The Pteridosperms from the Carboniferous-Permian of Zöbing, Niederösterreich

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Contents

Abstract	1
1 Introduction	3
2 Geographic and geologic setting	7
2.1 Geographic setting	7
2.2 Geologic setting	8
2.3 The Zöbing Palaeozoic	9
3 State of research	11
3.1 History of research	11
3.2 Lithostratigraphy	14
3.3 Flora & Biostratigraphy	16
3.4 Palaeoecology	16
4 Material	18
4.1 Samples	18
4.2 Preservation	18
5 Methods	20
5.1 Decryption & Preparation	20
5.2 Macrofossil analysis	20
5.3 Limitations	21
5.4 Utensils	22
5.4.1 Stereo microscopy	22
5.4.2 Images	22
5.5 Documentation	22
6 Results & Discussion	24
6.1 Elements of the flora	24
6.1.1 Alethopteris Sternberg 1825	24
6.1.2 Callipteridium WEISS 1870	30
6.1.3 Neuropteris sensu lato (BRONGNIART) STERNBERG 1825	33
6.1.4 Odontopteris (BRONGNIART) STERNBERG 1825	35
6.1.5 Dicksonites Sterzel 1881	37
6.1.6 Pseudomariopteris DANZÉ-CORSIN 1953	38
6.1.7 Sphenopteris (BRONGNIART) STERNBERG 1825	39
6.1.8 Foliage of unknown affinity Pub. Krahuletz-Ges. 2023/01 Berkholz/Zöbing	40

6.2 Quantitative analysis	
6.3 Systematics	
6.4 Plant architecture and development	
6.5 Palaeoecology	47
6.6 Biostratigraphy	
7 Conclusions	
Plates	
References	77
Appendix	

Abstract

In the lowermost Leopoldacker Siltstone Member of the Late Palaeozoic Zöbing Formation (Lower Austria), fossiliferous horizons above and below a small coal seam comprise a diverse fossil flora, dominated by pteridosperms and ferns. So far this flora lacks a taxonomic examination, which is important for the understanding of specific plant groups and single species, as well as for the comprehension of Late Palaeozoic floras, the palaeoecological environment and biostratigraphic correlations.

In this study, the pteridosperm foliage was determined by macrofossil analysis. Three previously identified species can be confirmed and several new taxa are revealed. Two groups of Late Palaeozoic pteridosperms are represented by the identified taxa: The Medullosales and the Callistophytales. Only two species belong to the latter one whereas the majority of the fossils can be attributed to the Medullosales. The dominance (~ 50 %) of the medullosan seed fern *Alethopteris zeilleri* is conspicuous. The predominant hygrophilous-mesophilous taxa possibly inhabited marginal areas of lakes or rivers. The highly fragmented remnants indicate a fluvial transport. Though, the irregular order of the plant fragments suggests a deposition under stagnant conditions. An unambiguous stratigraphic correlation based on the identified species is difficult, also in comprehension with the associated plant groups. Though, a late Stephanian age rather than a Rotliegend age can be assumed for the Leopoldacker Siltstone Member by the characteristics of the identified pteridosperms and the occurrence and abundance of other available plant groups. According to this evaluation, the suggested stratigraphic significance of the available species *Alethopteris schneideri* as an index fossil for the Rotliegend is challenged.

1 Introduction

Pteridosperms (Pteridospermatophyta) form a heterogeneous group of extinct gymnosperms characterised by fern-like foliage. In contrast to ferns, pteridosperms bear real seeds ("seed ferns") (Krings et al. 2006).

The earliest pteridosperms probably existed in the Upper Devonian, the latest are reported from the Triassic.

Seed ferns display a great diversity in morphology and growth habit: Some forms were small to medium-sized trees with upright trunks and massive fernlike fronds (Taylor et al. 2009). Some not completely self-supporting pteridosperms probably gained support by leaning against neighbouring trees, or by loosely intermingling with components of the surrounding vegetation via large fronds with wide-angled pinnae or even by intertwining foliage with closely growing other individuals of the same species (Krings & Kerp 2006). Yet other forms existed, featuring scrambling and/or climbing growth habits like vines and lianas (Krings et al. 2003, Krings & Kerp 2006).

