



## NEW DATA ON THE MACROFLORA OF THE BASAL ROTLIEGEND GROUP (REMIGIUSBERG FORMATION; GZHELIAN) IN THE SAAR-NAHE BASIN (SW-GERMANY)

DIETER UHL<sup>1,2,\*</sup>, ANDRÉ JASPER<sup>1,2</sup>

<sup>1</sup> Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; e-mail: dieter.uhl@senckenberg.de.

<sup>2</sup> Programa de Pós-Graduação em Ambiente e Desenvolvimento da UNIVATES (PPGAD/UNIVATES), Centro Universitário Univates, Rua Avelino Tallini, 171 – CEP 95.900-000, Lajeado, RS, Brazil.

\* corresponding author

Uhl, D., Jasper, A. (2016): New data on the macroflora of the basal Rotliegend group (Remigiusberg Formation; Gzhelian) in the Saar-Nahe Basin (SW-Germany). – *Fossil Imprint*, 72(3-4): 239–250, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

**Abstract:** New discoveries of fossil plant macroremains from the Remigiusberg Formation (lowermost Rotliegend group) considerably enlarge our knowledge about the flora of the basal-most part of the lithostratigraphically defined Rotliegend group within the Saar-Nahe Basin in SW-Germany. Most taxa are plants that grew in relatively humid habitats near rivers, or around margins of the lake in whose sediments the plant macroremains were found. This, together with previously reported palynological data, suggests that the wetlands in which these plants grew were large enough to act as taphonomical barriers against the deposition of plant macroremains from dryer habitats.

Based on some of the new taxa, it is also possible to constrain the base of the biostratigraphic *Autunia conferta* zone in this basin, a task that was not possible before, due to the scarcity of macrofloristic data from the basal Rotliegend group. The new data provide evidence that the upper part of the Remigiusberg Formation is probably not older than late Gzhelian. This corresponds to earlier biostratigraphic interpretations based on palaeozoological remains.

**Key words:** Pennsylvanian, Permian, biostratigraphy, flora, climate, diversity, taphonomy

Received: November 11, 2016 | Accepted: December 2, 2016 | Issued: December 30, 2016

### Introduction

The Saar-Nahe Basin in SW-Germany is the largest intramontane basin containing Carboniferous and Permian sediments within the Varican mountain chain that is currently exposed at the surface. The Remigiusberg Formation in this basin has attracted a lot of scientific interest during recent years, due to an increasing number of finds of some of the oldest European terrestrial vertebrates. The oldest sediments within the basin are known from the Yeadonian (Spiesen formation), and continental sedimentation continued, with several discontinuities, at least up to the Kungurian (Schindler 2007, Boy et al. 2012 and citations therein). Due to the commercial mining of coals that occur in the upper Pennsylvanian strata (i.e. Duckmantian – Gzhelian; Steinkohlen group), the macroflora from this period is known quite well (e.g. Kerp et al. 2007a, b, Cleal 2008 and citations therein). Workable coal seams occur up to the top of the Gzhelian Breitenbach formation, although the youngest seams never had great commercial value, and were mostly mined for local or regional usage (e.g. Schindler 2007).

The lithostratigraphically defined boundary between the Steinkohlen group and the Rotliegend group is at the top of

the Breitenbach Formation (e.g. Schindler 2007, Boy et al. 2012). The lithological changes are also reflected by changes in the composition of the basin's fossil fauna and flora (e.g. Boy and Schindler 2000, 2012, Kerp et al. 2007b, Boy et al. 2012). During deposition of the Rotliegend group, an aridization trend occurred in the basin, which mirrored a general trend in facies development (Stapf 1990, 1997, Kerp 2000). Parallel to these environmental trends, there is also a decrease of macrofloras dominated by basinal elements from permanently wet environments, and an increase of macrofloras dominated by hinterland elements from environments that were dry at least seasonally (e.g. Kerp 2000, Kerp et al. 2007b).

Additionally, sediments from the lower Rotliegend group (Glan subgroup; uppermost Gzhelian – Asselian) yield more frequently fossil plants than sediments from the upper Rotliegend group (Nahe subgroup; Asselian/Sakmarian – Kungurian). This led to increased patchiness of localities yielding fossil plant remains in the Nahe subgroup, as compared to the Glan subgroup (Kerp and Fichter 1985, Uhl et al. 2004, Kerp et al. 2007a, b).

Fossil macroflora of the Rotliegend deposits from this basin has been reviewed by Kerp and Fichter (1985), as well

**Table 1. Overview on plant taxa so far recognized from the Remigiusberg Formation.**

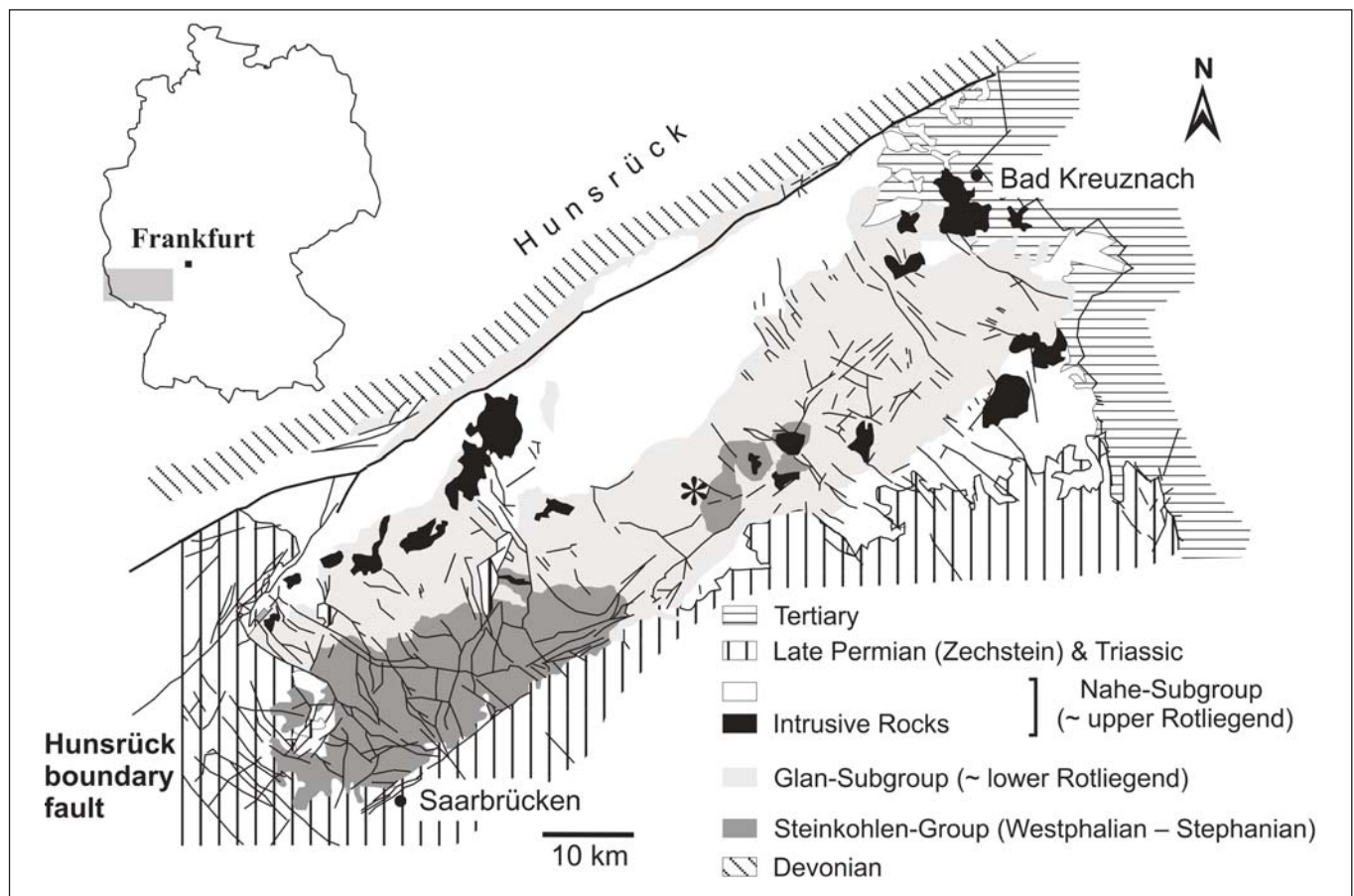
Taxon	Kerp and Fischer (1985)	This work
<i>Calamites</i> sp.		x
<i>Eucalamites cruciatus</i>		x
<i>Asterophyllites equisetiformis</i>		x
<i>Asterophyllites longifolius</i>	?	?
<i>Scolecopteris</i> sp.		x
<i>Pecopteris</i> cf. <i>cyathea</i> (= <i>Cyathocarpus</i> cf. <i>cyatheus</i> )	x	x
<i>Pecopteris</i> cf. <i>densifolia</i>		x
<i>Pecopteris</i> sp.	x	x
<i>Autunia conferta</i>		x
<i>Autunia naumannii</i>	x	
cf. " <i>Sphenopteris</i> " <i>germanica</i>		x
<i>Samaropsis</i> sp.	x	?
indet. seeds		x

as Kerp et al. (2007a, b), and a number of recent studies dealt with selected aspects of the macroflora (e.g. Lausberg and Kerp 2000, Lausberg 2002, Lausberg et al. 2003, Uhl and Heidtke 2003, Uhl 2006, 2008, Uhl and Lausberg 2008, Uhl

and Raisch 2009). However, for some stratigraphic levels in this basin, there are still gaps in our knowledge concerning fossil macroflora (cf. Uhl 2008).

