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Land plant diversity in selected latest Pennsylvanian?–Permian deposits from the Saar-Nahe Basin (SW-Germany) and the German Zechstein Basin³

(Figs 1–5; Tab. 1)

Abstract. For the first time, a quantitative analysis of the land-plant diversity during deposition of the Rotliegend (latest Pennsylvanian–Early Permian; Gzhelian – Sakmarian) of the Saar-Nahe basin (SW-Germany) and the Zechstein (Late Permian; Wuchiapingian) of the German Zechstein basin is given. A study of six taphofloras indicates that regionally not only the overall species richness declined, but also the diversity as represented by individual taphofloras. This decline occurred after the deposition of the Upper Rotliegend (Asselian–Sakmarian), leading to an extremely low species richness during the deposition of the Zechstein. Besides taphonomic differences between the individual localities considered here, possible reasons for the observed lower diversity include most probably a climatic deterioration/aridisation due to tectonic northwards movement of Pangaea.

As compared to the Late Pennsylvanian and the Early Permian, this climatic deterioration together with a contemporaneous decrease in topographic relief due to erosion and collapse of the Variscan Orogen, may also be the main reason for a decrease in habitat diversity and finally the decrease in land-plant diversity. However, based on the data presented here it is difficult to judge whether the observed regional diversity decline at individual localities can be generalized for the entire Euramerican floral province. Nevertheless, it can be concluded from other sources, that there are large gaps in the palaeobotanical record of this region, which may lead to underestimation of the “true” land plant diversity during this period within the Euramerican floral province.

Key words: land-plant diversity, Euramerica, Germany, Pennsylvanian, Permian.

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3 Accepted for publication on February 2, 2008.

INTRODUCTION

The Late Palaeozoic represents a time interval characterized by vast climatic and vegetational changes, that may be considered as analogues of those in the Late Quaternary (Gastaldo *et al.*, 1996). Climatically this period was characterized by two ice-ages, with major glaciations in the Late Westphalian (Moskopian) and the Early Permian (Sakmarian) (Frakes *et al.*, 1992). From the Stephanian (Kazimovian–Gzhelian) onward the climate became generally more seasonal and drier (DiMichele & Aronson, 1992; Phillips & Peppers, 1984) and during the Permian drier climates became prominent also in tropical lowlands and intermontane areas (Retallack, 1995).

Due to these climatic changes it is of considerable interest to know how land-plant diversity developed during this period and to what extent diversity changes may be interpreted as responses to changing climatic and environmental, but also palaeogeographic conditions (Rees, 2002). So far quantitative studies on Permian ecosystems, especially from the Euramerican floral province, are still largely missing. Although several previous studies included qualitative interpretations of the development of plant diversity in the Permian of Euramerica (Kerp, 1996, 2000), up to now only few studies have yielded semi-quantitative interpretations, either directly based on fossil assemblages combined from different localities (Schweitzer, 1962, 1986) or using data compiled from the literature (Haubold & Schaumberg, 1985). Two exceptions are the studies by Rees (2002) and Ziegler *et al.* (2002). Rees (2002) investigated quantitative changes in generic diversity throughout the Permian and the Triassic based on data from the literature. This author found that the development of plant diversity, as represented by genus diversity, differed between the floral provinces. In accordance with previous qualitative studies (Kerp, 1996, 2000), Rees (2002) found an almost continuous decrease in genus diversity throughout the Permian within the Euamerican floral province. However, such an approach gives a rather crude picture, and it is still difficult to reveal the influence of local climatic or environmental conditions and moreover taphonomic disturbances on the observed diversity patterns. For many Permian plants we are facing the additional problem of morphogenera of unknown systematic affinity (e.g., *Culmitschia* amongst the conifers [Visscher *et al.*, 1986; Mapes & Rothwell, 1991], or *Rhachiphyllum* amongst the pteridosperms [Kerp, 1988]), whose representatives may in fact represent several natural genera. In such cases, the use of morphospecies may give a less biased view of plant diversity (i.e. species richness). However, quantitative studies based on the (morpho-) species content of individual macrofloras from the Permian are largely missing, not only for the Euramerican floral province, but also on a global scale. An exception is the study by Ziegler *et al.* (2002), who investigated the development of land-plant diversity from the Lower Mississippian (Tournaisian) up to the Early Permian (Kungurian) of the Maritimes basin in Canada, based on genera and species counts. However, their data on Permian floras from this basin are scarce and no clear diversity trend could be observed within the Early Permian of this region.

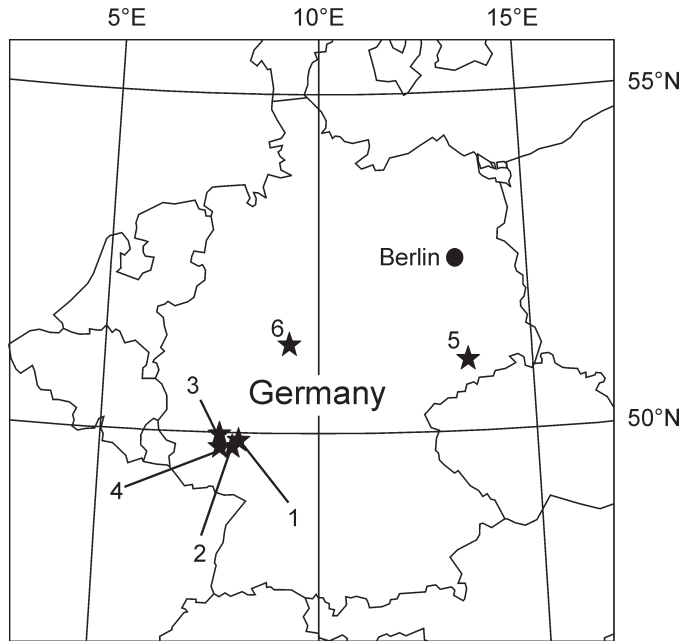


Fig. 1. Map showing the locations of the six Late Palaeozoic taphofloras considered in the present study

The current paper presents a detailed quantitative analysis of selected taphofloras from the latest Palaeozoic (latest Pennsylvanian?–Late Permian) of the Euramerican floral province on the highest taxonomic level available (i.e. natural and morpho-species). The floras investigated here come from the Rotliegend (Late Pennsylvanian?–Early Permian; Gzhelian?–Sakmarian) of the Saar-Nahe Basin in SW-Germany, as well as the Zechstein (Late Permian, Wuchiapingian) of NW-Hesse and Thuringia (Germany) (Fig. 1).

As the only quantitatively known floras from the latest Palaeozoic (latest Pennsylvanian?–Late Permian) occur in the Saar-Nahe Basin and the German Zechstein Basin we restricted our studies to these areas.

