The upper Carboniferous-Lower Permian flora of Zöbing, Lower Austria

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Earth, Life and Climate
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Abstract

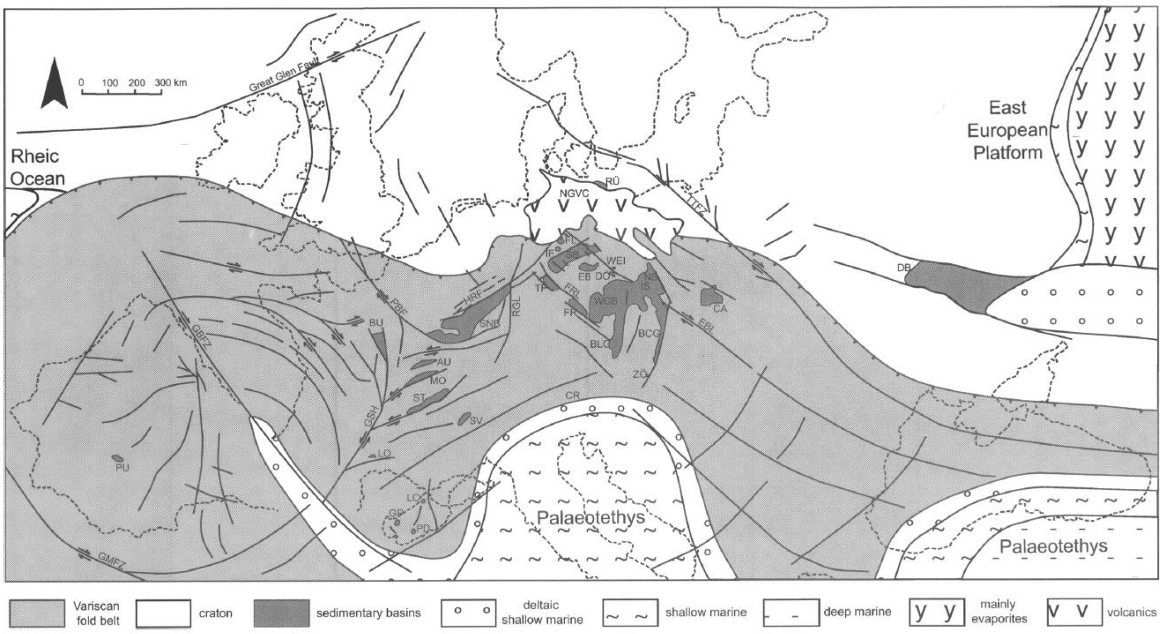
During the Late Carboniferous and early Permian, a major floristic change took place in Euramerica. Gymnosperms replaced the previously dominant pteridophytes. This reflects a climatic change, i.e. from wetland-dominated to more arid conditions. Extensive studies on the vegetation during this time interval have recently been carried out in the Czech Republic. The Zöbing formation in Austria, is of the same age of these Czech formations, but has not yet been compared to them. Material from the Zöbing formation has been examined and compared to Czech floras. A clear transition can be seen in the flora of the Zöbing formation, from a Stephanian tree fern and *Alethopteris zeilleri* dominated flora, to a Asselian flora dominated by peltasperms and conifers. There are clear similarities between the floras of the Zöbing formation and the different Czechian formations, despite notable differences in species composition and abundance between Zöbing and the Czech formations. This is especially true for the nearby Boskovice Basin.

1. Introduction

The Carboniferous period is well known for its coal swamps with large lycopods and large arthropods. However, at the end of the Westphalian stage (late Carboniferous), a major change in vegetation among tropical plant species took place. This event is often referred to as the Carboniferous rainforest collapse. After the C.R.C. the vegetation was dominated by tree ferns, medullosan pteridosperms, and sigillarian lycopsids, although dominant species patterns between localities could vary. (DiMichele, Phillips 1996) The earliest pollen from conifers date back to the early Carboniferous.(Stephenson, Millward et al. 2008) However, conifer macro fossils are extremely rare before the C.R.C. They become more abundant in the Late Carboniferous. This suggests the beginning of seasonally dry environments in the tropic region. Their presence, together with other more advanced seed plant like peltasperms, would become more common near the end of the Carboniferous and into the Permian.(DiMichele, Phillips 1996, Kerp 1996)

The super continent Pangea was not yet formed in the Early Carboniferous. Parts of modern China formed the island continent of Cathaysia situated in an equatorial position. Parts of modern Siberia formed the temperate continent Angara in the Northern Hemisphere. In the Southern Hemisphere Africa, South America, India, Australia and Antarctica formed Gondwana. This continent was centered around the south pole and partly covered by a large ice sheet. Gondwana moved northward towards the equator during the Carboniferous. Europe and North America formed the continent of Laurussia, which was slowly moving from to the equator to the Northern Hemisphere.

The collision between Gondwana and Laurussia was the beginning of the formation of the supercontinent Pangea that eventually resulted in the Variscan Orogeny. This meant that the southern half of Europe was uplifted including the Bohemian Massif(Kroner, Hahn et al. 2007). North of the Bohemian Massif the western and central Bohemian basins and the Intra Sudetic basin were situated, east of the Bohemian Massif the Boskovice Basin, and southeast the Zöbing Basin(Roscher, Schneider 2006). Sediments from the Boskovice Basin and Zöbing Basin where derived from different source areas, which makes it hypothetical whether these two basins were in contact with each other or not.



Basins are omitted. Relevant basins for this thesis are the BLG, Blanice Graben; BCG, Boskovice Graben; IS, Intra Sudetic Basin; NS, North Sudetic Basin; WCB, Western and Central Bohemian Basins; ZO, Zöbingen. After (Roscher, Schneider 2006)

The climate in the equatorial region gradually became drier, although it is marked by oscillations between drier and wetter phases.(Roscher, Schneider 2006) In the middle Carboniferous, Gondwanna collided with Laurussia. Thie Variscan Orogney caused an uplift of the equatorial lowlands, but mountain ranges probably did not exceed altitudes of over 2000 m,(Roscher, Schneider 2006). Wet lowland regions became drier highland regions, which exaggerated the effect of the drying climate.

The vegetation had to adapt to these changes, leading to the evolution of new plant orders in these habitats(DiMichele, Aronson 1992). However, most evolutionary innovations took place in ecologically stressed extrabasinal areas, which have yielded only few fossils(Looy, Kerp et al. 2014). The increasingly drier climate made enabled these newer orders to migrate into the lowland regions, were they replaced the old vegetation types that were dominated by wetland elements(DiMichele, Aronson 1992, Looy, Kerp et al. 2014).