One example is the macroflora of the Remigiusberg Formation, consisting of the basalmost sediments of the Rotliegend group within the Saar-Nahe Basin (Boy et al. 2012). Kerp and Fichter (1985), in their comprehensive review of then-known data about the macroflora from the Rotliegend of the Saar-Nahe Basin listed four plant bearing localities from this unit, each yielding one to four taxa, though rather badly preserved. In total, these authors recognized only five taxa from this stratigraphic level (cf. Tab. 1). Since that review, no new data concerning macroflora of the Remigiusberg Formation have been published.

However, in recent years, the Remigiusberg Formation has experienced considerable scientific interest, due to numerous findings of terrestrial vertebrates, including the so-far oldest amniote remains from Central Europe (e. g. Fröbisch et al. 2012, Voigt et al. 2014, Voigt and Uhl 2015). In the present study, new data on the macroflora of the Remigiusberg Formation are provided, based on new finds from two localities on Remigiusberg (a small mountain in the vicinity of the city of Kusel; Text-fig. 1), which is the type area of this formation. These finds considerably expand our knowledge about the flora during deposition of the Remigiusberg Formation, and they also help develop a better understanding of the habitats of the recently-discovered terrestrial vertebrates. Additionally, these new findings



**Text-fig. 1. Geological overview map of Saar-Nahe Basin (modified from Stapf (1990) and Uhl et al. (2004)). Asterisk (\*) marks position of localities at Remigiusberg.**

include several biostratigraphically relevant taxa, so it is possible for the first time to provide constraints for the base of the *Autunia conferta* zone (sensu Opluštil et al. 2016) of macropalaeobotanical biostratigraphy in this particular basin.

## Geology and stratigraphy

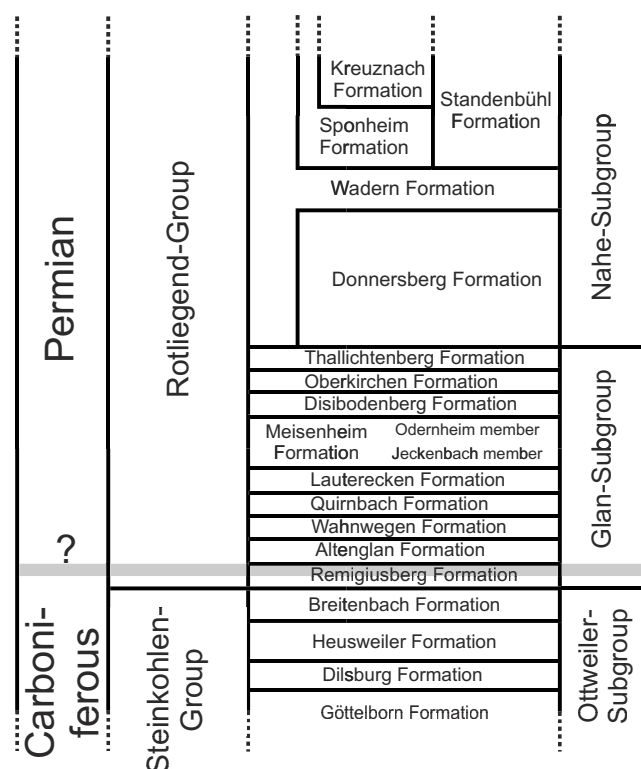
The Saar-Nahe Basin is a half-graben structure, with a surface extension of approximately 100 km from SW to NE, and 40 from NW to SE (Stapf 1990, Henk 1993). Within Central Europe, it is one of the largest and best exposed intramontane basins of the Variscan orogenic belt in Central Europe with a purely continental sedimentary infill (Schäfer 1986, Schäfer and Korsch 1998). Sedimentation started in the Yeadonian and lasted up to the Kungurian (Early Permian: Schindler 2007, Boy et al. 2012). Although some authors have claimed that there are no discordances or unconformities between the Breitenbach and Remigiusberg Formations in the Saar-Nahe Basin (Boy and Schindler 2000, Schindler 2007), palynological data hint towards at least a minor discontinuity at the top of the Breitenbach Formation (Cleal 2008).

Within the basin, the Rotliegend group is divided into the Glan subgroup (~ Lower Rotliegend; Gzhelian – Asselian) and the Nahe subgroup (~ Upper Rotliegend; Asselian – Kungurian) (Boy and Fichter 1982, German Stratigraphic Commission 2002, Menning et al. 2005, Boy et al. 2012).

So far, the exact position of the Pennsylvanian-Permian boundary within the Saar-Nahe Basin is controversial (e.g. Boy and Schindler 2000, 2012, Menning et al. 2005, Roscher and Schneider 2005, Schneider and Werneburg 2006, 2012, Uhl and Lausberg 2008, Boy et al. 2012). Absolute ages derived from volcanic markers beds within the Glan subgroup are contradictory, and provide inconsistent age models (see discussion in Menning et al. 2005). Also, biostratigraphic data are contradictory. Some authors place the Pennsylvanian-Permian boundary within the “Stephanian C” (Breitenbach Formation in the Saar-Nahe Basin), based on inter-basin correlations of selected biostratigraphic data, like shark-tooth and insect-zonations (e.g. Roscher and Schneider 2005, Schneider and Werneburg 2006, 2012). Others place the boundary within the Altenglan Formation, based on ecostratigraphic correlations (e.g. Boy and Schindler 2000, 2012, Boy et al. 2012). Up to now, it was not possible to use palaeobotanical data to provide any biostratigraphic constraints on the Pennsylvanian-Permian boundary in this basin, due to the scarcity of fossil plants from the basal Rotliegend group.

## Material

The material on which this study is based comes from two localities within the Remigiusberg Formation (Boy and Schindler 2000, Boy et al. 2012), which were temporarily exposed in 2007 at the western margin of the so called Southern-quarry at Remigiusberg in the vicinity of Haschbach village. The sediment containing most of the plant remains (locality No. 1) is a dark, blue-grey contact-metamorphous lacustrine claystone, directly overlying a volcanic intrusion. These volcanic rocks, a diorite variety locally named as Kuselite, have been quarried at Remigiusberg since the 19<sup>th</sup>



**Text-fig. 2. Overview of stratigraphy of Permian-Carboniferous succession in Saar-Nahe Basin (based on German Stratigraphic Commission (2002), Menning et al. (2005), Boy et al. (2012)). Stratigraphic position of localities at the Remigiusberg is marked by horizontal grey bar.**

century. Besides plant remains, the sediment contains isolated scales of relatively rare actinopterygians and osteolepid fishes (Boy et al. 2012). Other plant material comes from grey-green and red clay- and siltstones, which have been removed as overburden during quarrying of the Kuselite, and piled on spoil-tips at the western end of the Southern quarry (locality No. 2). These types of sediments are typical for the upper part of the Remigiusberg Formation (Boy et al. 2012), and can also be found in situ within the quarry.

