a).

Palaeoenvironmental adaptations include specific trichomes and tendrils which can be interpreted as evidence for a climbing and/or scrambling habit of a plant (Krings et al. 2003b) or as functional adaptations related to the defence against herbivorous arthropods (Krings et al. 2002, 2003a). Papillae on epidermal cells (Fig. 1F), deeply sunken stomata (Fig. 1E–F) and papillae which overarch the stomata (Fig. 1F) are other cuticular traits that may be interpreted as being effective in reducing transpirational stress and are found more often in taxa from arid than from mesic or even humid environments. These features have been observed from a number of taxa from the Upper Permian of central and southern Europe (Gothan & Nagalhard 1922, Schweitzer 1962, Poort & Kerp 1990, Uhl & Kerp 2002b, Uhl 2004a). Recently, Thévenard et al. (2005) provided an overview of such xeromorphic adaptations, including cuticular adaptations, in Mesozoic gymnosperms. However, it is difficult to quantify most of these adaptations and it is only possible to get qualitative information about palaeoenvironmental conditions from observations of such adaptations. Other cuticular charcteristics are the stomatal density (SD) and the stomatal index (SI), which may be quantified more easily (Salisbury 1927, Beerling 1999, Poole & Kürschner 1999).

SD and SI are of special interest with regard to changes in atmospheric CO_2 concentrations over the geological past, and have attracted a considerable amount of scientific interest in the last decades (cf. Royer 2001). This is due to the fact that CO_2 is an important, anthropogenically influenced, greenhouse-gas (Houghton et al. 1995). It has been demonstrated by many authors that SD and SI are negatively correlated with atmospheric CO_2 concentrations in many extant plants (Woodward 1987, Woodward & Bazzaz 1988, Beerling & Royer 2002). Correspondingly, changes of SD and SI in fossil cuticles are considered to represent excellent proxies for changes of CO_2 concentrations in the geological past, not only in the Cenozoic (Beerling 1993, van der Burgh et al. 1993, Kürschner et al. 1996, Kürschner 1997, Retallack 2001, 2002, Royer et al. 2001, Roth-Nebelsick et al. 2004), but also in the Mesozoic (McElwain et al. 1999, Retallack 2001, 2002) and even the Palaeozoic (McElwain & Chaloner 1995, 1996, McElwain 1998, Edwards et al. 1998, Cleal et al. 1999, Retallack 2001, 2002). However, some problems remain especially for most Mesozoic and Palaeozoic taxa which have no really close living relatives (same genus or species), which have to be solved before SD and SI may be used as reliable palaeoatmospheric proxies in the Pre-Cenozoic.

One of these problems is the natural variability of SD and SI in fossil plants. It is well known from studies on modern angiosperms, that the variability of both parameters can be relatively large, even within individual leaves (Poole et al. 1996, 2000, Bruschi et al. 2003). However, up to now systematic investigations on the variability of these parameters in most Mesozoic and Palaeozoic plants are rare, to date. Apart from some taxonomic studies in which larger numbers of cuticles have been investigated, mostly in order to use SD as a taxonomic character (Clement-Westerhof 1984), only few data are available on the variability of SD and SI in Mesozoic and Palaeozoic plants. Nevertheless, these studies show that SD and SI may vary considerably not only within individual leaves, but also within and between individual taphofloras (Uhl & Kerp 2005), probably depending on external parameters, such as (micro-)climatic and edaphic conditions. The data also suggest that taphonomic biases (i.e. fragmentation of individual needles, mixing of material from different micro-habitats, mixing of different taxa, time averaging) have to be taken into account when stomatal densities and indices of fossil plants are to be used for the reconstruction of palaeoatmospheric CO_2 concentrations. This is especially true when only a small sample size is available for investigation (Uhl & Kerp 2005).