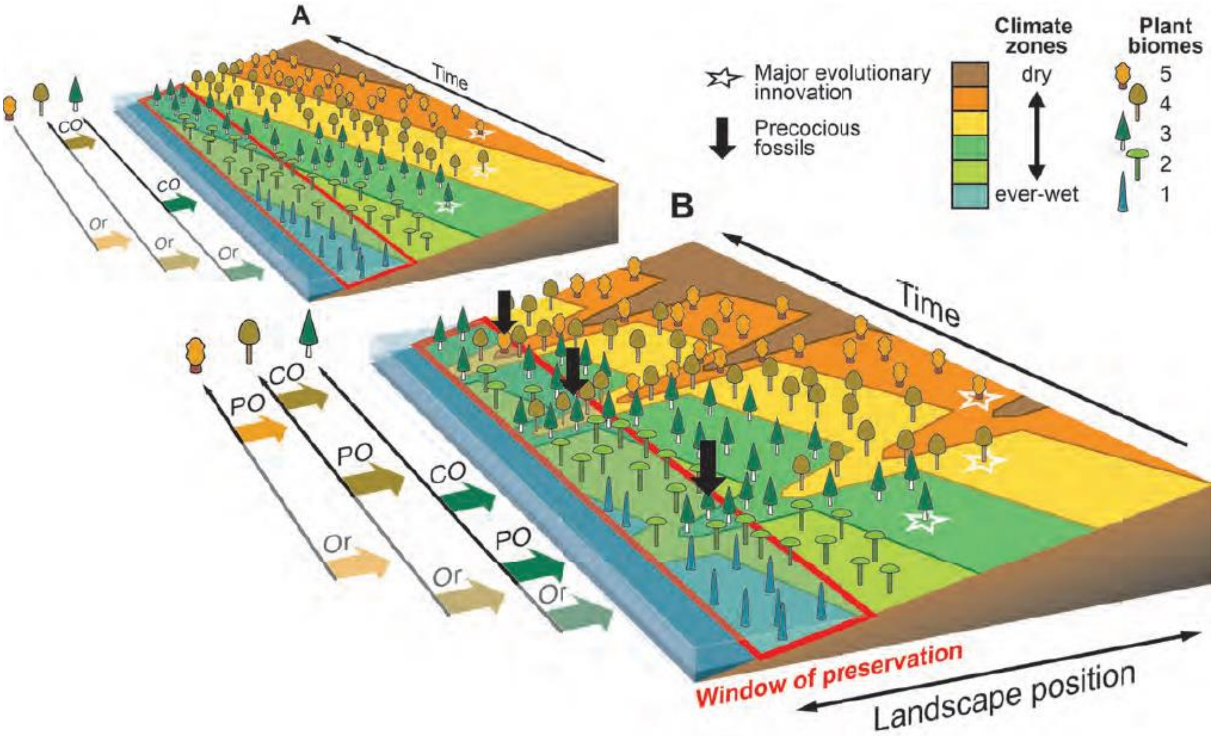


Figure 2 A is the general pattern based on an early incomplete knowledge of the fossil record.
B is the pattern that emerges after increased sampling of the fossil record. Precocious appearances reflect climate oscillations and accompanying tracking by plants, bringing new forms initially temporalily into the window of preservation during drier episodes. Or, origination of clades; PO, precocious occurrence of fossil floras; CO, common occurrence of fossil floras.

Studying these vegetation changes can tell a lot about climate, evolution and stratigraphy of the Late Carboniferous and early Permian. Recently the Boskovice Basin, Czech Republic, has been studied in detail by (Šimůnek, Martínek 2009). They concluded that the southern part of the basin is Late Carboniferous in age, and that the northern part is early Permian, based on the both the litho- and biostratigraphy. South of the Boskovice Basin, in lower Austria the Zöbing Formation was deposited. This formation has been studied in the past, but has not yet been compared to these new data from the Czech Republic. By comparing the fossil flora of the Zöbing Formation to that of the Boskovice Basin and other localities, it is possible to better date and understand the climatic conditions and floral chances in present-day Lower Austria during the Late Carboniferous and Early Permian.

2. Geography, Geology and Lithology

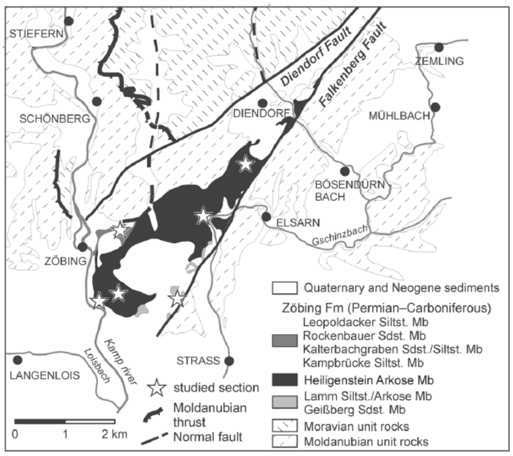


Figure 3 (Nehyba, Reinhard et al. 2012)

The Zöbing Formation is named after the nearby settlement within the municipality Langenlois. Which is located in the Krems-Land District in Lower Austria. The centre of Zöbing lies near the River Kamp. The outcrop of the Zöbing formation is located east of the river.

The sediments of the Zöbing Formation are of late Paleozoic age and preserved in a wedge-shaped half-graben of the Bohemian Massif, between the Diendorf Fault to the north west and the Falkenberg Fault in the south-east.(Nehyba, Reinhard et al. 2012)

The formation forms a more than 1000 m thick succession. It is found in an area that is 6,5 km long and 2,3 km at its broadest. The sediments are tectonically tilted, together with a crystalline basement (mainly granulite and ultrabasites)(Vasicek 1991, Nehyba, Reinhard et al. 2012).

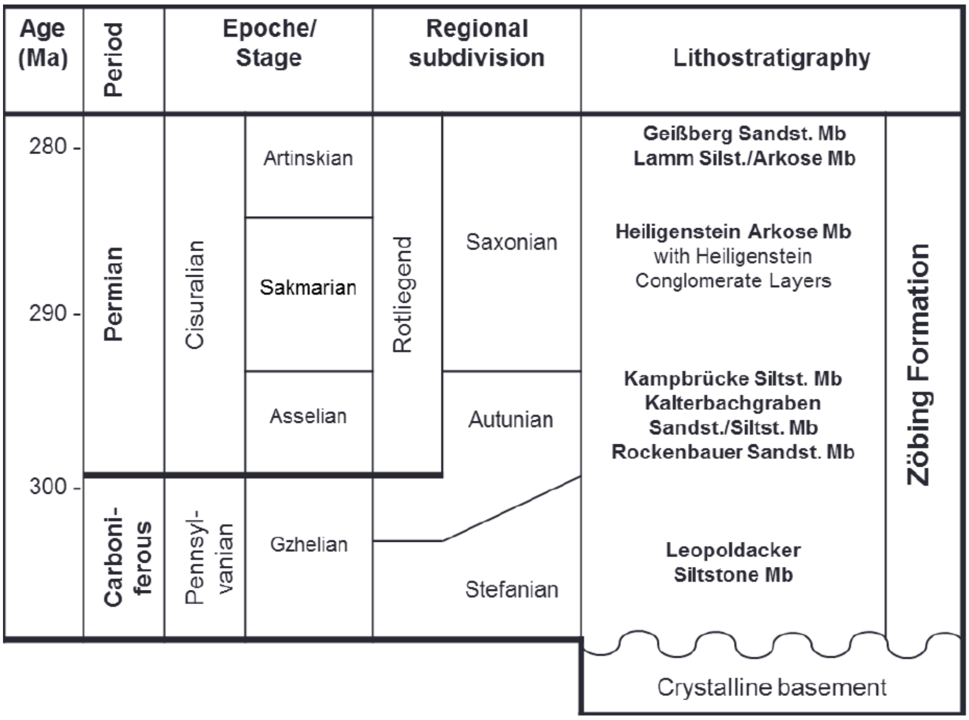


Figure 4 Lithostratigraphic correlation of the Upper Carboniferous—Permian sediments in the Boskovice Basin (modified after(Šimůnek, Martínek 2009))