REGIONAL FRAMEWORK

Within the Saar-Nahe Basin in SW-Germany, continental sediments have been deposited which more or less continuously span the Pennsylvanian–Permian transition and parts of the Early Permian (Gzhelian–Sakmarian). The latest Pennsylvanian (latest Gzhelian) to Early Permian (Asselian–Sakmarian) deposits of this area have been assigned to the lithostratigraphically defined Rotliegend group (German Stratigraphic Commission, 2002). Due to a long history of research (Kerp & Fichter, 1985), the macroflora from this basin is regarded as one of the best known regional Euramerican floras from this period (DiMichele & Hook, 1992). Unfortu-

nately, not all sediments from the Rotliegend of the Saar-Nahe Basin are equally rich in plant fossils. During the Lower Rotliegend (Glan Subgroup; uppermost Gzhelian/Asselian?) fossil plants have been more frequently preserved than in the Upper Rotliegend (Nahe Subgroup; Asselian – Sakmarian). This trend, that may be climatically induced (Stapf, 1990, 1997), has led to an increased patchiness of plant bearing localities in the Upper Rotliegend as compared to the Lower Rotliegend (Uhl *et al.*, 2004). Rotliegend deposits of this basin show a general trend from floras dominated by basinal elements towards floras dominated by hinterland elements together with a general trend in facies development (Lützner, 1988; Kerp, 2000). In contrast to the Lower Rotliegend with many localities with quite abundant and diverse macrofloras (Kerp & Fichter, 1985; Kerp *et al.*, 1990; Lausberg & Kerp, 2000; Uhl & Heidtke, 2003), the Upper Rotliegend generally contains few fossils (Kerp, 1996) and even less localities yielding diverse macrofloras have been discovered so far (Schuster, 1908; Kerp & Fichter, 1985; Kerp, 1988; Lausberg, 2002; Lausberg *et al.*, 2003, Kerp *et al.*, 2007a, b).

Plant bearing localities from the Upper Permian of Europe are even more rare than from the Upper Rotliegend of the Saar-Nahe Basin (Kerp, 2000; Uhl & Kerp 2002a, b). The majority of plant bearing deposits known so far, are from the marine Zechstein (Wuchiapingian) deposits of England, Germany and Poland (Schweitzer, 1962, 1986; Ullrich, 1964; Haubold & Schaumberg, 1985; Kerp, 1996, 2000; Uhl and Kerp, 2002a; Uhl, 2004b). Most plant remains from these deposits have been discovered due to the mining of copper-rich deposits, mainly in the 19th century, but also during parts of the 20th century (Haubold & Schaumberg, 1985; Uhl & Kerp, 2002a).

Most Zechstein floras have a very similar taxonomic composition, with conifers dominating at all localities currently known (Haubold & Schaumberg, 1985; Schweitzer, 1986). Of special interest for palaeobotanical studies are deposits from NW-Hesse, as well as Thuringia, because of their outstanding preservation (Uhl & Kerp, 2002a, b, 2005; Uhl, 2004b). Many Zechstein plants from these areas have yielded cuticles, which enable us to give reliable taxonomic determinations for these plants (Gothan & Nagalhard, 1922; Ullrich, 1964; Uhl & Kerp, 2002a, b, 2005), whereas in most other areas which yielded Zechstein plants only gross-morphological characters can be used for the (often unreliable) determination of such remains (Weigelt, 1928; Brandt, 1997). Generally fossil floras from the Zechstein seem to be of rather low taxonomic diversity (Schweitzer, 1962, 1986; Ullrich, 1964; Haubold & Schaumberg, 1985; Uhl & Kerp, 2002a), even when compared to many Rotliegend floras from the Saar-Nahe Basin and the total number of taxa known from the Zechstein (Schweitzer, 1986) is rather low in comparison to the Rotliegend (Kerp & Fichter, 1985). However, also the number of different depositional settings known from the Zechstein is comparatively low and so far no quantitative comparison between individual localities with comparable taphonomic histories exists.

The climate during the deposition of the Zechstein has been interpreted as being even more arid in Central Europe than during the Upper Rotliegend (Kerp, 1996,

2000; Rees, 2002; Fluteau *et al.*, 2001), although recent interpretations suggest more humid conditions due to the ingression of the Zechstein sea (Schneider *et al.*, 2006). Nevertheless most authors correlated the low taxonomic diversity (i.e. species richness) of the Zechstein palaeofloras with unfavourable climatic conditions in this area (Schweitzer, 1962, 1986; Kerp, 1996, 2000; Rees, 2002). However, so far no comprehensive quantitative study dealing with this question has been performed, which takes into account, that there is less material known from the Zechstein than from many Rotliegend localities.

However, in both, the Rotliegend of the Saar-Nahe Basin and the Zechstein of NW-Hesse and Thuringia, some localities yield abundant plant remains, which allowed for the first time to quantitatively analyse at least some individual palaeofloras from the entire Euramerican floral province. Based on six localities from Germany, the current study compares adpression (*sensu* Shute & Cleal, 1987) floras preserved within lacustrine and marginal marine sediments of Late Palaeozoic (i.e. latest Pennsylvanian?–Late Permian) age. As already stated by Rees (2002), such a study can help elucidate some of the effects of climate, geography and preservation bias on our evaluation of the regional diversity in Central Europe during the Latest Palaeozoic.

LOCALITIES

Rotliegend (Late Pennsylvanian–Early Permian; Gzhelian – Sakmarian)

The Rotliegend material studied here originates from four different localities in the Saar-Nahe Basin in SW-Germany (Figs 1, 2). This basin is one of the largest and best exposed Late Palaeozoic intramontane basins within the Variscan orogenic belt in Central Europe (Schäfer & Korsch, 1998). The surface extension of this half graben structure is about 100 km (SW–NE) × 40 km (NW–SE) (Henk, 1993; Stapf, 1990). The basinfill is purely continental (Schäfer, 1986). Its deposition started in the Early Westphalian (Henk, 1993) and lasted at least until the Early Permian (Sakmarian) without considerable hiatuses from the Barruelian (Kasimovian) upwards. According to Boy and Schindler (2000), there is no discordance or unconformity between the Late Pennsylvanian and the Early Permian in the Saar-Nahe Basin.

The Rotliegend strata (Late Pennsylvanian–Early Permian) of the basin are divided into the Glan Subgroup (~ Lower Rotliegend; Gzhelian/Asselian?) and the Nahe Subgroup (~ Upper Rotliegend; Asselian–Sakmarian) (Boy & Fichter, 1982; German Stratigraphic Commission, 2002; Menning *et al.*, 2005). Schäfer and Korsch (1998) as well as Schäfer (2005) correlated the base of the Nahe Subgroup with the Pennsylvanian–Permian boundary, but such an interpretation is not in agreement with absolute datings of volcanic marker beds (Menning *et al.*, 2005). At the moment, the precise lithostratigraphic position of the Pennsylvanian–Permian boundary within the Rotliegend of the Saar-Nahe Basin is still under discussion, due to inconsistencies with absolute datings of different volcanic marker beds within the Glan Subgroup (see discussion in Menning *et al.*, 2005). However, it