The material used for this study comes from the following collections:

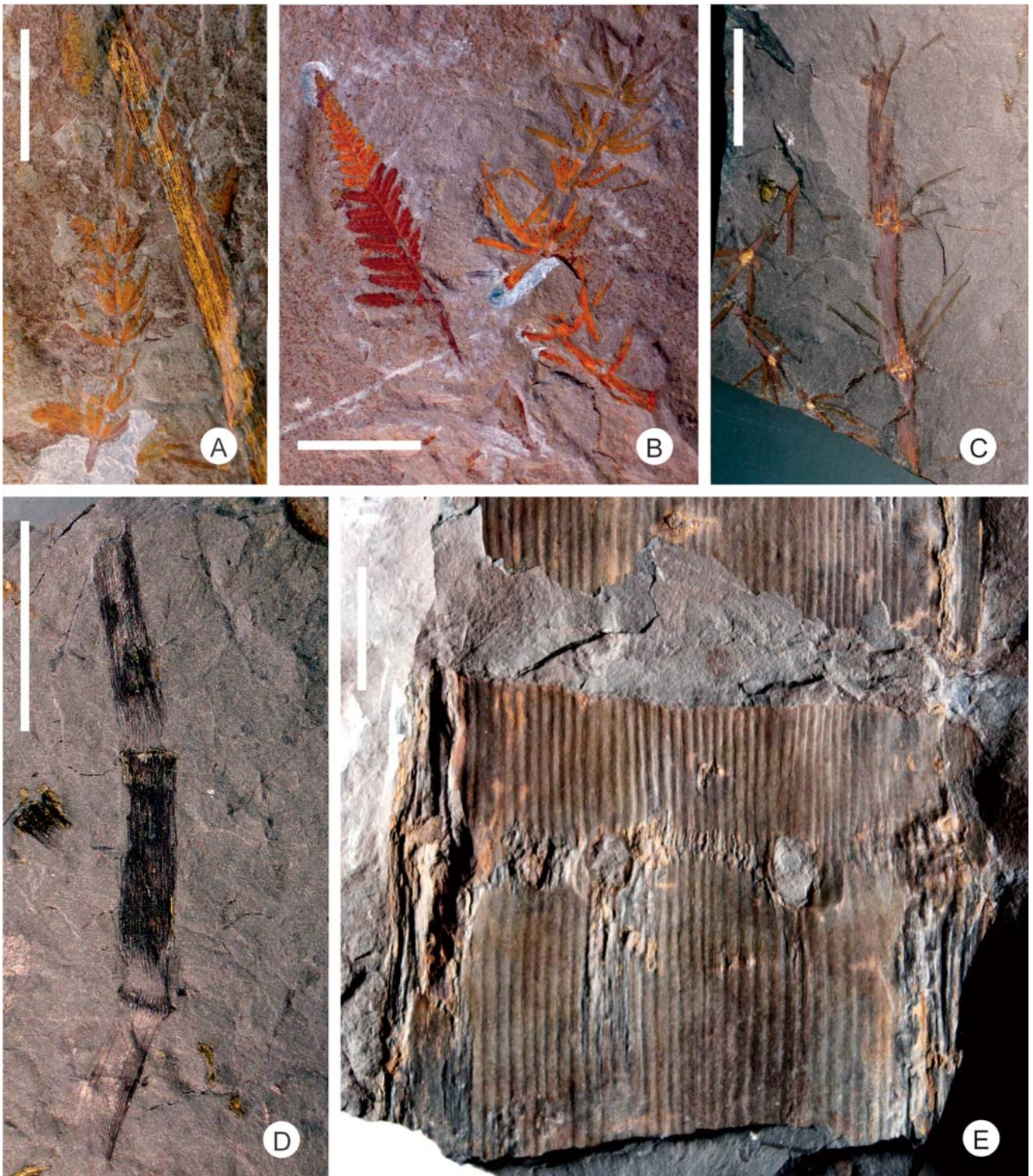
- Landessammlung Rheinland-Pfalz, Mainz, Germany (LS-RLP);
- Private collection O. Emrich, Kottweiler-Schwanden, Germany (SEK);
- Private collection Isbarn, Tiefenthal, Germany (SIT).

Additionally, we analyzed the published literature on the macroflora of this basin as a source for Text-fig. 7 (i.e. Kerp and Fichter 1985, Schindler et al. 2004, Kerp et al. 2007a, b, Cleal 2008, Uhl 2008).

## The flora

### Sphenophytes

Unidentifiable fragments of axis of sphenophytes (probably belonging to Calamitaceae) can be found in a number of horizons (mainly grey-green silt- and claystones) throughout the entire Remigiusberg Formation. In individual



**Text-fig. 3. Sphenophyte and fern remains from Remigiusberg Formation.** A) *Asterophyllites equisetiformis*, Inv.-Nr. PB 2010/5809 LS (LS-RLP), scalebar = 2.5 cm; B) *Asterophyllites equisetiformis* (right) and *Pecopteris* sp. (left), Inv.-Nr. PB 2010/5813 LS (LS-RLP), scalebar = 2 cm; C) Long-leaved variety of *Asterophyllites equisetiformis*, Inv.-Nr. PB 2010/5808 LS, scalebar = 2 cm; D) *Calamites* sp., Inv.-Nr. PB 2010/5804 LS (LS-RLP), scalebar = 2.5 cm; E) *Eucalamites cruciatus*, Inv.-Nr. PB 2016/5034 LS (LS-RLP), scalebar = 2 cm.

layers, these remains can be quite numerous, covering almost entire bedding-planes. Large fragments of *Calamites* are also frequent in the sediments at locality No. 1. A few of these specimens, exhibiting scars of branches in the nodal areas, can be assigned to *Eucalamites cruciatus* STERNBERG

(Text-fig. 3E). Besides these relatively large remains, smaller calamitalean axes also occur frequently (Text-fig. 3D).

*Asterophyllites equisetiformis* (SCHLOTHEIM ex STERNBERG) BRONGNIART (Text-fig. 3A–B), a foliage type which is most likely associated with *Calamites undulatus* STERNBERG

(Barthel 2004), is abundant at locality No. 1. This taxon represents the most common calamitacean foliage type in the entire Rotliegend of the Saar-Nahe Basin (Kerp and Fichter 1985, Uhl 2008), and is seen as a typical element of humid environments (Barthel 2004, DiMichele et al. 2006).

One specimen of *Asterophyllites* from the new material has relatively large leaves, and somewhat resembles *Asterophyllites longifolius* (STERNBERG) BRONGNIART (Text-fig. 3C), a taxon whose questionable occurrence in sediments of the Remigiusberg Formation had already been mentioned by Kerp and Fichter (1985). Based on the fragmentary remain with an (incomplete) leaf length of ca. 20 mm, it is not possible to proof an unequivocal affiliation of this remain to this species. As it occurs together with *Asterophyllites equisetiformis* on the same bedding plane, it seems possible that this specimen just represents a long-leaved variety of the latter species.

Sphenophytes represent the most abundant plant remains in all horizons of the Remigiusberg Formation (data presented here, and additional observations in the field), and thus it is somewhat surprising that this group has not been mentioned earlier in the literature from this formation (e.g. Kerp and Fichter 1985, Boy and Schindler 2010, Boy et al. 2012). This discrepancy can probably be explained by the fact that previous studies were mainly based on material in existing university and museum collections (H. Kerp pers. comm. 2001), in which the ubiquitous calamitalean remains had not been incorporated. This was probably due to the fact that they were too “common” to be considered as relevant by collectors, who mainly focused on other groups of organisms (e.g. vertebrate fossils). Such a sampling bias is also known from other localities, where the most common fossils in the outcrops are underrepresented in the corresponding collections.

### Filicophytes

Sterile as well as fertile fragments of pecopterids dominate the flora, besides the ubiquitous sphenophyte remains at locality No. 1. Due to rather poor preservation of the venation, and if present, sporangia caused by the contact-metamorphism, most of these remains cannot be determined down to the species level.

Most sterile specimens can thus only be assigned to the genus *Pecopteris* BRONGNIART, based on frond architecture and pinnule outline. It is even worse for most fertile specimens; it is not even clear to which genus they belong, due to the poor preservation of fine details of sporangia. Some of the specimens, like the one figured in Text-fig. 4E, most likely belong to *Asterotheca* PRESL, based on the form and position of the sporangia. Some sterile specimens can most likely be matched with *Pecopteris densifolia* GOEPPERT (Text-fig. 4A) and *Pecopteris cyathea* SCHLOTHEIM ex BRONGNIART (= *Cyathocarpus cyatheus* (SCHLOTHEIM ex BRONGNIART) MOSBRUGGER; for a detailed taxonomic treatment of the taxa see Cleal 2015) (Text-fig. 4B), based on the form and size of pinnules and poorly visible details of the venation (cf. Barthel 2005). However, as an unequivocal determination of these pecopterids down to the species level is not possible, and since the likely species are morphologically very similar, we can only state that several of the pecopterid remains from locality No. 1 seem to belong to the *Pecopteris arborescens/cyathea* group.

An interesting observation at locality No. 2 is the fact that, although sphenophytes clearly dominate in grey-green

silt- and claystones, unidentifiable remains of pecopterid ferns, though not frequent, are more abundant in red sediments intercalated between these grey-green sediments, whereas calamites are almost missing in this red facies.

### Pteridosperms

Remains of pteridosperms are rare at locality No. 1, and totally missing at locality No. 2. So far, only a single specimen of *Autunia conferta* (STERNBERG) KERP has been discovered at locality No. 1 (Text-fig. 5A). *Autunia naumanni* (GUTBIER) KERP, previously reported by Kerp and Fichter (1985) from the Remigiusberg Formation, is missing from both new localities. First occurrence of both taxa is frequently used to define the base of the *Autunia conferta* zone (e.g. Wagner and Álvarez-Vázquez 2010, Opluštil et al. 2016 and citations therein).