The sediments were divided into several members by (Vasícek 1983). The crystalline basement is overlain by a 300 m thick succession that can be divided into four members. The lowest is called the *Leopoldacker Siltstone Member* and mainly consist of dark-grey, fine-grained, laminated silt- and sandstones with small coal streaks and a high amount of organic remains. The siltstones contain fossils of freshwater bivalves, gastropods, ostracods and small fish teeth and scales(Schindler, Hampe 1996). The *Leopoldacker Siltstone Member* is overlain by the *Rockenbauer Sandstone Member.* These sediments often contain resedimented clay and sandstone pebbles(Vasicek 1991). Ostracods, fish teeth and coprolites were found in this member(Schindler, Hampe 1996). The overlying *Kalterbachgraben Sandstone/Siltstone Member* consist of an alternation of thick layers of arkoses and sandstones with dark-grey, laminated silt- and sandstones (Vasicek 1991, Vasícek 1983). Higher in the member, reddish siltstones and dark laminated limestones occur, the latter containing ostracods and fish teeth(Schindler, Hampe 1996). The uppermost member of the basal succession in the *Kampbrücke Siltstone Member* consists mainly of siltstone layers alternating in longer intervals with arkoses and sandstones(Vasícek 1983, Vasicek 1991).

The middle part of the Zöbing Formation is around 700 m thick and only consist of the *Heiligenstein Arkose Member*, which is made up of arkoses, sandstones and conglomerates. The grain size increases towards the top(Vasicek 1991, Nehyba, Reinhard et al. 2012). The Heiligenstein Member is overlain by the 400 m thick *Lamm Siltstone* Member, which forms the upper part of the Zöbing Formation(Vasícek 1983, Vasicek 1991). The *Geißberg Sandstone Member* forms the top of the Zöbing Formation. No biostratigraphic data are available of the upper two members.

3. Vegetation types

Two major vegetation types can be recognized in the Late Carboniferous and Early Permian, i.e. the wetland biome and the seasonally dry biome(DiMichele, Pfefferkorn et al. 2001). However, there is a taphonomic bias toward wet lowland biomes, because uplands or extrabasinal areas are rarely preserved in the fossil record(Pfefferkorn 1980). The wet biome is therefore much better studied and understood.

During the Stephanian tree ferns were most common and most dominant in these biomes, but other groups such as the cordaites, the medullosan pteridosperms or seed ferns and the calamites were also important groups in these wetland environments.

The early drier biomes in the Stephanian were dominated by seed plants and included early conifers, pteridosperms, and cordaites. Ferns and sphenopsids were present but less abundant compared to the wet biomes(DiMichele, Pfefferkorn et al. 2001).

4. Different taxonomic groups

4.1 Calamites and other sphenopsids

Sphenopsids are related to modern horsetails. They are spore-producing plants with a distinctive morphology with a central articulated stem with branches and microphyllous leaves standing in whorls. This makes this group relatively easy to identify in the fossil record(Taylor, Taylor et al. 2009). There were many different species during the Carboniferous and Permian, ranging from herbaceous to arborescent forms.(Taylor, Taylor 1993)

The calamites were the largest of these arborescent forms, which could grow up to a height of 18 m. The stem was divided into nodes and internodes; several stems were connected by a creeping rhizome(Taylor, Taylor et al. 2009). These trees grew in wet environments, such as swamps and along lakes and rivers.

4.2 Tree ferns

Arborescent ferns were quit common in the Stephanian and Early Permian. After the C.R.C., opportunistic tree ferns became the dominant vegetation elements in many wet biomes. During the Stephanian lager tree fern genera such as *Psaronius* with pecopterid foliage became more common (DiMichele, Phillips 1996). Their appearance is quite similar to that of modern tree ferns. The trunks do not contain secondary vascular tissue (wood); instead a mantle consisting of adventitious roots provided support. This characteristic is still present in all extant tree ferns(Taylor, Taylor et al. 2009).

4.3 Cordaites

The cordaites were seed plants that first appeared in the Early Carboniferous and survived well in to the Permian. They were predominantly arborescent, but also creeping forms are known. The arborescent forms had large trunks with secondary xylem. This might have allowed them to become the tallest trees in the Late Carboniferous and Permian forests (Taylor, Taylor et al. 2009). They occupied a range of different habitats, ranging from mangrove-like lowlands to drier uplands(Cleal, Thomas 1999). Cordaitean leaves are variable, but usually strap- or tongue-shaped, sometimes reaching a length up to 1 m and a width of 15 cm(Willis, McElwain 2002). Most leaves had longitudinally oriented parallel veins, but no central vein(Taylor, Taylor 1993). However, some cordaites had more needle like leaves with a single vein(Stewart, Rothwell 1993).

4.4 Pteridosperms

The Pteridosperms are a clade of extinct gymnosperms characterized by fern-like foliage that reproduced with true seeds. This is why there are often called seed ferns, although they were no ferns(Krings, Kerp 2006).

They form a paraphyletic clade and are more of a historical construct than a well-circumscribed phylogenetic lineage. This is partly why the wide range in ecological roles and ecomorphological attributes should not be surprising(DiMichele, Phillips et al. 2006). Pteridosperms can locally be the dominant canopy trees, prominent understory trees, form a scrambling ground cover, thicket-formers, or liana-like plants and vines. Some species appear to have been weedy opportunists, although this ecological strategy seems to be a minor part of the wide spectrum of pteridosperm life habits, but all had to some degree woody axes(DiMichele, Phillips et al. 2006).

At least eight orders of Palaeozoic pteridosperms are currently recognized(Taylor, Taylor et al. 2009). The two most important in Europe during the Stephanian and Early Permian were the Medullosales and the Peltaspermales.

4.5 The medullosan pteridosperms

Medullosans are considered a classical group of Pteridosperms(DiMichele, Phillips et al. 2006). The oldest medullosans were vine-like plants, but many later forms were real trees(DiMichele, Phillips et al. 2006). Their seeds were often relatively large, implying a K-strategy of life. Most medullosans occurred in the equatorial region in relatively wet biomes, on better drained soils. They were most diverse and most common in the middle Carboniferous, but they started to decline during the late Carboniferous. There are two important arborescent groups of medullosans, the alethopterids and the neuropterids. They both lived in woodlands and forests, but in they are almost never found together in the fossil record. It is suggested that *Alethopteris* is probably the most xeromophic of the two, but also many *Neuropterids* had xeromorphic adaptations(DiMichele, Phillips et al. 2006). The presence of xeromorphic traits in medullosans, shows that these pteridosperms were adapting to a drier climate at the end of the Carboniferous and the Permian. However, xeromorphic features may also point to physiologically “dry” conditions, such as low-pH and nutrient poor habitats in wetland habitats or brackish influences.