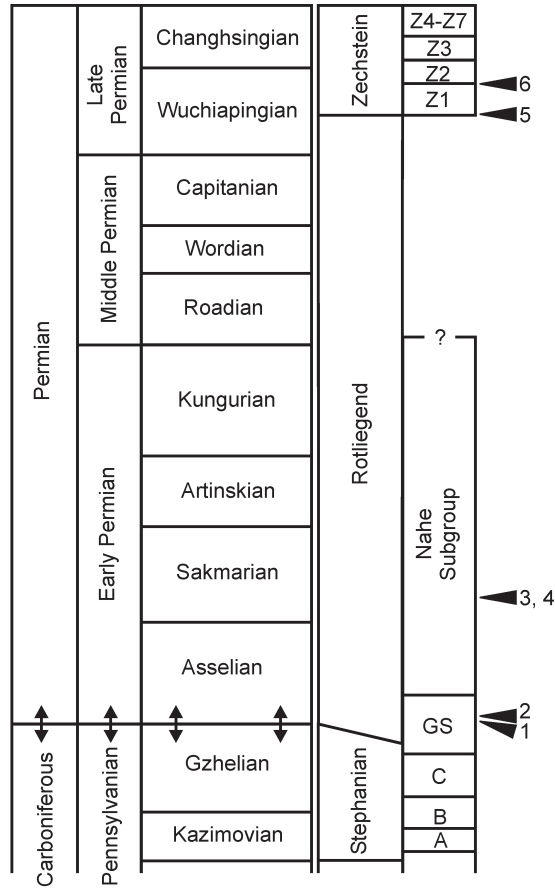


Fig. 2. Stratigraphical column showing the stratigraphical distribution of the six taphofloras (modified from German Stratigraphic Commission, 2002; Schäfer, 2005)

should be noted here, that following inter-basinal correlations based on biostratigraphical data, like shark-teeth- and insect-zonations, some authors (e.g. Roscher & Schneider, 2005; Schneider & Werneburg, 2006) recently placed the Pennsylvanian–Permian boundary within the Stephanian C (Breitenbach-Formation within the Saar-Nahe Basin). A solution of the obvious dilemma regarding the exact position of the boundary within the Saar-Nahe Basin is beyond the scope of the present work. Due to the inconsistencies with absolute datings and the scarcity of usable biostratigraphical data in the continental deposits of this basin, in our view at present neither a Pennsylvanian nor a Permian age can be confirmed for the Lower Rotliegend floras considered in the present study.

Alsensz (Lower Rotliegend, Meisenheim Formation, Jeckenbach Subformation, L-O 6 [*sensu* Boy & Fichter, 1982], Gzhelian?/Asselian?): One of the localities from the Lower Rotliegend, which can be considered as being sampled quantitatively, comes from Alsensz. This flora was first described by Trunkó and Munk

(1990) and comes from laminated, silty to clayey, lacustrine sediments. The material has been preserved as relatively small (up to 15 cm fragment length) but usually well identifiable adpressions. Recently a comprehensive revision based on additional collections has been published by Lausberg and Kerp (2000). These authors suggested the palaeoflora to be an allochthonous association of more or less typical dry-site taxa derived from the upland, which had been deposited in a relatively large palaeo-lake. More than 1000 specimens from this locality were examined.

Oberhausen (Lower Rotliegend, Meisenheim Formation, Jeckenbach Subformation, L-O 7 [*sensu* Boy & Fichter, 1982], Gzhelian): At Oberhausen, allochthonously deposited remains of a conifer dominated upland flora (Kerp *et al.* 1990), associated with *Dadoxylon*-type charcoal (Uhl *et al.*, 2004), have been discovered within grey-brown sandstones and grey-brown finely laminated siltstones deposited in a lacustrine environment. The material has been preserved as relatively small (up to 10–15 cm fragment length), but usually well identifiable adpressions (Kerp *et al.* 1990). For this study we used the data published by Kerp *et al.* (1990), who published a quantitative analysis of about 600 specimens from this locality.

Schallodenbach (Upper Rotliegend, Donnersberg Formation, RT III, Asselian–Sakmarian): The Schallodenbach locality is one of the oldest known plant bearing localities from the Upper Rotliegend of the Saar-Nahe Basin (Schuster, 1908). The sediments consist of airfall-tuffs from the Donnersberg volcano, about 25 km northeast of this locality, deposited in a lacustrine environment. The material has been preserved as small to medium sized (fragments up to 20–25 cm length are known from this locality), well identifiable adpressions. The flora is supposed to represent a parautochthonously deposited, hydrophilous environment with mesophilous influences (Lausberg, 2002). In some layers remains of gymnosperm charcoal are present, pointing to the occasional occurrence of wildfires (Uhl *et al.*, 2004).

Fischbach (Upper Rotliegend, Donnersberg Formation, RT ?III/IV, Asselian–Sakmarian): The Fischbach locality in the North of the Saar-Nahe Basin has also yielded parautochthonously deposited floral remains preserved as adpressions (Kerp, 2000; Lausberg, 2002; Kerp *et al.*, 2007b). Like in Schallodenbach, the subaquatic deposition is connected with rich ash falls derived from the Donnersberg volcano, about 45 km southeast of this locality. At Fischbach these ash falls probably caused a quick entombment without any indication for considerable transport. Consequently, the size of individual specimens is outstanding, ranging from 10 to 40 cm. Even more or less complete lateral branches of walchian conifers have been found at this locality (Lausberg, 2002). This locality can be interpreted as being more or less contemporaneous with Schallodenbach (Lausberg, 2002).

Zechstein (Late Permian, Wuchiapingian)

The Late Permian material studied here originates from two different localities from the Lower Zechstein of Germany (see Fig. 1). Despite a long sampling history, at the moment only a few plant bearing localities from the Central European

Zechstein basin can be considered to be sampled quantitatively. However, material from most localities is scattered across a large number of international collections and up to now only semi-quantitative diversity estimates for the individual localities have been published (e.g., Schweitzer, 1962, 1986; Haubold & Schaumberg, 1985). So far, quantitative data exist only for two localities (see Fig. 1), that have recently been studied in detail based on extensive museum collections, as well as own data from the field, i.e. Gera in Thuringia (Uhl, 2001; Uhl & Kerp, 2002a; Uhl & Brandt, 2004; Uhl, 2006a) and Geismar in NW-Hesse (Uhl & Kerp, 2002b, 2003, 2005, in prep.; Uhl, 2004a, 2006a, b).

Gera (Zechstein 1; Wuchiapingian): At the village of Trebnitz near Gera in eastern Thuringia, the Upper Permian Kupferschiefer (Lower Zechstein 1 [Z1]), a thin, 0.2–1.2 m thick layer that occurs throughout the entire Zechstein basin, has been mined for copper until the 19th century. Here fossil plants have been collected during the 19th century in large quantities (Geinitz, 1862, 1880; Ullrich, 1964; Uhl, 2001; Uhl & Kerp, 2002a; Uhl & Brandt, 2004). The Kupferschiefer generally represents a fully marine, anoxic sediment (Haubold & Schaumberg, 1985) and all plant remains have to be considered as allochthonous. However, in the case of Trebnitz, the Kupferschiefer has been deposited in an embayment of the Zechstein sea, and therefore this locality can be regarded as having been located near to the Late Permian shoreline (e.g., Ullrich, 1964), enabling us to compare this depositional setting with lacustrine settings from the Rotliegend. The source sediment is a finely laminated claystone and the material has been preserved as small to medium sized, well identifiable impressions (Uhl & Kerp, 2002a, b).