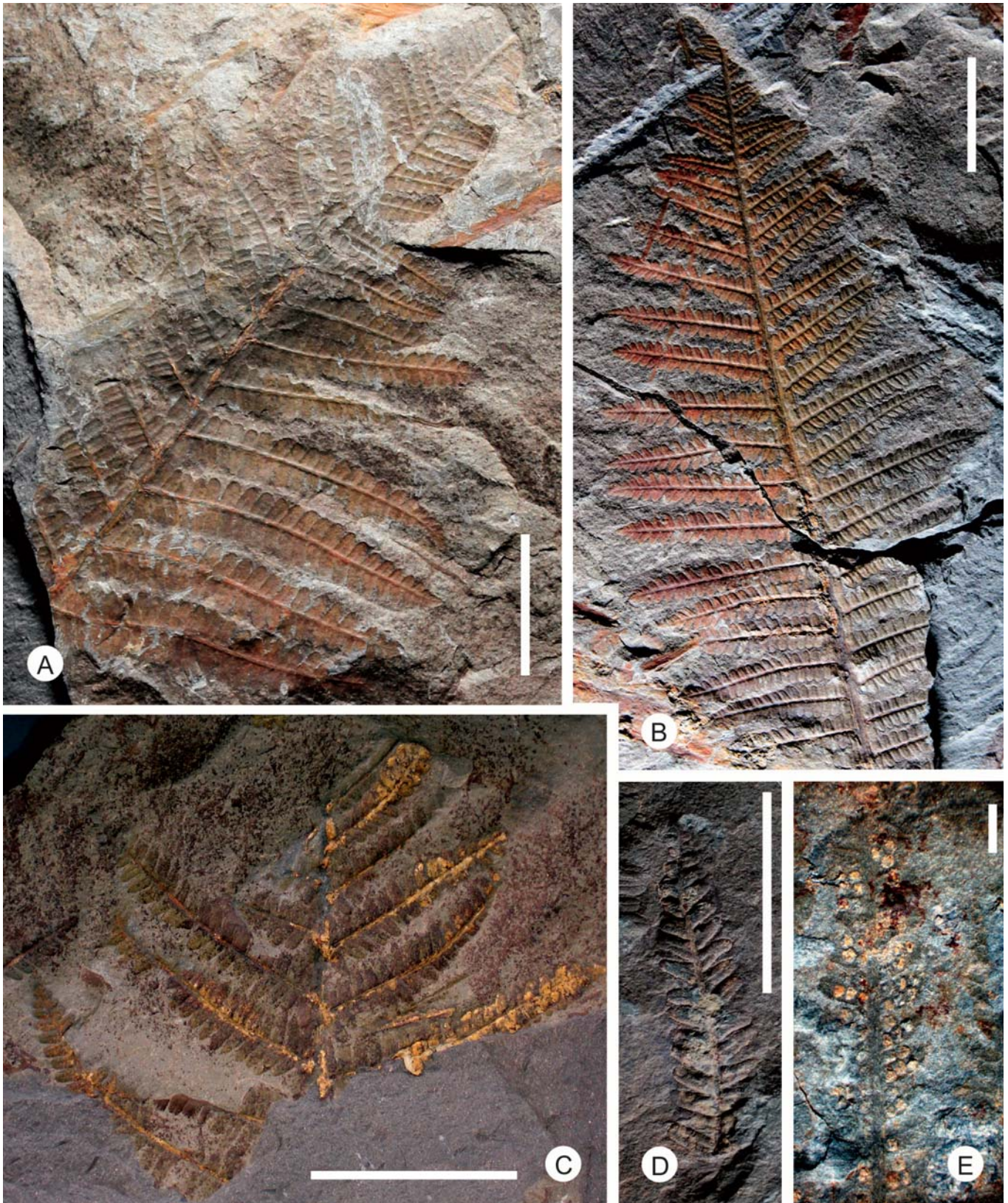
Three rather badly preserved specimens can best be matched with “*Sphenopteris*” *germanica* WEISS, based on their general morphology (Text-fig. 5B–C) (cf. Barthel 2006, DiMichele et al. 2013). This taxon represents a typical element of the mesophilous-xerophilous Rotliegend vegetation, growing at some distance from lakes and rivers (e.g. Gothan and Gimm 1930, Arnhardt 1972, Barthel 2006). It is relatively common in the Central European Rotliegend, e.g. in NW-Saxony, Thuringia and the Sudetic basins (e.g. Remy 1978, Barthel 2006). Although Barthel (2006), in a study on Rotliegend plants from the Thuringian Forest Basin mentioned the occurrence of this taxon in the Rotliegend of the Saar-Nahe Basin, there seems to be no confirmed published record of this taxon from this particular basin so far. An American record of this taxon from the Early Permian of Colorado (Pfefferkorn and Resnik 1980) was later questioned by Dimitrova et al. (2010) as a potential misidentification. However, a similar form has also been reported from the Pennsylvanian of Texas as “*Sphenopteridium* of the *Sphenopteris germanica* type” (e.g. DiMichele 2014: fig. 12). As pointed out by DiMichele et al. (2013), “*Sphenopteris*” *germanica* should be included in *Sphenopteridium* SCHIMPER, but since a formal synonymy (as announced by these authors) has so far not been published, we refrain from using the combination *Sphenopteridium germanicum* for the time being.

### Carpological remains

Seeds are abundant on some slabs from locality No. 1. All are rather badly preserved, and occur mostly as small dots with a shiny luster on the surface of rocks (not necessarily on bedding planes). Due to their overall poor preservation, it is not possible to determine whether these seeds are winged or not, although some larger ones exhibit a kind of shiny and flat halo around a rounded central body (Text-fig. 6A–B). These features resemble the genus *Samaropsis* GOEPPERT, which was previously mentioned by Kerp and Fichter (1985) from the Remigiusberg Formation, but due to the poor preservation of the material, an unequivocal affiliation to this taxon is not possible.

### Taphonomy and palaeoenvironment

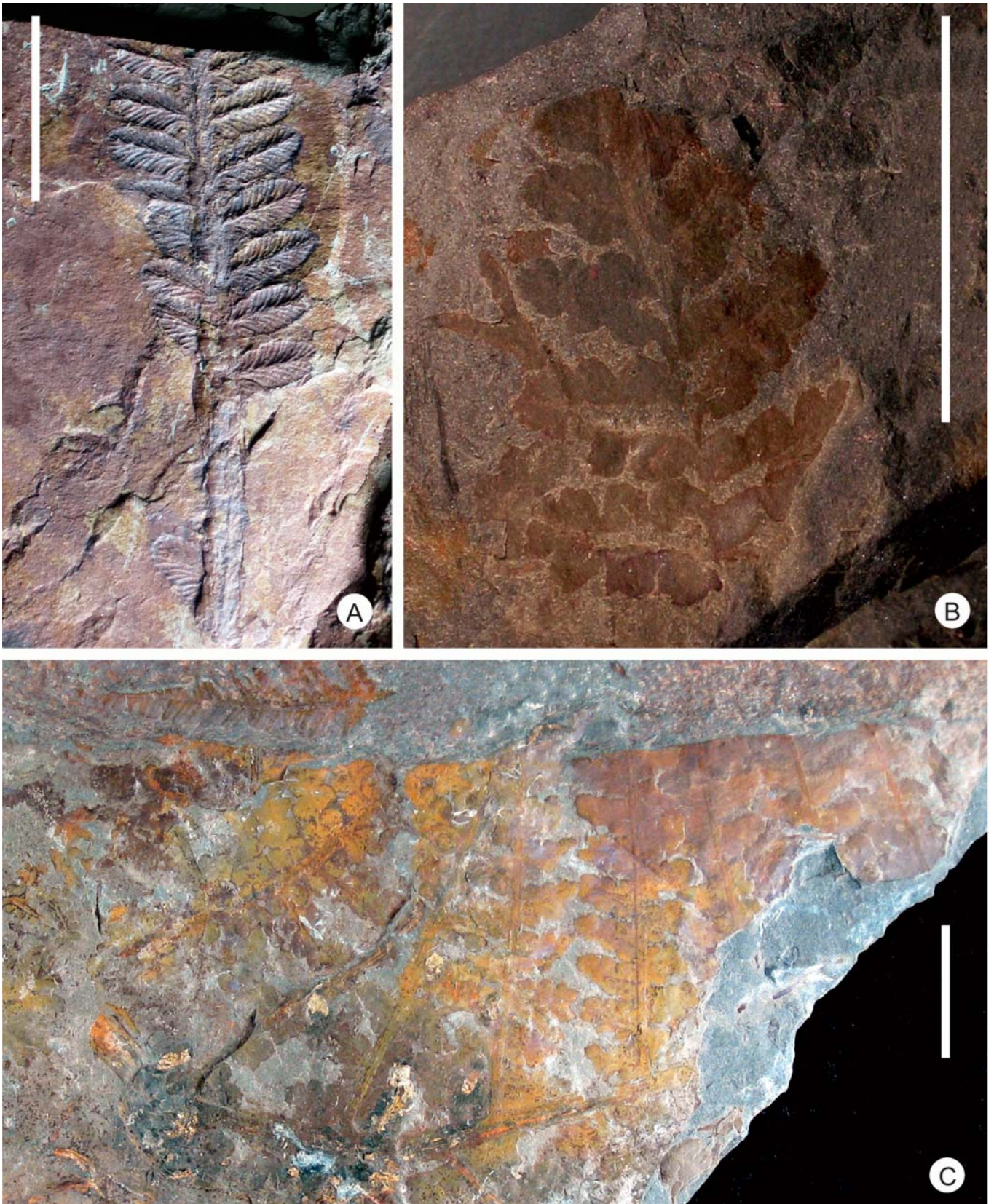
Based on palynological data (from an unpublished report), Boy and Schindler (2000) postulated that the more