4.6 The peltaspermalean pteridosperms

Peltasperms are a more derived group of pteridosperms. They are the only pteridosperms that had their main distribution in the Permian and persisted into the Mesozoic, but they first appeared during the latest Carboniferous(Kerp 1988). They had a global distribution in the tropics during the Early Permian(Naugolnykh, Kerp 1996). Their ecological range covered both wet but usually drier biomes. Most finds are associated with increased seasonality and generally drier conditions. The tolerance for a seasonal changing environment was probably one of the key factors why peltasperms thrived throughout the Permian and into the Mesozoic(DiMichele, Phillips et al. 2006).

5. Methods

A fossil collection of over 1500 specimens from the Leopoldacker, Kampbrücke and Rockenbauer members of the Zöbing Formation, that has been collected by Dr. Werner Vasìcek, was examined. An attempt was made to identify the specimens in this collections, using the recently published papers on the Rotliegend flora of the Thuringian Forest by (Barthel 2003, Barthel 2004, Barthel 2005, Barthel 2006, Barthel 2007, Barthel 2008)and Barthel & Brauner (2015) as main reference works. Most fossils had already been prepared and had only occasionally to be cleaned of dust. The fossils had been numbered by Vasìcek corresponding to the stratigraphic horizons in which they were found. The numbers, quality, species and extra information were all entered into a database. Most fossils were photographed for future reference, applying the techniques described in Kerp & Bomfleur (2011). Material of low quality and little interest was not photographed, due to time constrains.

Finally, the data was interpreted and compared to that of the Czech Boskovice Basin(Šimůnek, Martínek 2009) and the Western and Central Bohemian and Sudetic basins(Opluštil, Šimůnek et al. 2013)

6. Results

The fossils from the Leopoldacker Member, consist of two different groups. The first is mainly dominated by medullosans, making up 46,7% of the assemblage. One single species is dominant, *Alethopteris zeilleri*. Which makes up 29% of the entire assemblage. Other medullosans in this assemblage are *A. schneideri, A. pennsylvanica, Odontopteris schlotheimii*, *O. brardii*, *O.* sp. *Callipteridium gigas* and *Neurocallipteris* sp*.* The second most common group in this assemblage are ferns, containing the species *Senftenbergia plumosa*, *Scolecopteris arborescens*, *S. candollena, S. cyathea*, *S. hemitelioides*, *S. oreopteridia*, *S. polymorpha*, *S. pseudobucklandii*, *S. unita* and *Scoleropteris* sp. However, the most common is the tree fern *S. densiflora.* Sphenopsids are present but uncommon and mainly represented by *Sphenophyllum oblongifolium* and *S. verticilatum*. Calamites are present as well in the form of. Peltasperms, callistophytes, cordaites and conifers are rare but present in this assemblage and contain the species *Autunia conferta*, *A. naumannii*, *Dicksonites plukenetii*, *Cordaites* sp.*, Ernestiodendron filiciforme, Hermitia germanica* and *Walchia piniformis.* A little more than 1% of the assemblage consists of seeds, i.e. *Samaropsis* sp., *Cardiocarpus* sp. and *Trigonocarpus* sp.

The second Leopoldacker group is – just like the first – characterized by a high proportion of tree ferns, making up nearly one third of the assemblage. *Scoleropteris densiflora* is the most common tree fern species just like in the group described above. Other species present are *S. arborescens*, *S. cyathea*, *S. oreopteridia*, *S. polymorpha* and *S. pseudobucklandii*. Sphenopsids are rare and only *Sphenophyllum verticillatum* is present. Medulloscean pteridosperms make up a much smaller proportion of the total assemblage compared to the latter group, but alethopterids are still dominant. *Alethopteris schneideri* is the most common medullosan and *A. zeilleri, Odontopteris brardii and O.* sp. make up the rest of the medullosan diversity. Peltasperms, callistophytes, cordaites and conifers are all much more common in this assemblage with *Autunia conferta*, *A. naumannii* and *Rhachiphyllum schenkii* representing the peltasperm diversity. Conifers make up a higher proportion of the assemblage, but have decreased in diversity, with only the species *Walchia piniformis* being present.

The material collected from the Kampbrücke Member shows a much higher proportion and diversity of sphenopsids and calamites, compared to the associations from the Leopoldacker Member. The following species where found to be present: *Annularia spinulosa, A. spicata, A. carinata, A. sphenophylloides, Annularia* sp.*, Calamostachys tuberculata* and *Metacalamostachys dumasii.* Ferns make up only a small proportion of the Kampbrücke material. They include *Lobatopteris* sp.*,* Scolecopteris sp., *Remia pinnatifida* and *Aphlebia germarii*. Peltasperms constitute a significant portion of the assemblage, with *Autunia naumannii* being the dominant species, and *Autunia conferta* and *Dichophyllum flabellifera* occurring in low numbers. Quantitatively, medullosan pteridosperms occur in comparable numbers as in Group 2 from the Leopoldacker Member, but the species composition differs. *Neurocallipteris* sp., *Neurodontopteris* sp., *Neuropteris* sp., *Odontopteris lingulata, O. schlotheimii, O. subcrenulata, O.* sp., *Cyclopteris* sp. and a single specimen of *Alethopteris* sp., are present. Cordaites are rare in the Kampbrücke Assemblage. Conifers do not constitute a large part of the assemblage of the Kampbrücke Member. However, they show a higher diversity, with *Ernestiodendron filiciforme, Otovicia hypnoides*, *Feysia* sp. and W*alchia piniformis.* Some slabs also contain conifer dwarfshoots, scales and a cone. The most unique feature of the Kampbrücke assemblages is the present of the presumed cycad here provisionally identified as "*Pterophyllum*". Only two specimens where found in the entire Zöbing collection and both were part of the Kampbrücke assemblage.

The material from the Rockenbauer Member consist mainly of conifers with a significant percentage of sphenopsids, peltasperms and medullosan pteridosperms. The assemblage contains the following species: *Alethopteris zeilleri, Annularia carinata*, *Annularia spicata*, *Autunia conferta*, *Autunia naumannii*, *Calamostachys tuberculata, Callipteridium gigas, Ernestiodendron filiciforme*, *Neurocallipteris planchardii*, *Odontopteris brardii*, *O. lingulata*, *O. schlotheimii*, *O.* sp., *Sphenophyllum verticillatum* and *Walchia piniformis.* Only one fern *Scolecopteris* sp. was found to be present. Fructifications and seeds consist of *Schuetzia anomala* and *Samaropsis* sp.

Two assemblages corresponding to different stratigraphic units were not considered. The first assemblage consists of a single specimen of *Odontopteris schlotheimii*, which would fall in a third Leopoldacker group. The second assemblage that was omitted is associated to the Lauserkünette Member, which is not mentioned in the available literature. This assemblage consists of single specimens identified respectively as *Alethopteris* sp., *Walchia piniformis*, an unknown fragment and two specimens of *Odontopteris schlotheimii*. In total 134 specimens were omitted from the analyses, because it was not possible to determine to which assemblage they belong.

7. Correlation, comparison and interpretation

Leopoldacker Member

The flora of the Leopoldacker Member mostly resembles a flora that is characterized by relatively wet conditions.
The landscape of Zöbing consisted of a lake that was surrounded by a forest dominated by tree ferns and medullosan pteridosperms. However, the presence of conifers and peltasperms indicates drier conditions in the hinterland. The higher proportion of these meso- to xerophilous elements and decrease in medullosan pteriosperms in the second Leopoldacker group, suggests that either seasonality increased or the local elevation increased.