Geismar (Zechstein 1–2; Wuchiapingian): Another Zechstein-flora which can be considered as being sampled quantitatively comes from the locality Frankenberg-Geismar in NW-Hesse, Germany. This locality is well known for its permianized, mostly pyritized, plant remains, the so-called Frankenberger-Kornähren (Waldin, 1778; Ullmann, 1803; Bronn, 1828; Göppert, 1850; Solms-Laubach, 1884; Poort & Kerp, 1990; Uhl & Kerp, 2002b; Uhl, 2004a, 2006b). The flora is dominated by conifers, which originated most likely from the more arid hinterland. Wildfires, as evidenced by abundant charcoal remains, may have occurred regularly within the source flora(s) (Uhl & Kerp, 2003). The sediments belong to the top part of Z1, transitional zone to Zechstein 2 (Z2), the so-called Geismarer Kupferletten-Flöz (Kulick & Paul 1987), a marly layer that may attain a total thickness of 0.2 – 0.8 m (Kulick, 1987). The material has been preserved as small to medium sized, well identifiable impressions and permineralizations (Uhl & Kerp, 2002b). Like the Gera area, the Frankenberg area represents an embayment of the Central European Zechstein basin and the plant bearing marls were deposited in a marginal marine setting (Richter-Bernburg, 1955; Sauer, 1964; Kulick, 1987; Kulick & Paul, 1987).

Raw data for the six localities and information on the repositories of the material considered in this study can be found in the appendix.

METHODS

A taphoflora, in the sense used here, is represented by a collection made from a single depositional environment at a single locality, similar to the approach proposed by DiMichele and Aronson (1992). Most of the localities investigated here have a long sampling history and collections held in different institutions and museums are assumed to represent quantitative samples of the individual floras. Therefore, we based our investigation on already existing collections and not on *a priori* quantitative collections. However, one should be aware that this may introduce additional biases related to different sampling procedures and intensities, and thus complicating the interpretation of the results.

To overcome at least some problems associated with different taphonomic behaviour of different plant parts and duplication of organs representing the same plant, we restricted our study to vegetative organs like leaves (conifers, pteridosperms, other gymnosperms and ferns) or stems (sphenopsids and lycopsids) (Rees *et al.*, 1999). For most of the investigated localities plant remains were quantified by a method in which each slab of fossiliferous rock was regarded as a separate square (Pfefferkorn *et al.*, 1975) due to the relatively small size of most slabs at the majority of localities. Each taxon on a slab was scored as present, independently of the number of fragments belonging to the particular taxon observed on the slab. According to Wing and DiMichele (1995) this method of censusing is more appropriate for Palaeozoic floras than leaf counting. Ferns and pteridosperms have highly divided leaves, in sphenopsid and lycopsids stems are the major identifiable organ type and conifer branching systems may be easily fragmented due to decay or mechanical stress (Gastaldo, 1992), leading to great variations of the size of identifiable fragments in different taxa. If every identifiable fragment was counted as an “individual” this would lead to an overrepresentation of taxa which can be identified by small fragments (i.e., conifers) (Wing & DiMichele, 1995).

However, for data taken from the literature (Oberhausen) nothing is known about how the remains have been quantified. Considering the overall small size of slabs which can be collected at this locality (Kerp *et al.*, 1990 and our own observations during field work at this locality), it is not very likely that there would be considerable differences between the different censusing approaches. In contrast to the other localities, at Alsenz, as well as Fischbach, every identifiable specimen has been counted, due to the fact that here very large slabs (up to ~1 x 2 m) have been recovered during excavation (Alsenz: Trunkó & Munk, 1990; Fischbach: Kerp, 2000; Lausberg, 2002). Although such a mixing of different censusing techniques will probably interfere with the analysis of the data presented here, at the moment it seems justifiable to combine the data from all localities, considering the scarcity of quantitative data on land plant diversity from the Permian of the Euramerican floral province.

Rarefaction curves, rank-correlations and diversity indices were calculated using the software package *Biodiversity Professional, Version 2* (© 1997 The Natural History Museum/Scottish Association for Marine Science). Statistics were calcu-

lated with the STATISTICA 5.1 package (StatSoft, Inc.). Diversity indices were calculated using all taxonomic rankings and vegetative plant parts, assuming that each represented one distinct biological entity (Pryor & Gastaldo, 2000).

TAXONOMIC COMPOSITION

On the first view, the taxonomic composition of the individual taphofloras differs considerably between the Rotliegend and the Zechstein (cf. Appendix 1). However, there are also some remarkable similarities: though always a rare element, leaves of the Ginkgophyte form-species *Sphenobaiera digitata* (Brongniart) Florin are not only known from several Zechstein localities (Schweitzer, 1986; Uhl & Kerp, 2002a), but also from the allochthonous Rotliegend-floras of Alsenz (Lausberg & Kerp, 2000) and Oberhausen (Kerp *et al.*, 1990). The latter two localities also yielded radially symmetrical megasporophylls assignable to *Peltaspermum* (Kerp *et al.*, 2001), which is also a common constituent of almost all floras known from the Zechstein (Schweitzer, 1986; Poort & Kerp, 1990; Uhl & Kerp, 2002a). Another superficial similarity between the floras from the different periods is the occurrence of conifers belonging to the conifer genus *Culmitzschia*. However, in its current concept *Culmitzschia* is only regarded as a form genus of conifers of (probable) walchiacean affinity with known epidermal anatomy (Visscher *et al.*, 1986); thus a closer systematic relationship of different species is not implied by an assignment to this genus.

With the exception of the Schallodenbach locality, all localities investigated here are clearly dominated by conifers (Fig. 3, Appendix 1). The hitherto unidentified bifurcated leaves, which are the most abundant remains at the locality Alsenz, probably also belong to a conifer or conifer-like plant (Trunkó & Munk, 1990; Lausberg & Kerp, 2000), but such an affiliation has not yet been proved. In contrast to all other localities, Schallodenbach is dominated by pteridosperms and sphenopsids, with less than 15% conifer remains. This is also the only locality where remains of arborescent lycopsids play a considerable role in the palaeoflora, pointing to the fact that this plant group was on the decline during this period on the northern hemisphere. In all Rotliegend floras considered here ferns are represented only by a few remains, whereas in the Zechstein no plant has been unequivocally identified as a fern (although it is likely for the different taxa included in the genus *Sphenopteris*). Although not a dominant element, except in Schallodenbach, pteridosperms occur in all floras as important elements of the floras. Sphenopsids have been found in all floras except at the Fischbach locality (Upper Rotliegend) and the Geismar locality (Zechstein), although in varying abundance (Fig. 3).