Seed ferns are a paraphyletic group as resolved by most phylogenetic analyses which only provide a general sense of the relationships among pteridosperm groups. However, groups with shared morphological characteristics can be identified with relative certainty, even though subsequent relationships among these groups are often not well understood (DiMichele 2006).

Classic higher pteridosperm groups of the Late Pennsylvanian and Early Permian are the Medullosales (Carboniferous to Permian), encompassing rich taxonomic diversities, the Callistophytales (Pennsylvanian to Lower Permian), and the modern Peltaspermales (Pennsylvanian to Triassic) (DiMichele 2006, Taylor et al. 2009).

Pteridosperms are important elements of Late Palaeozoic landscapes (Taylor et al. 2009), where they inhabited a wide range of terra firma habitats (DiMichele 2006). They apparently reached wide distribution and their highest diversity in the warm and humid, palaeoequatorial swamp forests of Euramerica (Krings et al. 2003, 2006).

The extent of these coal swamp forests began to increase towards the end of the Middle Pennsylvanian, and at the end of the Late Pennsylvanian, the remains of these forests had almost disappeared in tropical Euramerica.

Since the Late Pennsylvanian, the climate in tropical Euramerica has been characterised by increasing temperature and aridity, oscillating between overall wet and seasonal drier periods. This trend continued into the Permian (Gastaldo et al. 1996, Opluštil et al. 2013).

These climatic and the resulting environmental changes in Euramerica were induced by glaciation periods and the Variscan Orogeny (DiMichele et al. 1992).

The Carboniferous was marked by a reduction of atmospheric CO_2 and significant cooling. Extensive glacial intervals caused sinking sea levels and lead to the development of cyclic marine sequences (cyclothems) in coal-bearing strata (Falcon-Lang & DiMichele 2010, McCann et al. 2008).

The collision of Gondwana and Euramerica (Laurussia) in the Middle Carboniferous resulted in the formation of the Variscan mountain chain (Fig. 1). Due to the large extent of this newly formed continent, dry climate prevailed over large regions (Stanley 2001). Peat swamp areas and thus large-scale peat formation decreased. Most Stephanian and Lower Permian (Rotliegend/Autunian) sedimentary strata of western and central Europe are preserved in intramontane basins (Fig. 2) and only a few locally developed coal seams are known from the Rotliegend (Kerp 1996b).

Furthermore, different regions were locally influenced by palaeogeographical changes and regional orogenic movements. These factors are correlated to topography and distance from the sea, the existence of rain shadows, and patterns of atmospheric circulation responsible for local climatic condition. Additionally, they affected the tectonic regime and subsidence rates, which again control the sedimentary environment, fluvial styles and water tables (DiMichele et al. 1992, Calder 1994, Opluštil & Cleal 2007).



Fig. 1: Palaeogeographic global map of the Pennsylvanian, showing Austrias approximate position (red dot) in the Variscan mountain chain; after http://cpgeosystems.com.

With the advent of climatic oscillations, the floral composition underwent intense changes (DiMichele et al. 2006, 2010).

Increasing aridity and seasonality lead to a decrease of wetland habitats in basinal lowlands, causing the replacement of assemblages consisting of spore-producing or primitive seed plants by vegetation dominated by gymnosperms (DiMichele et al. 2005, 2006, Kerp 1996a, Opluštil et al. 2013). While early Pennsylvanian swamp forests were mainly inhabited by arborescent lycopsids, and only in minor quantity by arborescent and herbaceous sphenopsids, ferns, seed-bearing cordaites and pteridosperms, in typical Stephanian swamp forests arborescent filicalean ferns were dominant and formed a relatively closed canopy. The Stephanian ecosystems were more dynamic and covered only small areas. The arborescent lycopsids disappeared almost completely during the Westphalian D-Stephanian transition and the frequency of scrambling and climbing forms of pteridosperms increased considerably within this group during the Stephanian (McCann et al. 2008, Kerp & Krings 1998). During the Late Stephanian, basinal vegetation consisted mainly of tree ferns, calamites and pteridosperms, whereas dry 'Hinterland' floras, were rarely preserved. The first significant macrofossil record of dryland floras, dominated by conifers and peltasperms, derives from the interval between the uppermost Stephanian and the early Permian (Opluštil et al. 2013, McCann et al. 2008, Kerp 2000).