An additional problem has to be taken in account with many Palaeozoic and Mesozoic plants: SD and SI in plants with stomata arranged in distinct patterns (many conifers with stomata arranged in rows) can not be used as potential indicators of atmospheric CO_2, due to the disturbing effects of these patterns (McElwain et al. 2002, Kouwenberg et al. 2003). Unfortunately this type of stomatal arrangement is present in many Palaeozoic and Mesozoic plants, especially conifers and other gymnosperms.

As a consequence the reliability of quantitative estimates of atmospheric CO_2 concentrations during the Palaeozoic and probably also the Mesozoic obtained by several authors during the last decade must be reconsidered (McElwain & Chaloner 1995, 1996, McElwain 1998, McElwain et al. 1999, Retallack 2001, 2002). In most of these studies only a small number of cuticles (in many cases only small cuticle fragments) have been used for determination of SD and SI. Considering the caveats based on the data from modern angiosperms

(Poole et al. 1996, 2000, Bruschi et al. 2003) as well as Palaeozoic conifers (Clement-Westerhof 1984, Uhl & Kerp 2005) the reliability of atmospheric CO_2 values estimated from these data must be questioned.

LEAF PHYSIOGNOMY

The fact that external forces may influence certain leaf physiognomic traits is known since the end of the 19th century (Stahl 1880, 1883, Schimper 1898). However, Bailey and Sinnott (1915, 1916) were the first to quantify the correlations between a certain leaf physiognomic trait and an external forcing factor. These authors demonstrated that within woody dicotyledonous angiosperms the type of leaf margin is strongly correlated with the mean annual temperature (MAT), entire margined taxa predominate in the tropics, and taxa with non-entire (toothed) margined leaves predominate in cold-temperate regions. A fact that has been corroborated by many additional studies since then (Wolfe 1979, Wilf 1997, Greenwood et al. 2004, Traiser et al. 2005). Besides the general botanical interest in such studies, leaf physiognomy represents also a widely used tool for palaeo-environmental and climatic studies. A variety of different methods based on leaf physiognomy are used (Wolfe 1979, 1993, Kovach & Spicer 1996, Wilf 1997, Wiemann et al. 1998, Jacobs 1999, 2002, Wolfe & Spicer 1999, Kowalski 2002). Although several attempts have been made to recognize the causal relationships between environmental parameters and leaf physiognomic traits (Roth et al. 1995, Baker-Brosh & Peet 1997, Sisó et al. 2001, Royer et al. 2005, Royer & Wilf 2006), they are not yet fully understood (Boyd 1994, Jordan 1997).

One of the problems concerning the applicability of many leaf physiognomic methods, is the fact that the relationships between leaf physiognomy and climatic parameters (i.e. leaf margin type and MAT) may not differ only in some special habitats within a larger region, like riparian forests (Burnham et al. 2001, Kowalski & Dilcher 2003), but also between different regions throughout the world (Wilf 1997, Kowalski 2002, Greenwood et al. 2004, Traiser et al. 2005). Although today there seems to be a global evolutionary convergence of leaf physiognomy in response to the selection of temperature in mesic habitats, there are also some differences between different regions worldwide, which may be attributed to differences in vegetation and climate history (Greenwood et al. 2004). Probably such differences also can be found in fossil floras, although this problem has been neglected to date. Interestingly the observed evolutionary convergence of leaf physiognomy in response to climate can not only be found in angiosperms, but also in late Palaeozoic gigantopterids (Glasspool et al. 2004, 2005).

Taphonomic biases and sampling techniques are problems which may have an impact on the use of leaf physiognomic methods (Boyd 1994, Jordan 1997, Wilf 1997, Wolfe 1993, 1995), although little work has been done so far on this subject (Burnham 1989, Greenwood 1992, Uhl et al. 2003, Traiser et al., 2005, Spicer et al. 2005). As expected, leaf physiognomic techniques, like leaf margin analysis, are influenced by low numbers of taxa and low specimen numbers (Uhl et al. 2003), although multivariate techniques like CLAMP seem to be less affected than the univariate leaf margin analysis (Uhl et al. 2006). This is in full agreement with previous assumptions to exclude samples with less than 15 (Povey et al. 1994) or even 30 taxa (Wolfe 1985) from any leaf physiognomic analysis.