TAPHONOMIC CONSIDERATIONS

One of the major problems of studies dealing with “palaeobiodiversity” is the fact that all studies have to work with assemblages that have been the subject of various taphonomic filters and biases (Ferguson, 1985, 1995; Spicer, 1989; Rössler & Barthel, 1998). These filters and biases have probably influenced the number of

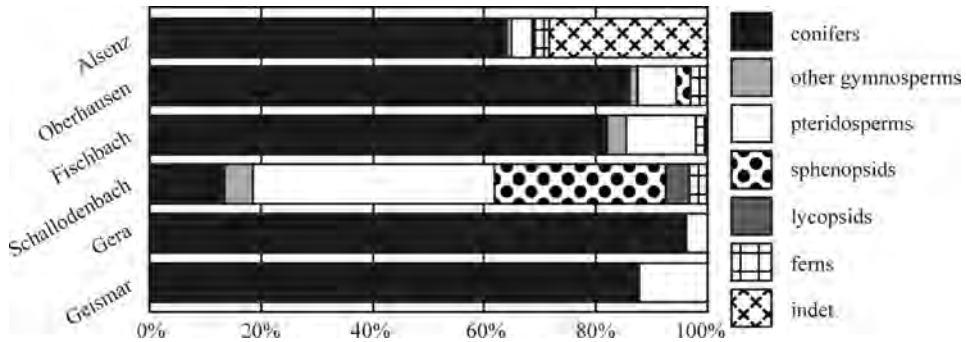


Fig. 3. Summarized taxonomic composition of the individual taphofloras

taxa, the size of fragments, the type of fragments (i.e. plant organs), the quality and type of preservation, as well as the abundance of fossil remains. Many of the problems associated with taphonomic biases can (at least partly) be overcome by following an isotaphonomic approach (Behrensmeier *et al.*, 1992). In the present study, deposits from large lakes from the Lower Rotliegend have been compared to marine deposits from the Zechstein, under the assumption that the depositional settings and taphonomical filters were rather similar for both types of deposits. Additionally deposits from somewhat smaller lakes from the Upper Rotliegend in which plant fossils have been deposited within airfall tuffs have been included, although these deposits represent slightly different depositional settings and have been affected by different taphonomical filters. However, due to the scarcity of plant bearing deposits, which allow for quantitative analysis of their fossil content, these localities have been included in the present study, although this will probably make the interpretation of the results more difficult.

Based on comparison with modern Araucarians, Gastaldo (1992) concluded, that the fragmentation of walchian conifers depends, amongst other parameters, on the residency time within the water column and “physical forces operating in the depositional environment, but is probably more a function of tissue decay at the leaf bases”. The same can be assumed for the various conifers from the Zechstein, which, like walchian conifers, show a superficial morphological similarity to modern Araucarians. It can therefore be assumed that many taphonomic filters influencing the fragmentation and sorting of conifer remains are quite similar for the Rotliegend and Zechstein deposits.

For most of the taphofloras investigated here, taphonomic filters favouring the deposition of conifers and remains from other durable plants have to be considered as a possible reason for their dominance, not only for the Rotliegend, but also for the Zechstein. Such filters may also be one of the reasons for the observed homogeneity of the Zechstein assemblages.

RESULTS AND INTERPRETATIONS

Species richness and “specimen richness”

The number of identified taxa differs markedly between the individual taphofloras considered in this investigation (Tab. 1; Appendix 1). The “raw” species richness at both Lower Rotliegend localities (23 & 16 taxa) is higher than the species richness at the Upper Rotliegend (13 & 14 taxa), as well as the Zechstein localities (both 10 taxa). Even when we combine the individual floras from the individual timeslices, the overall “raw” species richness is highest for the Lower Rotliegend (30 taxa), intermediate for the Upper Rotliegend (22 taxa) and lowest for the Zechstein (12 taxa). A somewhat naïve interpretation of this observation could be, that the species richness declined more or less continuous from the Lower Rotliegend to the Zechstein. However, there are also huge differences in the number of specimens known from the individual localities and both, Upper Rotliegend, as well as Zechstein localities, yielded significantly less specimens than the Lower Rotliegend localities.

When considering all localities, the number of taxa per locality is statistically significant correlated with the number of collected specimens per locality ($r^2 = 0.81$; $p < 0.05$). When considering only the Rotliegend localities, the r^2 value for the correlation between the number of taxa and the number of collected specimens goes up to 0.99 ($p < 0.01$).

These results seem to indicate that there is a relation between the number of specimens at a given locality and the observed diversity (i.e. species richness), implying that the potential decline of species richness could in fact be an artifact of sampling intensity. To test such an interpretation, additional methods for the quantification of diversity have to be used, which allow for a correction against sample size.

Table 1

Numbers of specimens, species and diversity indices at the individual localities

Locality	Age	Specimen number	Species richness (S)	Fisher's α index (α)	Simpson index (D)	Shannon index (H')	Evenness (e)
Alsenz	Gzhelian/	1573	23	3.82	0.15	0.96	0.31
Oberhausen	Asselian ?	564	16	3.06	0.29	0.70	0.25
Fischbach	Asselian-	144	13	3.47	0.22	0.82	0.32
Schallodenbach	Sakmarian	238	14	3.25	0.14	0.97	0.37
Gera	Wuchia-	245	10	2.10	0.27	0.64	0.28
Gismar	pingian	364	10	1.90	0.52	0.46	0.20

Rank correlations

Rank correlations based on raw data (Fig. 4A), as well as normalized values (percentages) (Fig. 4B), show no clear trends which could be interpreted in terms of the taphonomical history of the individual localities (allochthonous vs. parautochthonous; lacustrine vs. marine) or their stratigraphic age. The only locality that differs markedly from all other localities is Frankenberg/Geismar. However, at the moment it is not clear whether the abundance of remains of the conifer *Ullmannia bronniei* Goeppert (70.6%) at this locality is caused only by taphonomical reasons or not. In all localities, except Schallodenbach, the most dominant taxa belong to the