The floral composition of the Leopoldacker Member most closely resembles that of the Rosice-Oslavany Formation in the Boskovice Basin. This is due to the high abundance of ferns in both stratigraphic units. Pteriosperms are similar in species composition, but are rarer in the Rosice-Oslavany Formation. This is especially true for *A. zeilleri*, which is dominant in the first Leopoldacker Group, but not very common in the Roscive-Oslavany 2nd and 3rd coal seams. In only one site pteridosperms are dominant with *Odontopteris schlotheimii* as the most common species. The conifer diversity is almost identical in the upper part of the Rosice-Oslavany Formation, compared to the Leopoldacker Member association. However, they are completely absent in the lower part. Ferns are quite rare in the upper Rosice-Oslavany Formation. Therefore, the Flora of the Leopoldacker Member is intermediate between those of the 2nd and 3rd coal seam and that of the the 1st coal seam of the Rosice-Oslavany Formation. In species composition the Leopoldacker Member resembles that of the Line formation in the Western and central Bohemian basins and the Semily formation of the Sudetic basins. With many of the same species of ferns, pteridosperms and conifers being present. Only mayor divergence is the diversity of sphenoid’s in the Line formation, which exceeds that of the Leopoldacker Member, and the absence of certain peltasperms like *Autunia naumannii*.

Rockenbauer Member

The Rockenbauer Member contained the fewest specimens of all examined stratigraphic units. This hampers interpretations based on abundances. It is the only member in which conifers are dominant, in particular *Walchia piniformis.* Ferns and alethopterids are rare. This means that the landscape was dominated by a mesophilous conifer forest with some pteridosperms. There are no horizons in the Boskovice Basin that compare well to the flora of the Rockenbauer Member, which makes it difficult to date this member.

	Stratagraphic members						Boskovice basin			
plant groups	Leopoldacker 1	Leopoldacker 2	Rockenbauer	Kampbrucke	Rosice Olslavany formation, 2nd and 3rd coal seam	Rosice Olslavany formation, 1st coal seam	Padochov Zbýšov	Padochov Říčany	Letovice Zboněk-Svitávka	Letovice Lubě
Sphenopsids	5,10	3,16	11,63	18,77	7,90	3,10	3,20	1,40	2,50	
Ferns	36,26	33,68	2,33	3,45	82,30	6,70	3,20	12,20	8,90	13,50
Peltasperms	3,78	5,26	11,63	29,12						
Medulloscean	46,74	24,21	20,93	23,75	1,80	46,60	8,50	24,50	45,60	32,40
Callistophyts	1,13	6,32	-	-						
Cordaitaleans	2,46	11,58	-	1,53	7,90	22,40	11,40	18,40	3,80	5,40
Conifers	3,21	12,63	44,19	13,79	-	21,10	73,40	43,50	39,20	48,60
Cycads	-	-	-	0,77						
seeds	1,32	3,16	9,30	8,81						

Table 1 Proportions of all floristic groups, in the specific stratigraphic units.

Kampbrücke Member

The abundance of conifers in the Kampbrücke flora is comparable to that of Leopoldacker Group 2. However, a little more than 3% of the Kampbrücke flora consist of tree ferns. Peltasperms, which make up only a small part in the Leopoldacker Member, are dominant in the Kampbrücke Member. The sediments of the Kampbrücke Member can nevertheless be interpreted as mainly lacustrine, but with more fluvial influence. The lake was still surrounded by a forest, but the vegetation had become a much more tolerant to periods of drought. The rare presence of cycad fossils indicates that the influence of hinterland elements on the floral composition had increased considerably, which means that the wet type vegetation had declined significantly.

The Flora of Kampbrücke Member resembles that of the typical Asselian (Lower Permian) floras. This means that the Carboniferous-Permian boundary is probably situated between the Leopoldacker and Kampbrücke members. There are similarities between the Kampbrücke and the Vrchlabì Formation in the Sudetic basins. Autunian peltaspersms and walchian conifers are common in all flora's, however some localities in the Vrchlabì formation have a much larger proportion of ferns, while others are over 90% dominated by walchian conifers. The flora of the Padochov Zbýšov Unit in the Boskovice Basin, is most similar to that of the Kampbrücke Member. Even the rare cycad-like foliage here provisionally identified as "*Pterophyllum*" is present. However, the flora of the Padochov Zbýšov consist for more than 70% out of conifers, compared to 13 % in the Kambrücke Member. In species abundance, the Kampbrücke floral association resembles that of the Padochov Říčany flora. Both are dominated by Autunian peltasperms and share a lot of species. However, many elements known from the Kampbrücke floral association are missing in the Padochov Říčany flora and vice versa. Differences in local conditions, might be factors contributing to the differences between these two floras.

8. Discussion and conclusion

All fossils used in this study had been collected before the start of the study. It was therefore impossible to determine biases and to correct them. Fossil wood and roots were left out of the comparison, in order to correct for differences in taphonnomy between sites. The identification of the different species was mainly done with material based on fossils found in Thuringia (Germany). However, there are some differences between the fossil flora of the Bohemian Basin and in the Thuringian Forest in Germany. Hence, not all specimens could be identified. The mostly very fragmentary nature of the material was an additional problem. The diversity within certain groups, especially conifers might therefore be underestimated. Nevertheless, a clear change can be noticed in the floral composition of the lower Zöbing Formation. From a 'wet type'-dominated typical Stephanian flora in the Leopoldacker Member with abundant tree ferns and alethopterids, to a 'dry type'-dominated flora in the Rockenbauer Member and finally a relatively dry Asselian peltasperm-dominated vegetation. These floras show similarities to those of the Boskovice Basin and other Czech localities to which they can be correlated. However, there are some differences in abundance and species composition, showing that the vegetation in the Zöbing Basin was more similar to the Boskovice Basin compared to other Czech localities, but not completely identical to that of the Boskovice Basin. Local conditions might be the largest contributor to these differences. Comparing the flora of Zöbing to other localities in Europe and the us, will be necessary to answer this questions.

9. Acknowledgements

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10. Appendix

10.1 Species list

Presence of species in the different stratigraphic members of the Zöbing formation.
p, present; x, more than 2 % of assemblage; **X** more than 9 % of assemblage.