Considering the fact that not only species richness, but also the total sample size may influence the reliabilty of leaf physiognomic studies (Uhl et al. 2003), there are uncertainties in some published palaeoclimate reconstructions based on leaf physiognomic analyses, which are based on small sample size or which provide no information about the sample size at all. In fact, many published applications of leaf physiognomic methods do not include information on sample size (Povey et al. 1994, Davies-Vollum 1997) or the sample size used is well below 1000 specimens [Wiemann et al. 1998 (>500), Gregory 1994 (177), Gregory-Wodzicki 1997 (537)], a threshold suggested on the data presented by Uhl et al. (2003). Presumably, previous applications without sampling control may underestimate or overestimate the proportion of entire-margined leaves and, hence, MAT, depending on taphonomic effects. Therefore, future applications should be restricted to those leaf floras for which sample size is known to be sufficient, which amongst other factors, depends on the original species-richness of the source flora (Burnham 1989, 1994a, b, Burnham et al. 1992).

Some of the taphonomic effects on leaf physiognomic techniques may be significantly reduced in new collections, by sampling as many taxa, facies types, and the longest possible transect per stratigraphical level as possible, as suggested by Wilf (1997). However, for old collections, especially from localities that are no longer accessible, as it is often the case with "classical" localities in Europe, this may not be practicable. Many of these "classical" localities, whose floras have been described during the 19th or even the 20th century, were related to the commercial exploitation of mineral resources like coal, lignite or limestone. In many cases, the corresponding quarries or mines long since have been abandoned and the fossil-bearing strata are no longer accessible. Well known examples are the Oehningen limestone quarries (Heer 1855, 1856, 1859), and several large, open cast lignite mines in Germany (Mai & Walther 1978, 1985). In these cases, other solutions have to be found to enable extractation of reliable information about selected palaeoclimatic parameters on the basis of fossil plants. These solutions may include the development of new calibration datasets for the use of uni- and multivariate leaf physiognomic approaches (Greenwood et al. 2004, Traiser et al. 2005), as well as the constant improvement of methods based on the nearest living relative (NLR) approach.

NEAREST LIVING RELATIVES (NLR)

Apart from the taphonomy and preservation of fossil plants, as well as anatomical and morphological adaptations of different plant organs, information about palaeoenvironmental conditions can be obtained by using the NLRs of fossil plants (where applicable). The NLR approach is one of the oldest palaeoenvironmental techniques (cf. Chaloner & Creber 1990, Mosbrugger 1999). Qualitative information has been derived from comparisons with assumed NLRs of fossil plants since the true nature of fossils was recognized by early natural philosophers (Waldin 1778). The first true quantitative reconstructions based on the NLR approach occurred in the middle of the 19th century by the Swiss palaeontologist Heer (1855, 1856, 1859, 1868) and since this time a variety of modifications of the NLR aproach has been applied to fossil plants. For a detailed overview of the NLR approach and its application to fossil floras see Mosbrugger (1999).

However, it should be clear that the accuracy of NLR methods decreases with the increasing age of a palaeoflora and, consequently, the NLR approach may be applied most reliably to Cenozoic floras (Mosbrugger 1999). Many Cenozoic plant taxa can be compared directly to extant taxa from the same family or even genus. Hence, the taxonomic composition of a taphoflora can provide information to which modern vegetation type the fossil vegetation may have been similar. This knowledge allows for quantitative statements about palaeoclimatic conditions (Wolfe 1985, Mai 1995). However, the climatic resolution of such an approach is not very high because most vegetation types have a rather wide climatic tolerance (Mosbrugger 1999). Nevertheless, this method has been used widely for palaeoclimate reconstructions in the Tertiary (cf. Mai 1995, Kvaček & Walther 2001). Although it is not always possible to reconstruct truly quantitative data with such an approach, it is possible to reconstruct the general type of climate (sensu Köppen 1923) under which a flora lived.