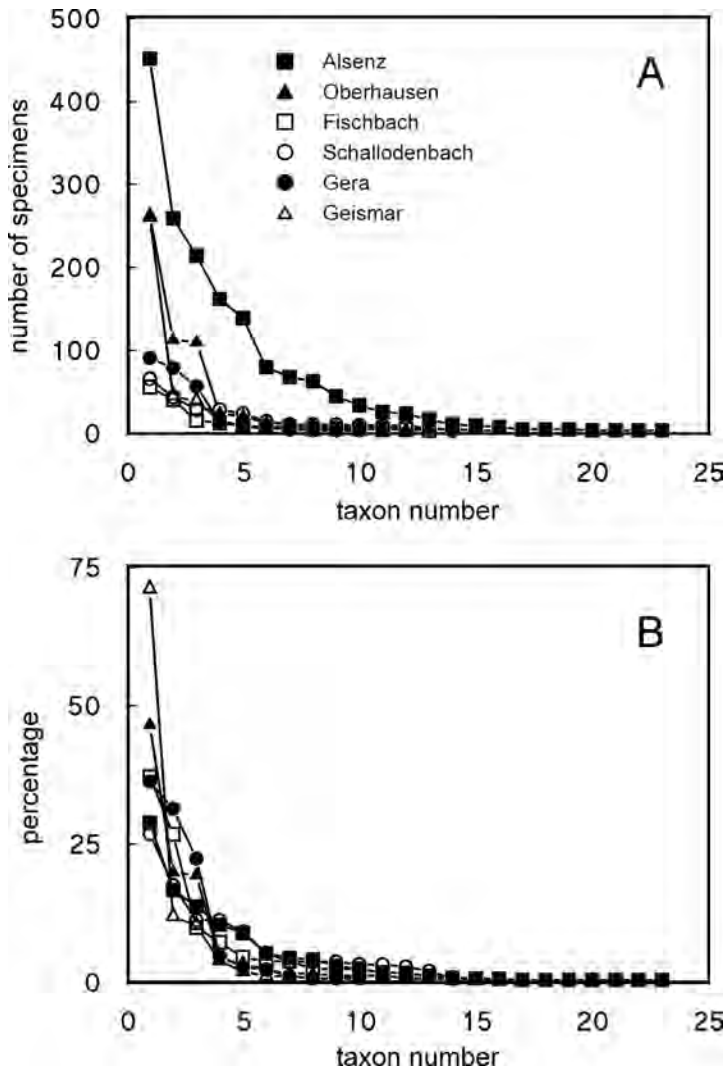


Fig. 4. Rank correlations of the individual taphofloras. (A) raw data, (B) normalized data

conifers, followed by different taxa belonging to the pteridosperms. In Schalldenbach the most dominant taxa are the peltasperm *Autunia conferta* and different sphenopsids. Here the most abundant coniferophyte (*sensu lato*) is *Dicranophyllum hallei* Remy & Remy, a ruderal plant, which probably inhabited frequently disturbed habitats, like banks and watersides of lakes, creeks and rivers (Barthel & Noll, 1999).

Diversity indices

When looking on different diversity indices it can be noticed that both Zechstein floras have the lowest values for Fisher's α index, as well as the Shannon index (Tab. 1). Although Geismar has also the highest value for the Simpson index and the lowest Evenness value, the values for Gera show no differences as compared to the Rotliegend localities. There is also no clear trend within the Rotliegend localities towards generally higher or lower values for an individual locality.

Standard diversity indices and evenness values are very low for all floras investigated in the present study. A possible interpretation for such low diversity indices may point to the assumption that the source communities existed under physically or chemically stressed conditions or that they experienced other environmental instabilities (e.g., Hughes, 1986). Similar low indices have been found for Late Pennsylvanian, gymnosperm dominated tropical dryland vegetation from an alluvial plain in Nova Scotia, stressed by seasonal droughts and regularly occurring wildfires (Falcon-Lang, 2003). Furthermore, it is well known from numerous studies of modern ecosystems, that stressed environments may easily experience an increase in dominance, a decrease in species richness and a decrease in the values of the diversity indices used in our study (e.g., Magurran, 1988) also supporting such a possible interpretation for the results presented here. However, these results from the Late Palaeozoic cannot be directly compared with results or interpretations obtained from modern environments. Again taphonomic filters and their influence on the abundance of individual taxa and plant parts have to be taken into account, as well as the fact that the number of fossil plant remains probably better reflects biomass than the number of individual organisms in an original flora. Nevertheless, these results may also point to a reduced diversity for the individual Zechstein floras as compared to the Rotliegend ones, but there is no clear indication for any diversity trends within the Rotliegend.

Rarefaction

A rarefaction analysis of all localities reveals that the rarefied diversities of both Zechstein localities are below the rarefied diversities of all Rotliegend localities (Fig. 5). Rarefied diversities of both Upper Rotliegend floras are between the diversities of both Lower Rotliegend floras and thus no clear within-Rotliegend diversity trend is visible.

This demonstrates that not only the overall Zechstein flora is less rich in taxa than the Rotliegend flora (Kerp, 1996, 2000), but also that individual Zechstein

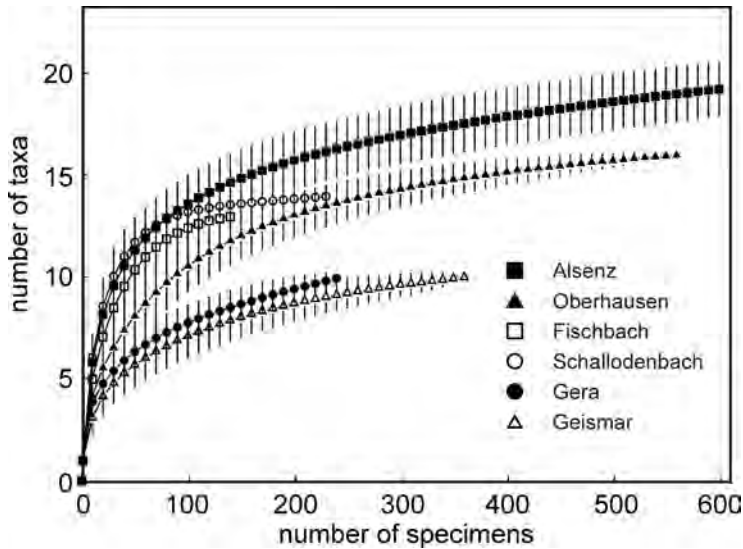


Fig. 5. Rarefaction curves for the individual taphofloras

taphofloras are less diverse than all of the individual Rotliegend taphofloras considered here, even when corrected against sample size. However, despite the observed climatic and environmental differences between the Upper and Lower Rotliegend, no clear trends towards higher or lower diversities can be seen in correlation with the stratigraphic age within the Rotliegend or with the depositional setting of the individual localities. Although it is not clear how much these results and interpretations have been influenced by different depositional settings and taphonomic histories of the Lower and Upper Rotliegend floras, it seems to indicate that there is no drastic change of land plant diversity within the Rotliegend of the Saar-Nahe Basin, at least within the vegetation types represented by the selected taphofloras. Nevertheless, our data provide no definitive evidence to reject influence of different depositional settings as either primary or secondary factor as a potential cause for the lower diversity of the Zechstein floras.

CLIMATIC AND PALAEOGEOGRAPHIC FORCING OF DIVERSITY?

In modern vegetation there is a strong tendency for dry climate vegetation to have fewer plant species (Gentry, 1988). According to palaeoclimatic-modelling (Fluteau *et al.*, 2001), the areas bordering the Zechstein-sea experienced more arid climates during the Late Permian than during the Rotliegend or the Upper Pennsylvanian. A well developed equator to pole temperature gradient existed during the Permian (Rees *et al.*, 1999, 2002; Gibbs *et al.*, 2002) and biome arrangement was similar to that of today: a relatively dry zone (evaporite belt, *sensu* Ziegler *et al.*, 2003) seems to demarcate the tropical humid zone from its temperate counterparts in the north and south, which are associated with coal deposits (Ziegler *et al.*, 2003).

The Zechstein floras considered here, have been deposited within this relative dry zone, about 20° (>2000 km) farther to the north than the intra-tropical Rotliegend deposits, due to the northward drift of Pangaea during this period (Ziegler *et al.*, 1997), although the absolute geographical distance is only about 200 to 400 km, with even less latitudinal difference (~150 km).