	Stratagraphic members			
spiecies	Leopoldacker 1	Leopoldacker 2	Kampbrucke	Rockenbauer
Annularia spinulosa	p		X	
Annularia spicata			X	p
Annularia carinata			p	p
Annularia sphenophylloides			p	
Annularia sp.	p		X	
Asterophyllites equiformis	p			
Calamostachys tuberculata	p		X	p
Calamites sp.	p	X		
Metacalamostachys dumasii	p		X	
Pecopteris monyi	p		p	
Pecopteris potoniei	p			
Pecopteris mertensioides	p			
Scolecopteris sp.	X	**X**	p	p
Scolecopteris candolleana	p			
Scolecopteris unita	p			
Scolecopteris pseudobucklandii	X	p		
Scolecopteris densiflora	**X**	**X**		
Scolecopteris polymorpha	p	p		
Scolecopteris arborescens	X	p		
Scolecopteris cyathea	X	X		
Scolecopteris oreopteridia	X	p		
Scolecopteris hemitelioides	p			
Remia pinnatifida			p	
Sphenophyllum obligifolium	p			
Sphenophyllum verticilatum	p	X		p
Sphenophyllum longifolium	p			
Sphenophyllum sp.	p			
Alethopteris zeilleri	**X**	X		p
Alethopteris schneideri	**X**	**X**		
Alethopteris pennsylvanica	p			
Altheopteris sp.			p	
Asterotheca sternbergii	p			

Autunia conferta	X	X	p	p
Autunia naumannii	X	p	**X**	X
Alphlebia germarii			p	
Callipteridium gigas	p			p
Senftenbergia plumosa	p			
Dicksonites plukenetii	p	X		
Dichophyllum flabellifera			X	
Lobatopteris sp.	p	p	p	
Lobatopteris geinitzii	p			
Lobatopteris viannae	p			
Pseudomariopteris busquetii	p	X		
Rhachiphyllum schenkii		p		
Cyclopteris sp.			p	
Odontopteris sp.	X	X	**X**	p
Odontopteris lingulata			p	p
Odontopteris schlotheimii	p		X	p
Odontopteris subcrenulata			p	
Odontopteris brardii	p	p		p
Neurocallipteris planchardii				p
Neurocallipteris sp.	p		X	
Neuropteris sp.			p	
Neurodontopteris sp.			p	
"Pterophyllum"			p	
Cordaites sp.	X	**X**	p	
Hermita germanica	p			
Walchia sp.	p		p	
Walchia piniformis	X	**X**	X	**X**
Otovicia hypnoides			p	
Ernestiodendron filiciformis	p		X	X
Feysia sp.			p	
Samaropsis sp.	p	p		p
Cardiocarpus sp.	p		X	
Trigonocarpus sp.	p	p	p	
Rhapdocarpus sp.			p	
Schuetzia sp.			p	X

10.1 References

BARTHEL, M., 2008. Die Rotliegendflora des Thüringer Waldes Teil 6: Wurzeln und fertile Organe. *Algen und Bakterien.Vegetation.Veröffentlichungen des Naturhistorischen Museums Schleusingen,* **23**, pp. 41-67.

BARTHEL, M., 2007. Die Rotliegendflora des Thüringer Waldes–Teil 5: Ginkgophyten. *Coniferophyten.Veröff.Naturhist.Mus.Schleusingen,* **22**, pp. 41-67.

BARTHEL, M., 2006. Die Rotliegendflora des Thüringer Waldes. Teil 4: Farnsamer und Farnlaub unbekannter taxonomischer Stellung. *Veröffentlichungen Naturhistorisches Museum Schleusingen,* **21**, pp. 33-72.

BARTHEL, M., 2005. Die Rotliegendflora des Thüringer Waldes. Teil 3: Farne. *Veröffentlichungen Naturhistorisches Museum Schleusingen,* **20**, pp. 27-56.

BARTHEL, M., 2004. Die Rotliegendflora des Thüringer Waldes. Teil 2: Calamiten und Lepidophyten. *Veröff.Naturhist.Mus.Schleusingen,* **19**, pp. 19-48.

BARTHEL, M., 2003. Die Rotliegendflora des Thüringer Waldes. Teil 1: Einführung und Keilblattpflanzen (Sphenophyllales)
. *Veröffentlichungen Naturhistorisches Museum Schleusingen,* , pp. 3-19.

CLEAL, C.J. and THOMAS, B.A., 1999. Plant fossils: the history of land vegetation.

DIMICHELE, W.A. and ARONSON, R.B., 1992. The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. *Evolution,* , pp. 807-824.

DIMICHELE, W.A., PFEFFERKORN, H.W. and GASTALDO, R.A., 2001. Response of Late Carboniferous and Early Permian Plant Communities to Climate Change 1. *Annual Review of Earth and Planetary Sciences,* **29**(1), pp. 461-487.

DIMICHELE, W.A. and PHILLIPS, T.L., 1996. Climate change, plant extinctions and vegetational recovery during the Middle-Late Pennsylvanian transition: The case of tropical peat-forming environments in North America. *Geological Society, London, Special Publications,* **102**(1), pp. 201-221.

DIMICHELE, W.A., PHILLIPS, T.L. and PFEFFERKORN, H.W., 2006. Paleoecology of Late Paleozoic pteridosperms from tropical Euramerica 1. *The Journal of the Torrey Botanical Society,* **133**(1), pp. 83-118.

KERP, H., 1996. Post-Variscan late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. *Review of palaeobotany and palynology,* **90**(3), pp. 263-285.

KERP, J., 1988. Aspects of Permian palaeobotany and palynology. X. The West-and Central European species of the genus Autunia Krasser emend. Kerp (Peltaspermaceae) and the form-genus Rhachiphyllum Kerp (callipterid foliage). *Review of palaeobotany and palynology,* **54**(3), pp. 249-360.

KRINGS, M. and KERP, H., 2006. Neuropteris attenuata, a narrow-stemmed, leaning or lianescent seed fern from the Upper Pennsylvanian of Lower Saxony, Germany. *Flora-Morphology, Distribution, Functional Ecology of Plants,* **201**(3), pp. 233-239.

KRONER, U., HAHN, T., ROMER, R.L. and LINNEMANN, U., 2007. The Variscan orogeny in the Saxo-Thuringian zone—heterogenous overprint of Cadomian/Paleozoic peri-Gondwana crust. *Geological Society of America Special Papers,* **423**, pp. 153-172.

LOOY, C., KERP, H., DUIJNSTEE, I. and DIMICHELE, B., 2014. The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. *The Sedimentary Record,* **12**(4), pp. 4-18.

NAUGOLNYKH, S.V. and KERP, H., 1996. Aspects of Permian palaeobotany and palynology. XV. On the oldest known peltasperms with radially symmetrical ovuliferous discs from the Kungurian (uppermost Lower Permian) of the Fore-Urals (Russia). *Review of palaeobotany and palynology,* **91**(1), pp. 35-62.

NEHYBA SLAVOMÍR, REINHARD, R. and MAŠTERA LUBOMÍR, 2012. *Provenance analysis of the Permo-Carboniferous fluvial sandstones of the southern part of the Boskovice Basin and the Zöbing Area (Czech Republic, Austria): implications for paleogeographical reconstructions of the post-Variscan collapse basins.*

OPLUŠTIL, S., ŠIMŮNEK, Z., ZAJÍC, J. and MENCL, V., 2013. Climatic and biotic changes around the Carboniferous/Permian boundary recorded in the continental basins of the Czech Republic. *International Journal of Coal Geology,* **119**, pp. 114-151.

PFEFFERKORN, H.W., 1980. A note on the term “upland flora”. *Review of palaeobotany and palynology,* **30**, pp. 157-158.

ROSCHER, M. and SCHNEIDER, J.W., 2006. Permo-Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. *Geological Society, London, Special Publications,* **265**(1), pp. 95-136.

SCHINDLER, T. and HAMPE, O., 1996. Eine erste Fischfauna (Chondrichthyes, Acanthodii, Osteichthyes) aus dem Permokarbon Niederösterreichs (Zöbing, NE Krems) mit paläoökologischen und biostratigraphischen Anmerkungen. *Beiträge zur Paläontologie,* **21**, pp. 93-103.