Text-fig. 4. Fern remains from Remigiusberg Formation. A) pectopterid remain belonging to *Pecopteris arborescens/cyathea* group, Inv.-Nr. PB 2016/5033 LS (LS-RLP), scalebar = 2 cm; B) pectopterid remain belonging to *Pecopteris arborescens/cyathea* group, Inv.-Nr. PB 2016/5029a+b LS (LS-RLP), scalebar = 2 cm; C) *Pecopteris* sp., Inv.-Nr. PB 2010/5809 LS (LS-RLP), scalebar = 2.5 cm; D) *Pecopteris* sp., Inv.-Nr. PB 2016/5029b LS (LS-RLP), scalebar = 2 cm; E) *Asterotheca* sp., Inv.-Nr. PB 2010/5812 LS (LS-RLP), scalebar = 2 mm.

meso- to xerophilous “hinterland” vegetation spread into basal habitats during deposition of the Remigiusberg Formation, in some places even replacing plants which grow

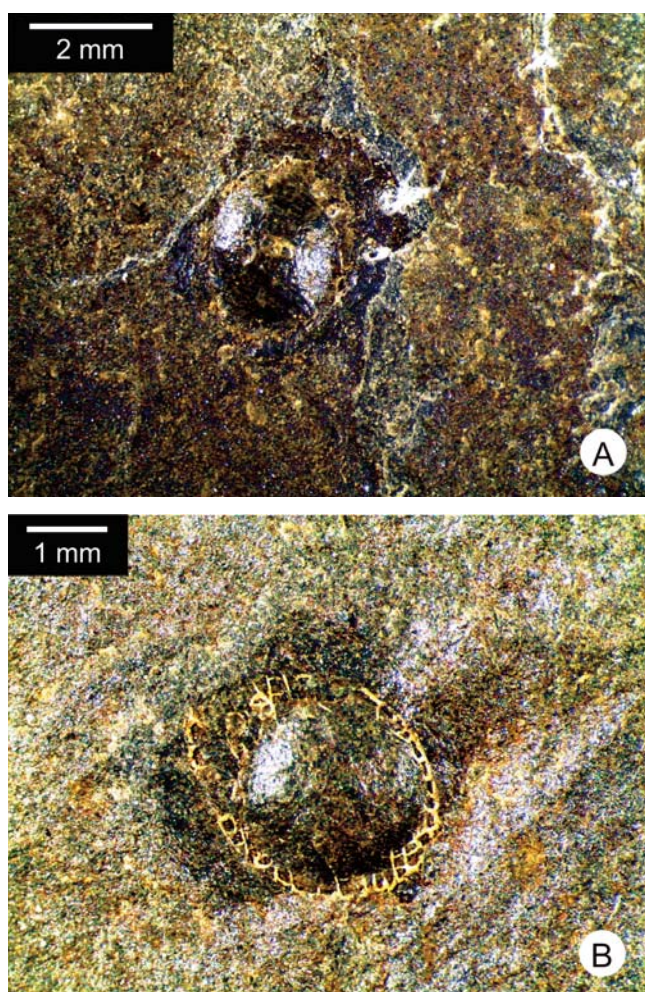
in substrates saturated with water for longer periods of time, like most ferns and sphenophytes from the riparian zone. Such an increase of more dry-adapted plants, and a



Text-fig. 5. Pteridosperm remains from Remigiusberg Formation. A) *Autunia conferta*, coll. Emrich, scalebar = 2 cm; B) “*Sphenopteris*” *germanica*, Inv.-Nr. PB 2010/5806 LS (LS-RLP), scalebar = 2.5 cm; C) “*Sphenopteris*” *germanica*, Inv.-Nr. PB 2016/5029b LS (LS-RLP), scalebar = 2 cm.

replacement of typical wetland vegetation from riparian habitats (or wet lands in a wide sense) is so far not indicated by the macroflora from this formation. However, palyno-

logical data and macrofloral data do not necessarily contradict each other, if some basic taphonomic aspects are considered. Palynomorphs are usually transported over larger



**Text-fig. 6.** Selected carpological remains from Remigiusberg Formation. A) cf. *Samaropsis* sp., Inv.-Nr. PB 2016/5038 LS (LS-RLP); B) cf. *Samaropsis* sp., Inv.-Nr. PB 2016/5029a LS (LS-RLP).

distances than most plant macroremains, and thus typical hinterland palynomorphs can occur in depositional systems, like lacustrine or marine environments, even if the source habitats are located some distance from these environments (e.g. Traverse 2007). For most macroremains, riparian vegetation can provide effective barriers for the transport from the source habitat into such areas of deposition (e.g. Ferguson 1985). Only when the wetland “belt” becomes smaller, and a (hypothetical) taphonomic threshold is crossed, the probability that a considerable number of non-wetland macroremains can be transported into the areas of deposition increases significantly. The rather low number of typical elements from the “hinterland” vegetation, adapted to seasonal or continuous dry conditions in the Remigiusberg Formation, and the dominance of plants adapted to (at least seasonally) wet conditions, like sphenophytes and ferns, implies that the riparian vegetation was still dominated by typical wetland plant communities, and that the riparian belt still acted as a considerable taphonomic barrier, preventing a significant input of mesophilous (rare) or even xerophilous remains (so far completely missing) into the lake.

Thus we can reconstruct the margin of the lake (and probably also the margins of its major tributaries) as colonized by a typical wetland community, consisting of

sphenophytes and ferns. Some distance from the lake and its major tributaries (maybe less than a hundred meters), the habitats of the more mesophilous plants, like the two *Autunia* species and “*Sphenopteris*” cf. *germanica* might have been located. At the moment, nothing can be said about how far this mesophilous “belt” stretched, or where habitats of xerophilous plants, like conifers, were located in relation to the lake margin, but palynological data hint at their presence somewhere in the “hinterland” of the lake.

In contrast with the palynoflora of the Remigiusberg Formation, which contains a number of “modern”, meso-xerophilous hinterland-elements (cf. Boy and Schindler 2000), the macroflora is dominated by “archaic” elements from wet habitats. This discrepancy can probably be explained by taphonomic filters, and differences between this flora and the flora from the unconformably (?) underlying Breitenbach Formation (“Stephanian C”, Gzhelian) (Cleal 2008), as well as a hinterland flora from the Heusweiler Formation (“Stephanian B”, Kazimovian – Gzhelian) (Kerp et al. 2007b) can probably be explained by climatic and/or tectonic changes, which also led to considerable changes in the depositional systems of the basin (e.g. Boy et al. 2012). These changed from a landscape dominated by braided rivers and extensive, long lasting coal swamps (the permanently most humid end member of plant habitats) to a landscape dominated by meandering rivers and lakes in the lower Rotliegend (Glan subgroup). This led to a spatial reduction of wetlands, which covered large landscapes during the Carboniferous, to marginal “wet spots”. Such a change is typical for the development of the vegetation all over Euramerica during the Carboniferous-Permian transition (e.g. DiMichele et al. 2006).