One of the reasons for a potential overall lower land-plant diversity as well as the lower diversity of the individual, allochthonous taphofloras within the Zechstein may be a reduced habitat disparity, as compared to the uppermost Pennsylvanian and Early Permian of the Euramerican province. Studies on modern ecosystems suggest that factors like topographic relief, soils and the geological underground influence habitat disparity on a regional scale, with a high habitat disparity leading to high plant-diversity (Whitaker, 1977; Shmida & Wilson, 1985). An Early Permian coastal flora from West Texas indicates that habitat differentiation was well developed within the tropical lowlands during the Late Palaeozoic (DiMichele *et al.*, 2000). Such a habitat differentiation can also be observed for the Rotliegend of the Saar-Nahe Basin (Kerp & Fichter, 1985; Lausberg, 2002; Kerp *et al.*, 2007a, b). Here different vegetation “types” are preserved at different localities, pointing to a spatial, but probably also temporal heterogeneity of habitats. In contrast, all floras known so far from the Zechstein, that show a much wider geographical distribution than the Rotliegend deposits, are very uniform and may have originated from a more uniform source vegetation, probably representing a reduced habitat diversity as compared to the latest Pennsylvanian and Early Permian. Only a few Zechstein taxa seem to have a somewhat restricted distribution pointing to some kind of habitat differentiation. For example, the conifer *Culmitzschia florinii* Ullrich is so far only known from the Zechstein of Thuringia (E-Germany) (Ullrich, 1964; Uhl & Kerp, 2002a) and Poland, even farther to the East (Clement-Westerhof, 1984). Although it is very likely that this taxon is congeneric with the Upper Permian genus *Ortiseia*, known from the Alps (Florin, 1964; Clement-Westerhof, 1984; Visscher *et al.*, 2001), it has never been found in the central or western part of the Central European Zechstein deposits. Nevertheless, *Nuskoisporites dulhuntyi* Potonié & Klaus, the prepollen of *Ortiseia*, occurs not only in the Alps, but is also frequent in Central and Western European deposits of Late Permian age (Poort *et al.*, 1997), pointing to a relative wide distribution of the source taxon, despite the lack of macro-remains in large areas.

However, due to the general scarcity of Late Permian plant deposits known from the Euramerican floral province, it is possible that the Zechstein flora represents a rather specialized vegetation type adapted to relatively humid coastal environments bordering the Zechstein sea, whereas the arid hinterlands had only a rather scarce vegetation cover (Schweitzer, 1962). However, rare contemporaneous continental deposits from Saxony and Thuringia in Germany yielded the same taxa as the fully marine Kupferschiefer near Gera (Ullrich, 1964; Uhl & Kerp, 2002a). Some of the anatomical and morphological traits of many Zechstein plants, like sunken stomata or prominent papillae overarching the stomatal pores, [e.g., *Peltaspermum martinsii* (Germar) Poort & Kerp] that have been interpreted as adapta-

tions to rather dry conditions (Schweitzer, 1962, 1986; Poort & Kerp, 1990; Thévenard *et al.*, 2005), could also be interpreted as adaptations to edaphic salinity, occurring in coastal habitats (Poort & Kerp, 1990). However, the same adaptations can also be found in specimens coming from contemporaneous continental deposits in N-Italy, Saxony and Thuringia (Ullrich, 1964; Poort & Kerp, 1990; Uhl & Kerp, 2002a), for which extreme saline conditions can be excluded (Ullrich, 1964; Poort & Kerp, 1990). Besides climatic changes, a decrease in topographic relief, due to the erosion and collapse of the Variscan Orogen, which took place during the Late Pennsylvanian and the Permian (Henk, 1997), may have affected the reduction of habitat disparity.

Non-quantitative data from the Bad Sobernheim flora, the youngest known palaeoflora from the Rotliegend of the Saar-Nahe Basin, indicate a higher species richness for this locality than for all other Rotliegend floras from this area (> 30 taxa; Kerp & Fichter, 1985; Kerp *et al.*, 2007b), whereas somewhat younger Middle – Late Permian localities in Germany indicate rather low diversities (i.e. low species richness; < 5 taxa) well before the onset of the Upper Permian Zechstein transgression (Munk *et al.*, 1993; Schweitzer, 1996). The first marine strata of the Frankenberg-area have been deposited directly on a Middle Permian land-surface shortly after the transgression of the Zechstein sea, and already yield a flora consisting of the typical Zechstein taxa, like *Peltaspermum martinsii* (Germar) Poort & Kerp, *Pseudovoltzia liebeana* (Geinitz) Florin and *Ullmannia brononii* Goeppert. The time or the region(s) in which these plants evolved are not known at the moment, but there is no unequivocal record of these plants from pre-Zechstein sediments within Europe. However, an Early Permian (Late Leonardian [Late Kungurian]) flora from north-central Texas which is younger than the floras from the Rotliegend (Gzhelian – Sakmarian) of Central Europe and older than the Late Permian (Wuchiapingian) Zechstein floras has a “mixed” species composition. Typical Zechstein plants like *Ullmannia*, *Pseudovoltzia liebeana* (Geinitz) Florin and *Taeniopteris eckardtii* Kurtze occur together with elements more typical for older Euramerican floras, like *Wattia* sp., *Walchia* sp. and *Dicranophyllum* sp. Additional plant remains resembling typical Mesozoic elements like *Podozamites* sp., *Dioonitocarpidium* and a *Swedenborgia* like seed-scale have been discovered at the same localities (DiMichele *et al.*, 2001), although the taxonomic affinity of many of these specimens is unclear at the moment (C. Looy, pers. comm. 2006). These findings show, that there is a large gap in the fossil record of these plants during the Middle and Upper Permian, which can probably be attributed to taphonomic biases and the scarcity of sediments suitable for the preservation of fossil plants. It is therefore extremely difficult to judge whether the observed decrease of land-plant diversity in the Late Permian of Germany can be generalized for Central Europe or even the complete Euramerican floral province. At the moment also the exact timing of the observed diversity decline remains unclear.

CONCLUSIONS

1) A quantitative analysis of the land-plant diversity of six taphofloras from the latest Pennsylvanian and Permian of Germany (i.e. from the Saar-Nahe Basin, SW-Germany, and the German Zechstein), basin supports the assumption that regionally (within these areas) a diversity decline occurred after the deposition of the Upper Rotliegend (Early Permian) sediments, leading to an extremely low species richness during the Zechstein (Late Permian).

2) Despite taphonomic differences between the individual localities considered here, possible reasons for the observed lower diversity include most probably a climatic deterioration/aridisation due to tectonic northwards movement of Pangaea.

3) This climatic deterioration, as well as a contemporaneous decrease in topographic relief due to erosion and collapse of the Variscan Orogen, may also be the main reasons for a decrease in habitat diversity, as compared to the Late Pennsylvanian and the Early Permian, which further amplified the decrease in land-plant diversity.