One of the more sophisticated methods based on NLRs is the Coexistence Approach (CA) developed by Mosbrugger and Utescher (1997) and applied repeatedly for Tertiary palaeoclimate reconstructions in Europe (Pross et al. 1998, Utescher et al. 2000, Kvaček et al. 2002, Uhl et al. 2003, 2006, Roth-Nebelsick et al. 2004), as well as East Asia (Liang et al. 2003). The CA determines for all taxa of a given fossil flora the NLRs and their climatic tolerances (i.e., minimum and maximum value) with respect to various climate parameters including mean annual temperature (MAT) or mean annual precipitation (MAP). The coexistence intervals are determined for these climate parameters within which all (or at least a great number of) NLRs of the fossil plants can coexist (cf. Fig. 2). It is assumed that the coexistence intervals best describe the palaeoclimate of the fossil flora (for a more detailed discussion of the general advantages and disadvantages of the CA, as well as other methods based on the NLR approach see Mosbrugger 1999).

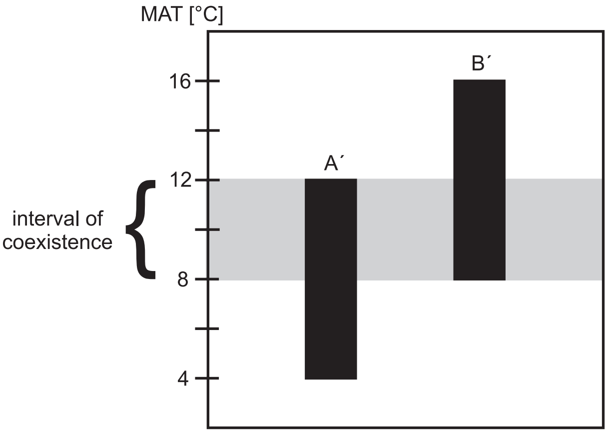

Fig. 2. Illustration of the basic principle of the Coexistence Approach. A´ and B´ are the NLRs of the fossil taxa A and B. Black bars represent the MAT ranges tolerated by A´ and B´. In the MAT interval between 8°C and 12°C both extant taxa can (at least theoretically) coexist. This interval of coexistence is considered to be the best estimate for MAT of a fossil flora with the fossil taxa A and B (redrawn from Mosbrugger & Utescher 1997)

Although CA and various leaf physiognomic techniques frequently have been used for palaeoclimate reconstructions (Gregory 1994, Wolfe 1995, Gregory-Wodzicki 1997, Mosbrugger & Utescher 1997, Pross et al. 1998, Wiemann et al. 1998, Utescher et al. 2000, Kvaček et al. 2002, Liang et al. 2003, Mosbrugger et al. 2005), direct comparisons based on the same source-floras are very rare to date (e.g. Mosbrugger & Utescher 1997, Utescher et al. 2000, Kvaček et al. 2002, Liang et al. 2003, Uhl et al. 2003, 2006). In most of these examples leaf physiognomic techniques provided temperatures that are considerably cooler than CA estimates. Additional data from independent sources often support the estimates derived from CA rather than those derived from physiognomic techniques (Mosbrugger & Utescher 1997, Kvaček et al. 2002, Uhl et al. 2006). Nevertheless, in a few cases CA and leaf physiognomic techniques produced temperature estimates that agreed well with each other (Uhl et al. 2003, Roth-Nebelsick et al. 2004).