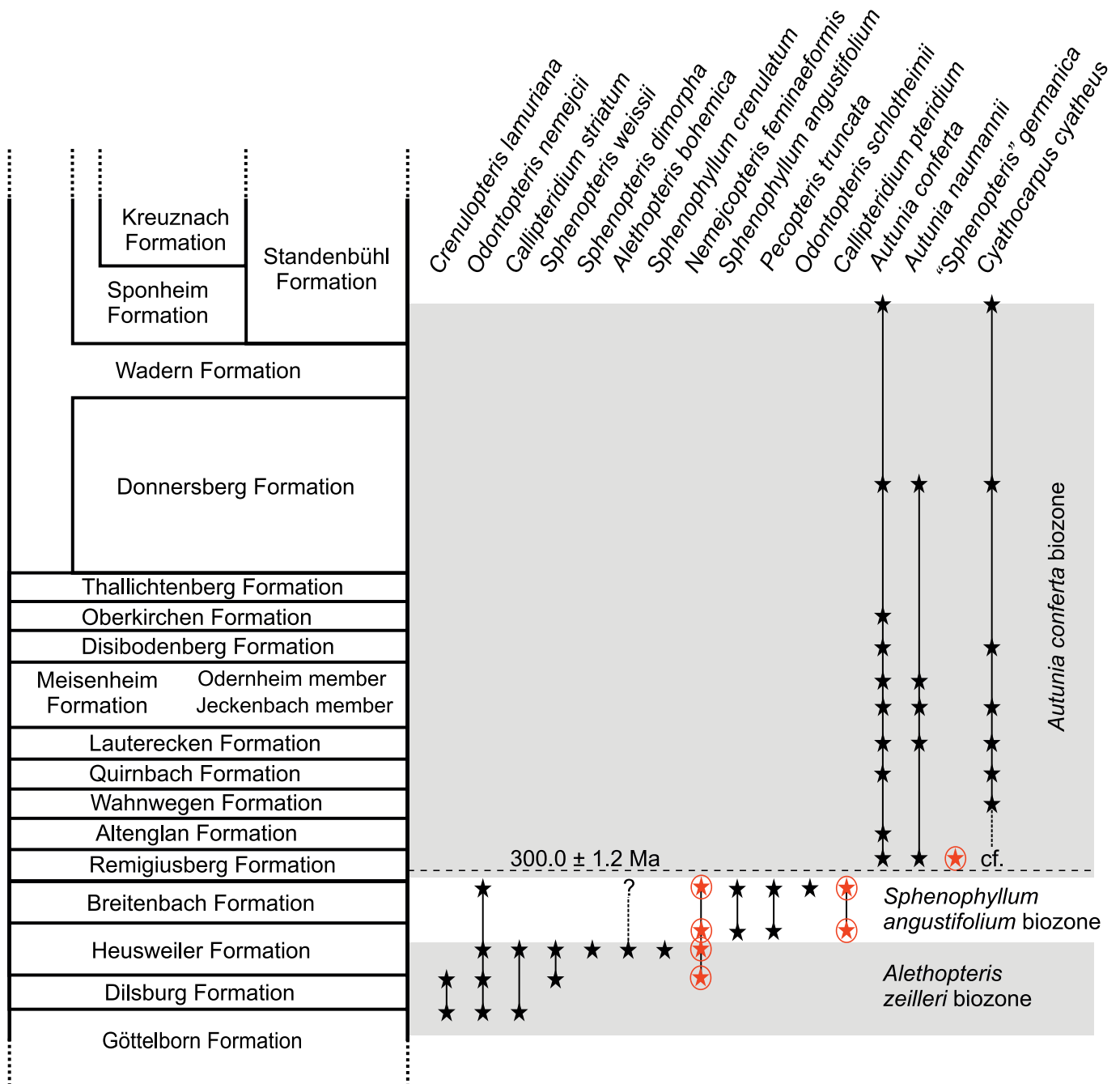
## Biostratigraphic implications

The most important marker for the base of the *Autunia conferta* biozone is the first occurrence of the name-giving pteridosperm *A. conferta*. Originally it was assumed that this taxon would be an index fossil for the Permian (e.g. Jongmans 1928, Jongmans and Gothan 1937), but subsequent work uncovered an earlier appearance in the late Pennsylvanian (Stephanian; e.g. Havlena 1970, Remy 1978, Kerp 1988).

Recently Barthel (2006) stated that *Autunia conferta* would only occur in the Lower Permian parts of the profiles in the Central European Rotliegend basins, and cited W. Gothan and W. Remy as authorities for such a statement, unfortunately without providing explicit references published by these eminent palaeobotanists. In any case, Opluštil et al. (2016) demonstrated that the taxon indeed appeared in the Late Pennsylvanian in many Central and Eastern European sedimentary basins.

Besides the name-giving taxon, other representatives of the genus *Autunia* are frequently used to support the base of this biozone (e.g. Opluštil et al. 2016, and citations therein). “*Sphenopteris*” *germanica* is also considered as an index fossil for the *Autunia conferta* zone (e.g. Remy 1978), and in many (but not all) other contemporary basins, *Cyathocarpus cyatheus* has its first appearance near the base of the *Autunia conferta* zone (e.g. Opluštil et al. 2016).





★ taxa that reach higher up into the *A. conferta* zone in other Rotliegend basins

Text-fig. 7. Stratigraphic ranges of selected, biostratigraphically relevant taxa from Late Pennsylvanian and Early Permian of Saar-Nahe Basin. Based on data from Kerp and Fichter (1985), Lausberg et al. (2003), Schindler et al. (2004), Kerp et al. (2007a, b), Cleal (2008) and Uhl (2008). Absolute age of  $300.0 \pm 1.2$  Ma in middle of Remigiusberg Formation based on Ar-Ar dating of sanidins published by Burger et al. (1997).

This places the oldest evidence for the *Autunia conferta* zone within the Saar-Nahe Basin in the upper part of the Remigiusberg Formation, whereas the top of the underlying Breitenbach Formation belongs to the *Sphenophyllum angustifolium* zone (Cleal 2008, cf. Text-fig. 7).

In other Central and Eastern European basins, the base of the *Autunia conferta* zone is clearly located in the late Gzhelian, but it became also clear that the base of the *A. conferta* zone is diachronous across Europe (Opluštil et al. 2016). This implies that the upper part of the Remigiusberg Formation is probably not older than the late Gzhelian. Cleal

(2008) suggested the possibility of a minor discontinuity at the top of the Breitenbach Formation ("Stephanian C" – Gzhelian), and thus it is not clear if a part of the late Gzhelian (or even a part of the lower Asselian) is missing in this basin. An Asselian age of the plant bearing sediments cannot be excluded based on the palaeobotanical data alone, as the *Autunia conferta* zone reaches widely up into the Early Permian.

Following Henderson et al. (2012), the best interpolation for the base of the Asselian and thus the entire Permian provides an age of  $298.9 \pm 0.2$  Ma. For the Saar-Nahe Basin,

Burger et al. (1997), based on Ar-Ar dating of sanidins, provided an absolute age of  $300.0 \pm 1.2$  Ma for a tuff near the “Stephanian C”/Rotliegend boundary in the northern part of the Saarland. According to Boy et al. (2012), this age comes from the so-called “Dirmingen-Tuff”, which is situated in the middle part of the Remigiusberg Formation. It would thus be slightly older than the new plant remains described here. However, as pointed out by different authors (e.g. Davydov et al. 2012), the Ar-Ar technique often provides rather imprecise age dates, compared to other techniques, due to intrinsic analytical and systematic errors. Thus such ages have to be interpreted with great care.

Considering only the numerical errors of both absolute age data, the Gzhelian-Asselian boundary could be within the middle to upper part of the Remigiusberg Formation. Without the errors, the “Dirmingen” tuff would clearly be of late Gzhelian age, supporting a late Gzhelian age for the only slightly younger plant-bearing sediments of the Remigiusberg Formation, but unfortunately this age has still to be considered with great care, as it might be rather imprecise, due to technical reasons (cf. Davydov et al. 2012). If this age were precise, it would imply that the Gzhelian-Asselian (Pennsylvanian-Permian) boundary is either near the top of the Remigiusberg Formation or within the following Altenglan Formation, as previously suggested by Boy and Schindler (2000, 2012), based on ecostratigraphic data. In contrast, both alternatives would contradict other biostratigraphic schemes based on inter-basinal correlations of palaeozoological remains (e.g. Roscher and Schneider 2005, Schneider and Werneburg 2006, 2012). Due to inconsistencies and technical problems with absolute ages derived from different volcanic marker beds within the Saar-Nahe Basin (cf. Menning et al. 2005, Davydov et al. 2012), there is still a big problem using such data from this basin. Thus it is still not possible to provide an unambiguous solution for positioning the Gzhelian-Asselian boundary within the Saar-Nahe Basin.