ŠIMŮNEK, Z. and MARTÍNEK, K., 2009. A study of Late Carboniferous and Early Permian plant assemblages from the Boskovice Basin, Czech Republic. *Review of palaeobotany and palynology,* **155**(3–4), pp. 275-307.

STEPHENSON, M., MILLWARD, D., LENG, M. and VANE, C., 2008. Palaeoecological and possible evolutionary effects of early Namurian (Serpukhovian, Carboniferous) glacioeustatic cyclicity. *Journal of the Geological Society,* **165**(6), pp. 993-1005.

STEWART, W.N. and ROTHWELL, G.W., 1993. *Paleobotany and the evolution of plants.* Cambridge University Press.

TAYLOR, E.L., TAYLOR, T.N. and KRINGS, M., 2009. *Paleobotany: the biology and evolution of fossil plants.* Academic Press.

TAYLOR, T.N. and TAYLOR, E.L., 1993. *The biology and evolution of fossil plants.* New Jersey, USA.: Prentice Hall.

VASÍCEK, W., 1983. Vasícek W. 1983: 280 Millionen Jahre alte Spuren der Steinkohlenwälder von Zöbing. *Katalogreihe des Krahuletz-Museums* 4, 15-50. *280 Millionen Jahre alte Spuren der Steinkohlenwälder von Zöbing.,* Katalogreihe des Krahuletz-Museums(4), pp. 15-50.

VASÍCEK, W., 1991. Das Jungpaläozoikum von Zöbing. *Nagel, D. & Rabeder, G. (Hrsg.): Exkursionen im Jungpaläozoikum und Mesozoikum Österreichs,* , pp. 1-21.

WILLIS, K. and MCELWAIN, J., 2002. The evolution of plants.

11.Plates

Plate 1 leopoldacker 1

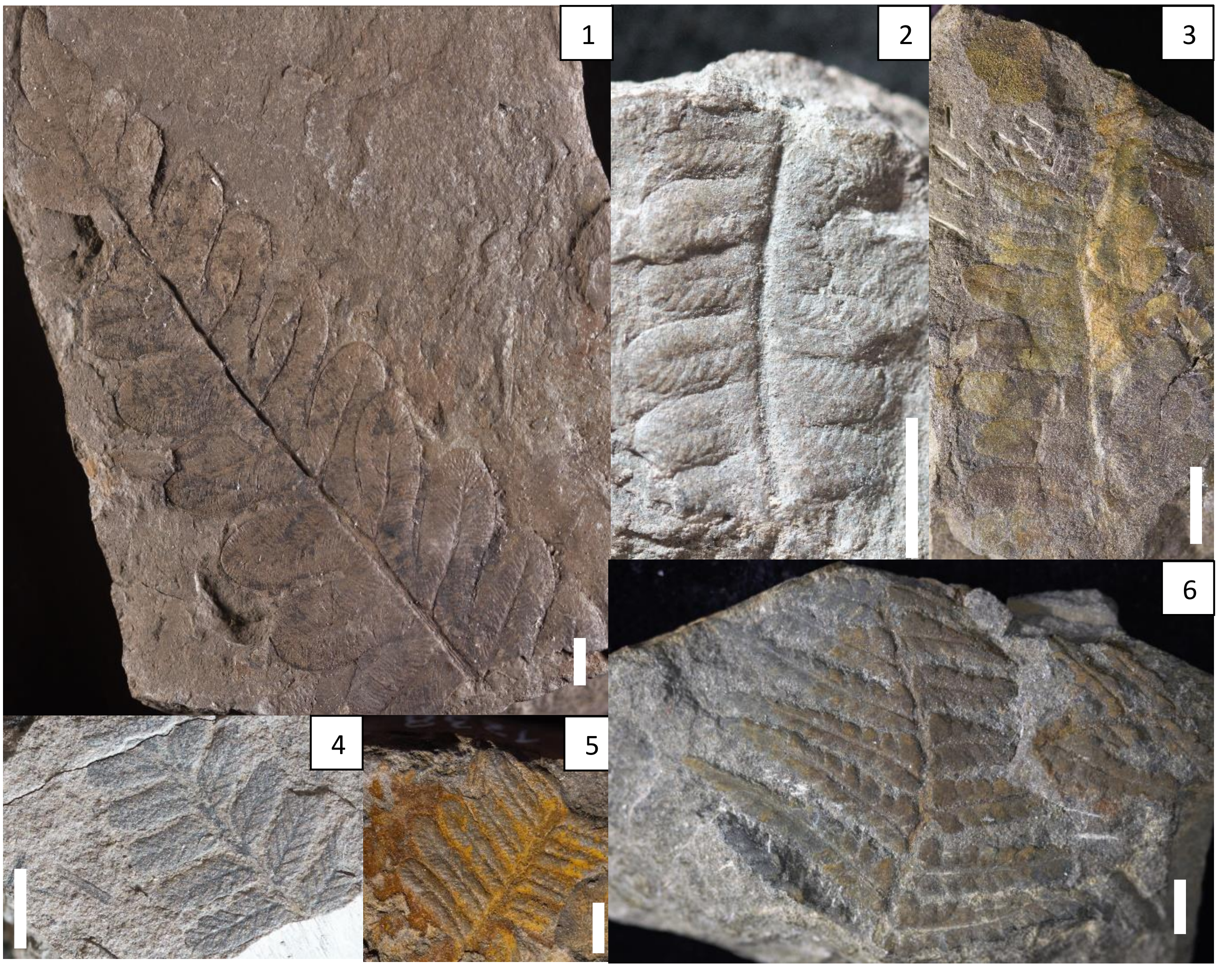

Plate 1; 1 *Alethopteris Zeilleri*, 2 *Scolecopteris arborescens*, 3 *Scolecopteris oreopteridia,*
4 *Scolecopteris hemitelioides*, 5 *Scolecopteris densiflora*, 6 *Senftenbergia plumosa.*
Scale is 5 mm.