Recently, the robustness of the CA against taphonomic biases has been tested (Uhl et al. 2003). In contrast to several leaf physiognomic methods, results based on the CA were less influenced by taphonomic biases. A widening of the intervals of coexistence has been observed in samples with rather low numbers of taxa, and such biases are similar to the results obtained by other authors (Pross et al. 1998). Such behaviour was predicted by Mosbrugger (1999) based on theoretical considerations. Another example for this dependency of CA on taxonomic richness, but also for the decreasing accuracy with an increasing age is given in Figure 3. These results again demonstrate that the CA still remains one of the most robust methods for the estimation of selected palaeoclimate parameters derived from Tertiary floras (cf. Mosbrugger 1999). However, due to taxonomic limitations of the underlying database, the application of this (and other NLR methods) may be restricted to certain geographic areas or stratigraphic intervals at the moment.

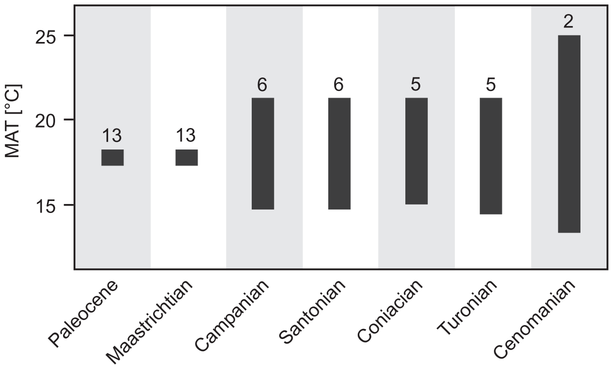

Fig. 3. CA estimates of mean annual temperature (MAT) intervals for carpofloras from the Paleoecene and Cretaceous of Central Europe (based on taxonomical data from Knobloch & Mai 1986). With increasing age the number of useable NLRs (on the generic level) that can be included in a CA analysis (number of taxa indicated above interval of coexistence) decreases and consequently the width of the interval of coexistence increases

Another advantage of the CA is the fact that it can be used with palaeofloristic data (i.e. reliable taxa lists of leaves, fruits/seeds or pollen/spores) from the literature to estimate palaeoclimatic data. Although it is possible in some cases to use the literature for leaf physiognomic analysis (cf. Uhl et al. 2003), published monographs on fossil leaf floras do not include all leaf physiognomic characters in many cases, which may be needed for such an analysis. Hence, the CA (as well as other quantitative methods based on NLRs) may be preferred to quantitative leaf physiognomic methods, when only literature is available for analysis. Such a uniform dataset may be necessary to compare the results of climate models with proxy data on a continental or even global scale (Mosbrugger & Schilling 1992, Steppuhn 2002, Micheels 2003).

CONCLUSIONS

Although various methods for the reconstruction of palaeoclimatic and palaeoenvironmental information have been developed during the last 200 years, only a few existing methods are able to produce reliable, quantitative estimates for selected palaeoclimatic and palaeoenvironmental parameters. Most information that can be extracted from fossil plants is qualitative. However, even this qualitative information can contribute significantly to our understanding of the interactions between fossil plants and their environments in many cases.

Different preservational modes may allow for the reconstruction of different, and sometimes complementary palaeoenvironmental information. An analysis of anatomical and morphological adaptations provides information about palaeoenvironmental conditions during growth (growth rings within wood, cuticular adaptations, stomatal density and –index), whereas an analysis of their preservational state can give us information about palaeoenvironmental conditions and events that occurred during the transfer of these remains from the biotic to the abiotic realm. However, there is undoubtedly an information loss through taphonomic processes, and taphonomical biases must be taken into account, especially when using quantitative methods. Depending on the method, these taphonomic biases may have more or less considerable influence on the results obtained by individual techniques (e.g. NLR versus leaf physiognomy).

It should be clear that the accuracy of these methods, not only the accuracy of the NLR approach, decreases with an increasing age of a palaeoflora. Consequently, all quantitative methods may be applied most reliable to Cenozoic floras.

Based on the overview presented here, it is suggested that a combination of different, independent techniques and proxies is needed, not only to overcome the shortcomings, limitations, and problems associated with the application of individual methods, but also to combine their advantages. Such a procedure can lead to more reliable information about palaeoenvironmental conditions, improving our knowledge about the comparability and applicability of individual methods.

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