## Acknowledgements

We thank Prof. em. Dr. Ortwin Emrich, Kottweiler-Schwanden, for loan of specimens, for alerting us to the new locality exposed in 2007, and for support during field work; Robert Noll, Tiefenthal/Pfalz, for loan of specimens; Dr. Gunter Isbarn, Tiefenthal/Pfalz, for the opportunity to investigate material collected at locality No. 2; Dr. Michael Wuttke, formerly at Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Direktion Landesarchäologie, Referat Erdgeschichte in Mainz, for loan of material (LS-RLP), Dr. Thomas Schindler, Spabrücken, for information concerning the stratigraphic position of the localities at the Remigiusberg and last but not least Dr. Sebastian Voigt, Urmuseum GEOSKOP, for many fruitful discussions about the fossil fauna and flora of the Remigiusberg Formation. A. Jasper acknowledges CAPES (Brazil – 8107-14-9) and the Alexander von Humboldt Foundation (Germany BRA 1137359 STPCAPES), and the financial support from FAPERGS and CNPq (305436/2015-5). D. Uhl acknowledges financial support from CAPES (“Science without Borders Program” – A072/2013). Furthermore, we thank Chris Cleal, Milan Libertín and Josef Pšenička for their constructive reviews, which helped to improve the manuscript considerably.

## References

- Arnhardt, A. (1972): Tektonik, Stratigraphie und Flora des Stefan und Rotliegenden im Thüringer Wald. – Berichte der deutschen Gesellschaft für geologische Wissenschaften, A17(1): 81–100.
- Barthel, M. (2004): Die Rotliegendflora des Thüringer Waldes. Teil 2: Calamiten und Lepidophyten. – Veröffentlichungen, Naturhistorisches Museum Schleusingen, 19: 19–48.
- Barthel, M. (2005): Die Rotliegendflora des Thüringer Waldes. Teil 3: Farne. – Veröffentlichungen, Naturhistorisches Museum Schleusingen, 20: 27–56.
- Barthel, M. (2006): Die Rotliegendflora des Thüringer Waldes. Teil 4: Farnsamer und Farnlaub unbekannter taxonomischer Stellung. – Veröffentlichungen, Naturhistorisches Museum Schleusingen, 21: 33–72.
- Boy, J. A., Fichter, J. (1982): Zur Stratigraphie des saarpfälzischen Rotliegenden (Ober-Karbon - Unter-Perm; SW-Deutschland). – Zeitschrift der Deutschen Geologischen Gesellschaft, 133: 607–642.
- Boy, J. A., Haneke, J., Kowalczyk, G., Lorenz, V., Schindler, T., Stollhofen, H., Thum, H. (2012): Rotliegend im Saar-Nahe-Becken, am Taunus-Südrand und im nördlichen Rheingraben. – In: Lütznert, H., Kowalczyk, G., Deutsche Stratigraphische Kommission (eds), Stratigraphie von Deutschland X. Rotliegend. Teil I: Innervariscische Becken. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, 61: 254–377.
- Boy, J. A., Schindler, T. (2000): Ökostratigraphische Bioevents im Grenzbereich Stephanium/Autunium (höchstes Karbon) des Saar-Nahe-Beckens (SW-Deutschland) und benachbarter Gebiete. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 216: 89–152.
- Boy, J. A., Schindler, T. (2012): Ökostratigraphie des Rotliegenden. – In: Lütznert, H., Kowalczyk, G., Deutsche Stratigraphische Kommission (eds), Stratigraphie von Deutschland X. Rotliegend. Teil I: Innervariscische Becken. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, 61: 143–160.
- Burger, K., Hess, J. C., Lippolt, H. J. (1997): Tephrochronologie mit Kaolin-Kohlesteinen: Mittel zur Korrelation paralischer und limnischer Ablagerungen des Oberkarbons. – Geologisches Jahrbuch, A, 147: 3–39.
- Cleal, C. J. (2008): Macrofloral biostratigraphy of the Ottweiler group in Saar-Lorraine and its consequences for Stephanian palynostratigraphy and geochronology. – *Studia Geologica Polonica*, 129: 9–23.
- Cleal, C. J. (2015): The generic taxonomy of Pennsylvanian age marattialean fern frond adpressions. – *Palaeontographica*, Abt. B, 292: 1–21
- Davydov, V. I., Korn, D., Schmitz, M. D. (2012): The Carboniferous Period. – In: Gradstein, F. M., Ogg, J. G., Schmitz, M. D., Ogg, G. M. (eds), *The Geological Timescale 2012*, vol. 2. Elsevier, Amsterdam, pp. 603–651.  
<https://doi.org/10.1016/b978-0-444-59425-9.00023-8>
- DiMichele, W. A. (2014): Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. – *International Journal of Plant Sciences*, 175: 123–164.  
<https://doi.org/10.1086/675235>

- DiMichele, W. A., Tabor, N. J., Chaney, D. S., Nelson, W. J. (2006): From wetlands to wet spots: Environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. – In: Greb, S. F., DiMichele, W. A. (eds), *Wetlands Through Time*. – GSA Special Papers, 399: 223–248.
- DiMichele, W. A., Wagner, R. H., Bashforth, A. R., Álvarez-Vázquez, C. (2013): An update on the flora of the Kinney Quarry of central New Mexico (Upper Pennsylvanian), its preservational and environmental significance. – *Bulletin, New Mexico Museum of Natural History and Science*, 59: 289–325.
- Dimitrova, T. K., Zodrow, E. L., Cleal, C. J., Thomas, B. A. (2010): Palynological evidence for Pennsylvanian (Late Carboniferous) vegetation change in the Sydney coalfield, eastern Canada. – *Journal of the Geological Society*, 45: 388–396.
- Ferguson, D. K. (1985): The origin of leaf-assemblages – new light on an old problem. – *Review of Palaeobotany and Palynology*, 46: 117–188.  
[https://doi.org/10.1016/0034-6667\(85\)90041-7](https://doi.org/10.1016/0034-6667(85)90041-7)
- Fröbisch, J., Schoch, R. R., Müller, J., Schindler, T., Schweiss, D. J. (2011): The oldest amniote from Germany: a sphenacodontid synapsid from the Saar-Nahe Basin. – *Acta Palaeontologica Polonica*, 56: 113–120.  
<https://doi.org/10.4202/app.2010.0039>
- German Stratigraphic Commission (ed.) (2002): *Stratigraphic Table of Germany 2002*. – GeoForschungsZentrum, Potsdam, 1 p.
- Gothan, W., Gimm, O. (1930): Neuere Beobachtungen und Betrachtungen über die Flora des Rothliegenden in Thüringen. – *Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine*, 2(1): 39–74.
- Havlena, V. (1970): Einige Bemerkungen zur Phytogeographie und Geobotanik des Karbons und Perms. – *Compte Rendu 6e Congrès International de Stratigraphie et Géologie du Carbonifère (Sheffield 1967)*, 3: 901–912.
- Henderson, C. M., Davydiv, V. I., Wardlaw, B. R. (2012): The Permian Period. – In: Gradstein, F. M., Ogg, J. G., Schmitz, M. D., Ogg, G. M. (eds), *The Geological Timescale 2012*, vol. 2. Elsevier, Amsterdam, pp. 653–680.  
<https://doi.org/10.1016/b978-0-444-59425-9.00024-x>
- Henk, A. (1993): Late orogenic basin evolution in the Variscan Internides: the Saar-Nahe Basin, southwest Germany. – *Tectonophysics*, 223: 273–290.  
[https://doi.org/10.1016/0040-1951\(93\)90141-6](https://doi.org/10.1016/0040-1951(93)90141-6)
- Jongmans, W. J. (1928): *Congress pour l'étude de la stratigraphie du Carbonifère dans les différents centres houillers de l'Europe*. – *Compte Rendu Congrès pour l'avancement des études de Stratigraphie Carbonifère (Heerlen 1927)*, 1: 1–48.
- Jongmans, W. J., Gothan, W. (1937): *Betrachtungen über die Ergebnisse des Zweiten Kongresses für Karbonstratigraphie*. – *Compte Rendu 2ème Congrès pour l'avancement des études de Stratigraphie Carbonifère (Heerlen 1935)*, 1: 1–40.
- Kerp, J. H. F. (1988): Aspects of Permian Palaeobotany and Palynology. X. The West- and Central European species of the genus *Autunia* Krasser emend. Kerp (Peltaspermaeae) and the form-genus *Rhachiphyllum* Kerp (callipterid foliage). – *Review of Palaeobotany and Palynology*, 54: 249–360.  
[https://doi.org/10.1016/0034-6667\(88\)90017-6](https://doi.org/10.1016/0034-6667(88)90017-6)
- Kerp, H. (2000): The modernization of landscapes during the Late Paleozoic–Early Mesozoic. – *Paleontological Society Papers*, 6: 79–113.
- Kerp, H., Fichter, J. (1985): Die Makroflora des saarpfälzischen Rotliegenden (? Ober-Karbon – Unter-Perm; SW-Deutschland). – *Mainzer geowissenschaftliche Mitteilungen*, 14: 159–286.
- Kerp, H., Noll, R., Uhl, D. (2007a): Übersicht über Pflanzengruppen und Vegetationsentwicklung im Permokarbon des Saar-Nahe Beckens. – In: Schindler, T., Heidtke, U. H. J. (eds), *Kohlesümpfe, Seen und Halbwüsten – Dokumente einer rund 300 Millionen Jahre alten Lebewelt zwischen Saarbrücken und Mainz*. POLLICHA Sonderveröffentlichung, 10: 42–74.
- Kerp, H., Noll, R., Uhl, D. (2007b): Vegetationsbilder aus dem saarpfälzischen Permokarbon. – In: Schindler, T., Heidtke, U. H. J. (eds), *Kohlesümpfe, Seen und Halbwüsten – Dokumente einer rund 300 Millionen Jahre alten Lebewelt zwischen Saarbrücken und Mainz*. POLLICHA Sonderveröffentlichung, 10: 76–109.
- Lausberg, S. (2002): *Neue Kenntnisse zur saarpfälzischen Rotliegendeflora unter besonderer Berücksichtigung der Coniferentaxonomie und des Hinterlandes*; Ph.D. Thesis. – MS, Westfälische Wilhelms-Universität Münster, Münster, Germany, 266 pp. (copy on-line urn:nbn:de:hbz:6-85659550011)
- Lausberg, S., Kerp, H. (2000): Eine Coniferen-dominierte Flora aus dem Unterrotliegend von Alsenz, Saar-Nahe-Becken, Deutschland. – *Feddes Repertorium*, 111: 399–426.  
<https://doi.org/10.1002/fedr.20001110706>
- Lausberg, S., Noll, R., Kerp, H. (2003): Die Floren der Rhyolithischen Tuffserien im Rotliegend des Saar-Nahe-Beckens: Olsbrücken (RT II). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 227: 63–92.
- Menning, M., Weyer, D., Wendt, I., Drozdowski, G., Hambach, U. (2005): Eine Numerische Zeitskala für das Pennsylvanium in Mitteleuropa. – In: *Deutsche Stratigraphische Kommission (ed.), Stratigraphie von Deutschland V – Das Oberkarbon (Pennsylvanium) in Deutschland*. Courier Forschungs-Institut Senckenberg, 254: 181–198.
- Opluštil, S., Schmitz, M., Cleal, C. J., Martinek, K. (2016): A review of the Middle–Late Pennsylvanian west European regional substages and floral biozones, and their correlation to the Geological Time Scale based on new U–Pb ages. – *Earth-Science Reviews*, 154: 301–335.  
<https://doi.org/10.1016/j.earscirev.2016.01.004>
- Pfefferkorn, H. W., Resnik, D. A. (1980): The occurrence of *Sphenopteris germanica* (pteridosperm, Autunian, Lower Permian). – *Journal of Paleontology*, 54: 81–84.
- Remy, W. (1978): Die *Sphenopteris-germanica*-Gruppe in den Sueplinger-Schichten (Flechtlinger Höhenzug). Ein Beleg für das Autun-Alter. – *Argumenta Palaeobotanica*, 5: 161–165.
- Roscher, M., Schneider, J. W. (2005): An annotated correlation chart for continental Late Pennsylvanian and Permian basins and the marine scale. – In: Lucas, S. G.,