4) Based on the data presented here it is difficult to judge whether the observed diversity decline at individual localities can be generalized for the entire Euramerican floral province, although it can be concluded from other sources, that there are large gaps in the palaeobotanical record of this region, which may lead to underestimations of the “true” land plant diversity during this period.

Acknowledgements

Establishment of the database used in this study was possible due to financial support by the Deutsche Forschungsgemeinschaft (DFG grants Ke 584/5-1, Ke 584/5-2, Ke 584/9-1). D.U. acknowledges financial support by the Alexander von Humboldt-Foundation and the Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO). We thank Hans Kerp (Münster, Germany) for his support of our studies on Late Palaeozoic floras, all the keepers of the museums and collections who provided access to their collections, and Th. Schindler (Spabrücken, Germany) and Ronny Rössler (Chemnitz, Germany) for fruitful discussions regarding the Pennsylvanian–Permian boundary within the Saar-Nahe Basin. We thank Chris Cleal (Cardiff, Great Britain) and Ronny Rössler (Chemnitz, Germany) for their reviews, that helped to improve the manuscript. This paper is a contribution to IGCP 469 – *Late Variscan terrestrial biotas and palaeoenvironments*.

Appendix 1

List of taxa and number of specimens occurring at the localities investigated

	Alsenz Lower Rotliegend, Meisenheim Formation, lacustrine silts and clays	Oberhausen Lower Rotliegend, Meisenheim Formation, lacustrine silts and sandstone	Fischbach Upper Rotliegend, Donnersberg Formation, lacustrine, subaquati- cally deposited airfall-tuffs	Schalloden- bach Upper Rotliegend, Donnersberg Formation, lacustrine, subaquati- cally deposited airfall-tuffs	Gera Zechstein Z 1, Kupfer- schiefer, marginal marine, laminated clay	Geismar Zechstein, Z 1-2, marginal marine, marls
<i>Dicranophyllum hallei</i>			2	26		
cf. <i>Dicranophyllum gallicum</i>		7				
<i>Culmitzschia angustifolia</i>	2					
<i>Culmitzschia florinii</i>					11	
<i>Culmitzschia laxifolia</i>	5		53			
<i>Culmitzschia parvifolia</i>	77					
cf. <i>Culmitzschia speciosa</i>	23		3			
<i>Ernestiodendron filiciforme</i>	65		10	7		
<i>Hermitia</i> sp.			6			
<i>Hermitia</i> sp. A	256					
<i>Hermitia</i> sp. B	14					
<i>Hermitia arnhardtii</i>	60					
cf. <i>Hermitia bertrandii</i>	2					
<i>Hermitia germanica</i>	211	107	38			
<i>Otovicia hypnoides</i>	136	260	5			
<i>Pseudovoltzia liebeana</i>					88	13
<i>Quadrocladus orobiformis</i>					5	3
<i>Quadrocladus solmsii</i>						1
<i>Quadrocladus</i> sp.						6
<i>Ullmannia</i> sp.					1	2
<i>Ullmannia brononii</i>					54	257
<i>Ullmannia frumentaria</i>					76	36
<i>Walchia piniformis</i>	159	110	1			
<i>Cordaites</i> sp.	1	2	5	12		
<i>Baieridium aphlebiaeforme</i>		1				
<i>Sphenobaiera digitata</i>	7	5			1	1
<i>Autunia conferta</i>			2	63		
<i>Autunia naumanni</i>				8		
<i>Dicksonites leptophyllum</i>		1				
<i>Dichophyllum stabellifera</i>	8		3			
<i>Neuropteris</i> cf. <i>cordata</i>		5				
<i>Odontopteris</i> sp.	31					
<i>Odontopteris lingulata</i>	21	21				
<i>Peltaspermum martinsii</i>					6	42

Appendix 1 (continued)
List of taxa and number of specimens occurring at the localities investigated

	Alsensz Lower Rotliegend, Meisenheim Formation, lacustrine silts and clays	Oberhausen Lower Rotliegend, Meisenheim Formation, lacustrine silts and sandstone	Fischbach Upper Rotliegend, Donnersberg Formation, lacustrine, subaquati- cally deposited airfall-tuffs	Schalloden- bach Upper Rotliegend, Donnersberg Formation, lacustrine, subaquati- cally deposited airfall-tuffs	Gera Zechstein Z 1, Kupfer- schiefer, marginal marine, laminated clay	Geismar Zechstein, Z 1-2, marginal marine, marls
<i>Rhachiphyllum schenkii</i>	1	8	13	8		
<i>Rhachiphyllum lyratifolia</i>	1			21		
<i>Rhachiphyllum subauriculata</i>	1					
<i>Sphenopteris</i> sp.					2	3
<i>Gracilopteris bergeronii</i>		5				
<i>Calamites</i> sp. 1		2				
<i>Calamites</i> sp. 2		2				
<i>Calamites multiramis</i>				8		
<i>Calamites gigas</i>	2	10		26		
<i>Calamites alternans-variens-insignis</i>				41		
<i>indet. sphenopsids</i>					1	
<i>Asolanus</i> sp.				4		
<i>Sigillaria brardii</i>				6		
<i>Pecopteris</i> sp.			3			
<i>Pecopteris polymorpha</i>				7		
<i>Pecopteris oreopteridea</i>				1		
<i>Remia pinnatifida</i>	42	18				
<i>indet. bifurcated leaves (conifers?)</i>	448					

Appendix 2
List of collections considered for this study

Collection	localities
Staatliches Museum für Naturkunde, Karlsruhe, Germany	1
Institute of Geology, University of Mainz, Mainz, Germany	1, 2
Naturhistorisches Museum, Mainz, Germany	1, 3
Laboratory for Palaeobotany and Palynology, Utrecht, The Netherlands	2, 4
Paläontologisches Museum, Nierstein, Germany	2, 3
Collection Schmitt-Riegraf, Münster, Germany	3
Forschungsstelle für Paläobotanik, University of Münster, Münster, Germany	4
Collection Noll, Tiefenthal, Germany	4
Museum für Naturkunde Gera, Gera, Germany	5
Museum für Mineralogie und Geologie, Dresden, Germany	5
Institute of Geology, University of Göttingen, Göttingen, Germany	5, 6
Institute of Geology, TU Bergakademie Freiberg, Freiberg, Germany	5, 6
Naturhistorisches Museum Schloß Bertholdsburg, Schleusingen, Germany	5, 6
Institute of Geology, University of Marburg, Marburg, Germany	6
Museum für Naturkunde, Humboldt-University Berlin, Berlin, Germany	5
Collection R. Goßmann, Bonn, Germany	6
Collection H. Kauffmann, Burgwald, Germany	6
Naturmuseum Senckenberg, Frankfurt/Main, Germany	6
Museum der Natur, Gotha, Germany	5
Institut für Spezielle Botanik, University of Jena, Jena, Germany	6
Collection W. Munk, Walzbachtal, Germany	6

1 – Alsenz; 2 – Oberhausen; 3 – Fischbach; 4 – Schallodenbach; 5 – Gera; 6 – Geismar

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