Fig. 2: Geographic position of important Permo-Carboniferous basins; Position of the Zöbing Palaeozoic marked (ZÖ), after Roscher & Schneider 2006.

In Zöbing (Niederösterreich/Lower Austria) a huge amount of plant fossils was collected during excavations at several localities in the late 1970s. These fossils derive from different horizons of a sedimentary succession preserved in a half-graben. Presumably, the sediments were deposited across the Carboniferous-Permian boundary (Vasícek 1991).

Most recent studies regarding the flora of Zöbing suggest a Stephanian to Autunian/Rotliegend age, on the basis of only few identified plant species (Vasícek 1991, Vasícek & Steininger 1996). However, until now no detailed and comprehensive taxonomic palaeobotanical studies and analyses of this flora were done, that might contribute to the understanding of single species and entire Carboniferous and Permian floras.

The examination of the heterogeneous group of pteridosperms provides an appropriate start for these studies due to their value for palaeoecological inferences and the suitability of some foliage types as biostratigraphic markers for biozonation (DiMichele et al. 2008, Taylor et al. 2009).

2 Geographic and geologic setting

2.1 Geographic setting

Zöbing is a small cadastral community within the municipality Langenlois in the Krems-Land District in Lower Austria (Fig. 3). It is situated at a narrow sector of the Kamptal about 70 km NW of Vienna (48.49068 N, 15.69385 E; http://retorte.ch). The centre of Zöbing is located near a river bend of the Kamp (Vasícek 1983).

Lower Austria is the largest of Austria's nine federal provinces, located in the northeast of the country, and encloses the federal province and Austrian capital Vienna in its centre.

Moreover, it is bordered by Upper Austria in the west, the Czech Republic in the north, Slovakia in the northeast, the Burgenland in the southeast and Styria and the Eastern Alps in the south. It is horizontally divided by the river Danube (http://noe.gv.at).

Zöbing is located in the Waldviertel, one of four historical regions in Lower Austria situated in the northwest. Typical features of the Waldviertel are high moor land areas and granite rocking stones ("Wackelsteine"). The other provinces are the Weinviertel in the northeast and the Mostviertel and the Industrieviertel south of the river Danube (Schuster et al. 2013, http://noe.gv.at).



Fig. 3: Left: Map of Europe, showing the rough position of Zöbing (Lower Austria); after http://zonu.com. Right: Geographic and geologic map of the Zöbing area, displaying important geological units and the location of the studied section (star); after Nehyba et al. 2012.

2.2 Geologic setting

The Late Palaeozoic sediments of Zöbing are preserved in a half-graben on the crystalline basement of the Bohemian Massif (Nehyba et al. 2012).

The Bohemian Massif encompasses a small part of Austria and extends into adjacent parts of the Czech Republic, Germany and Poland (Opluštil et al. 2013). In Austria, it only crops out in the NW of the country (i.e. Waldviertel, Dunkelsteiner Wald and Amstettener Bergland) (Fig. 4).

In the South and East the Bohemian Massif is bordered by the Molassebasin, which then again merges into the Alps (Wessely 2006).

The Bohemian Massif is the most important inlier of basement rocks in Central Europe and constitutes the easternmost segment of the Variscan orogenic belt (Opluštil et al. 2013, Linnemann et al. 2008). It results from the mid-Carboniferous collision of the continent Euramerica (Laurussia) with the northward drifting continent Gondwana and related microplates (Dallmeyer et al. 1995, Schuster et al. 2013).



Fig. 4: The main geological units of Austria and the geographic position of Zöbing in Lower Austria (dashed line); after http://bgfeldkirch.at.