- Zeigler, K. E. (eds), The Nonmarine Permian. – Bulletin, New Mexico Museum of Natural History and Science, 30: 282–291.
- Schäfer, A. (1986): Die Sedimente des Oberkarbons und Unterrotliegenden im Saar-Nahe-Becken. – Mainzer geowissenschaftliche Mitteilungen, 15: 239–365.
- Schäfer, A., Korsch, R. J. (1998): Formation and sediment fill of the Saar-Nahe Basin (Permo-Carboniferous, Germany). – Zeitschrift der Deutschen Geologischen Gesellschaft, 149: 233–269.
- Schindler, T. (2007): Geologie, Stratigraphie und Genese des permokarbonischen Saar-Nahe-Beckens. – In: Schindler, T., Heidtke, U. H. J. (eds), Kohlesümpfe, Seen und Halbwüsten – Dokumente einer rund 300 Millionen Jahre alten Lebewelt zwischen Saarbrücken und Mainz. – POLLICHIA Sonderveröffentlichung, 10: 4–37.
- Schindler, T., Uhl, D., Noll, R., Bach, T., Höhn, W., Poschmann, M., Rahm, B., Schweiss, D., Wuttke, M. (2004): Erstfunde von *Sigillaria*-Stämmen in situ in Rotliegend-Ablagerungen (Ober-Karbon bis Unter-Perm) der Nordpfalz (Südwestdeutschland). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 233: 1–26.
- Schneider, J. W., Werneburg, R. (2006): Insect biostratigraphy of the Euramerican continental Late Pennsylvanian and Early Permian. – In: Lucas, S. G., Cassinis, G., Schneider, J. W. (eds), Non-marine Permian biostratigraphy and biochronology. – Special Publication, Geological Society, 265: 325–336. <https://doi.org/10.1144/GSL.SP.2006.265.01.15>
- Schneider, J., Werneburg, R. (2012): Stratigraphie des Rotliegend mit Insekten und Amphibien. – In: Lützner, H., Kowalczyk, G., Deutsche Stratigraphische Kommission (eds), Stratigraphie von Deutschland X. Rotliegend. Teil I: Innervariscische Becken. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, 61: 110–142.
- Stapf, K. R. G. (1990): Fazies und Verbreitung lakustriner Systeme im Rotliegend des Saar-Nahe-Beckens (SW-Deutschland). – Mainzer geowissenschaftliche Mitteilungen 19: 213–234.
- Stapf, K. R. G. (1997): Rotliegend lacustrine sediments of the Saar-Nahe Basin (SW-Germany). – Gaea heidelbergensis, 4: 15–28.
- Traverse, A. (2007): Paleopalynology, 2<sup>nd</sup> ed. (Topics in Geobiology, vol. 28). – Springer, Dordrecht, 813 pp.
- Uhl, D. (2006): Ein Baumfarn der Gattung *Caulopteris* Lindley et W. Hutton aus dem Rotliegend (Oberkarbon – Unterperm) des Saar-Nahe-Beckens (SW-Deutschland). – Mitteilungen der POLLICHIA, 92: 5–8.
- Uhl, D. (2008): Die Paläoflora aus dem Rotliegend (Oberkarbon – Unterperm; Meisenheim formation; M5) von Niedermoschel (Saar-Nahe-Becken, SW-Deutschland). – Mainzer geowissenschaftliche Mitteilungen, 36: 7–36.
- Uhl, D., Heidtke, U. H. J. (2003): *Crossothea* Zeiller und *Caulopteris* Lindley et W. Hutton aus dem Rotliegend (Ober-Karbon – Unter-Perm) des Saar-Nahe-Beckens (SW-Deutschland). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 2003(6): 663–675.
- Uhl, D., Lausberg, S., (2008): Land plant diversity in selected Latest Pennsylvanian?–Permian deposits from the Saar-Nahe Basin (SW-Germany) and the German Zechstein basin. – Studia Geologica Polonica, 129: 81–106.
- Uhl, D., Lausberg, S., Noll, R., Stapf, K. R. G., (2004): Wildfires in the Late Palaeozoic of Central Europe – An overview of the Rotliegend (Upper Carboniferous – Lower Permian) of the Saar-Nahe Basin (SW-Germany). – Palaeogeography, Palaeoclimatology, Palaeoecology, 20: 23–35. <https://doi.org/10.1016/j.palaeo.2004.01.019>
- Uhl, D., Raisch, M. (2009): Die fossile Schachtelhalmbeblätterung *Calamariophyllum* im Rotliegend des Saar-Nahe Beckens – Fundmitteilung. – Mitteilungen der POLLICHIA, 94: 1–4.
- Voigt, S., Fischer, J., Schindler, T., Wuttke, M., Spindler, F., Rinehart, L. (2014): On a potential fossil hotspot for Pennsylvanian-Permian non-aquatic vertebrates in central Europe. – Paläontologie, Stratigraphie, Fazies (22), Freiburger Forschungshefte, C, 548: 39–44.
- Voigt, S., Uhl, D. (2015): Das Rotliegend (Oberkarbon – Unterperm) im Saar-Nahe-Becken (SW-Deutschland). – ZfB-Scriptum: Veröffentlichungen des Zentrums für Biodokumentation, 4: 60–80.
- Wagner, R. H., Álvarez-Vázquez, C. (2010): A redescription of the Stephanian species *Callipteridium virginianum* (Fontaine & White, 1880) comb. nov. and *Alethopteris leonensis* Wagner, 1964. – Scripta Geologica, Special Issue, 7: 93–139.