Plate2 Leopoldacker 2

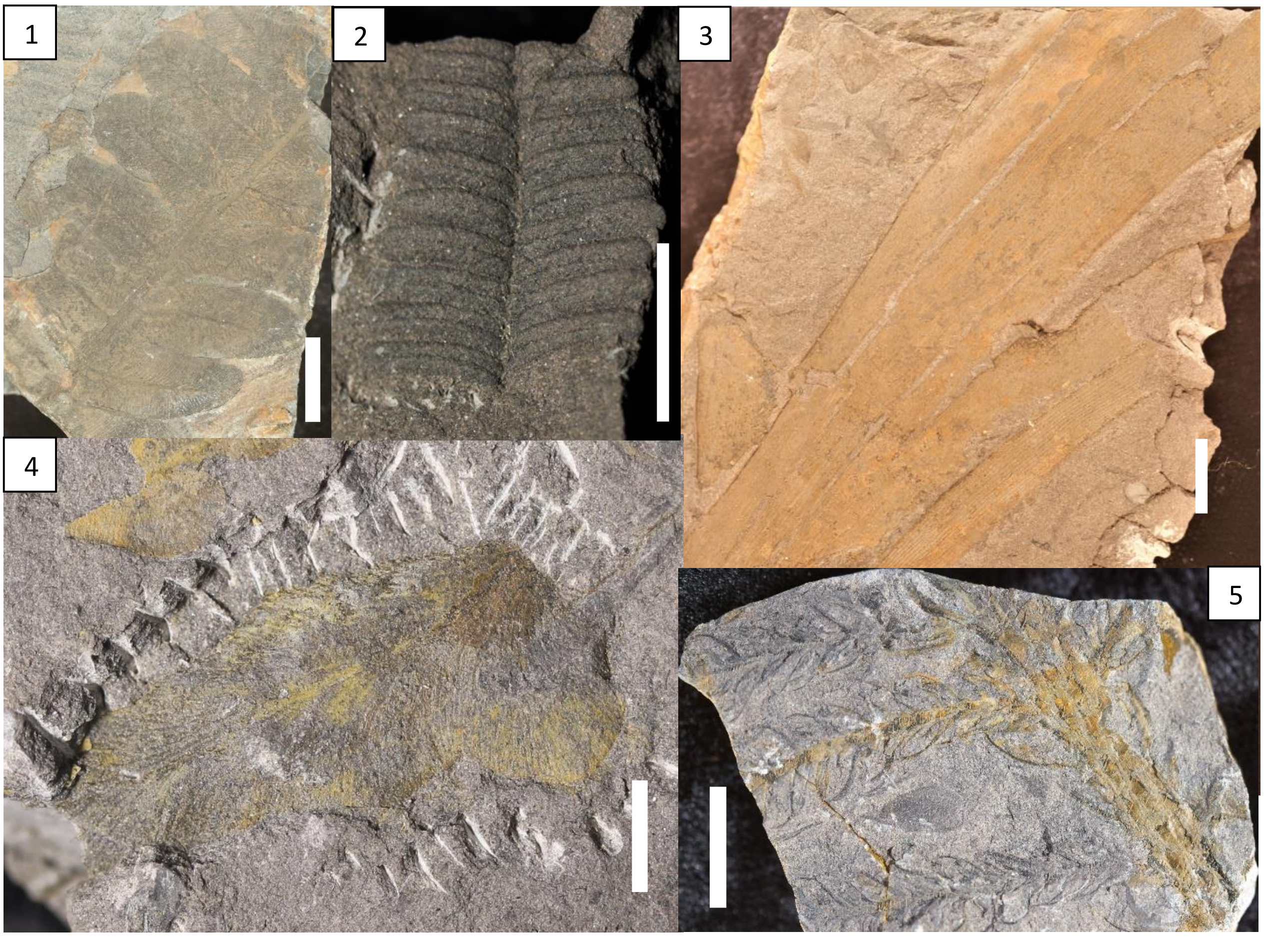

Plate 2; 1 *Alethopteris schneideri*, 2 *Scolecopteris densiflora*, 3 *Cordaites sp*., 4 *Odontopteris sp.*,
5 *Walchia piniformis*.
Scale is 1 cm.

Plate 3 Kambrücke

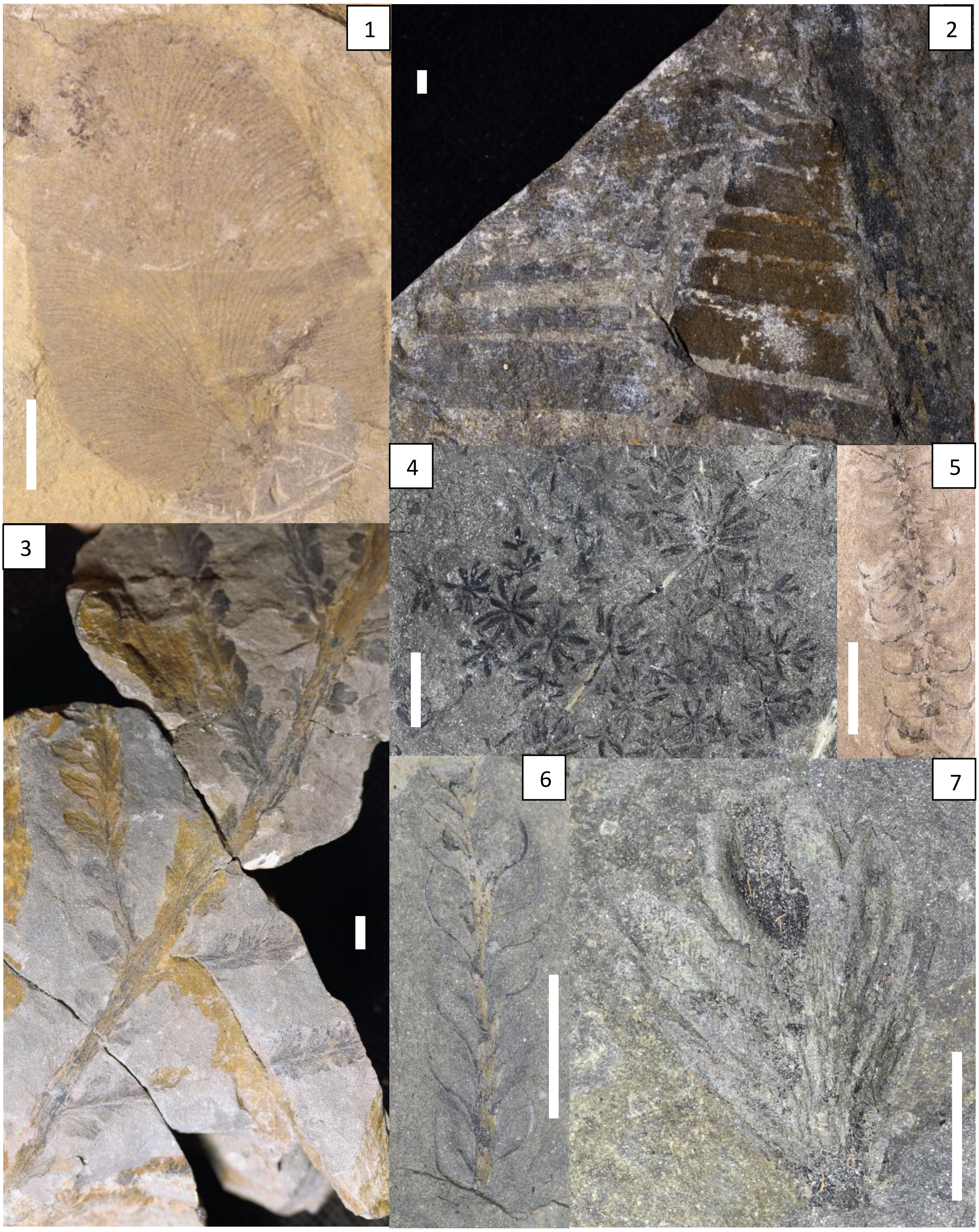

Plate 3; 1 *Odontopteris sp*., 2"*Pterophyllum*", 3 *Autunia naumannii*, 4 *Annularia spicata*, 5 *Ernestiodendron filiciformis*, 6 *Walchia piniformis*, 7 *Walchia piniformis*.
Scale is 5 mm.

Plate 4 Rockenbauer

Plate 4; 1 *Autunia naumannii,* 2 *Walchia piniformis,* 3 *Ernestiodendron filiciformis,*
4 *Schuetzia sp.*