Further collisional processes lead to crustal thickening, uplift and exhumation of granites and high-grade metamorphic rocks. Post-Variscan sedimentary deposition mainly started in the high mountain stage ('Hochgebirgsphase'), but not until the early Westphalian when uplift and orogenetic processes decreased.

Subsequently, the rotation of Gondwana induced normal and strike-slip faulting which lead to the formation of continental basins (Fig. 2). These basins developed in two periods (Matura 2006, Oplustil et al. 2013 and references therein).

During the younger period of basin formation, spanning the Upper Carboniferous and Lower Permian, the Blanice, Boskovice and Orlice half-grabens were formed. Also, two sinistral faults occurred in the crystalline basement of the Waldviertel and formed a tectonic half-graben in the surroundings of Zöbing (Matura 2006, Opluštil et al. 2013).

In this tectonic basin structure remnants of a large Upper Carboniferous to Permian sedimentary cover were preserved, tectonically tilted with the crystalline basement (Nehyba et al. 2012).

These exposed Late Palaeozoic sediments are mainly surrounded by crystalline rocks of the Moldanubicum, i.e. amphibolite and 'Gföhl gneiss', as well as granulite ('Granulite of Zöbing-Diendorf'), mica-schist and schist gneiss (Fig. 3). Northeast of the Zöbing Palaeozoic also rocks of the Moravian unit, i.e. granites, 'Biteš gneiss' and mica-schists occur (Nehyba et al. 2012, Vasícek 1996, Vasícek & Steininger 1996).

The Molanubicum is the easternmost part of the Moldanubian zone and constitutes, as well as the Moravian unit as part of the Moravo-Silesian zone, a section of the Bohemian Massif (Linnemann et al. 2008).

A considerably larger area is occupied by the Moldanubicum, extending between Moldova and the Danube. However, the Moravian unit represents a marginal area, which is predominantly exposed in Moravia (Czech Republic) and extends into a small part of the eastern Waldviertel (Schuster et al. 2013). Both units received their last metamorphic overprint in the Variscan era. A major east vergent thrust fault where the Moldanubicum was thrusted over the Moravicum separates the units (Prey 1980).

2.3 The Zöbing Palaeozoic

Inside a wedge-shaped half-graben structure between the Diendorf fault in the northwest and the Falkenberg fault in the southeast (Fig. 2), the Late Palaeozoic sediments were preserved and protected from further influences like erosion (Nehyba et al. 2012).

The distribution of the sediments longitudinally extends about 6.5 km in SW-NE direction between Zöbing and Diendorf-Olbersdorf. At the southern end, the transversal extension reaches a maximum of 2.3 km (Matura 2006, Nehyba et al. 2012).

Today, these Late Palaeozoic sediments mainly crop out at the Heiligenstein east to southeast of Zöbing (Nehyba et al. 2012).

The western border of this sedimentary succession continues over the edge of the Heiligenstein to the hillside of the Geißberg. In NNE direction of the Geißberg, the sediments are limited by the Falkenberg fault, along which they extend in northeastern direction. The northern border of the Palaeozoic sediments runs from the northern end of Zöbing in northeastern direction, crosses the Lausergraben and the Wolfbachgraben and proceeds southeast of the Pösingerberg to Diendorf-Olbersdorf (Nehyba et al. 2012, Vasícek 1983, 1991).

The succession is about 1300 m thick and generally tilted downward to S to SE. At the crystalline contact at the northern end of the occurrence, the sediments are tilted about 60° , in the main part of the profile about 30° to 45° and steeper again in the uppermost part (~ 80°) (Vasícek 1977, 1991).

3 State of research

3.1 History of research

The sedimentary succession of the Zöbing Formation is known since the 19th century and was studied by several scientists, first of all by Philipp A. Holger (1842). Paul Partsch (1843/44) firstly recorded this succession in a map and correlated it to the Rotliegend (early Permian). Afterwards, Cžjžek (1849) mapped the deposits more precisely (Nehyba et al. 2012, Vasícek 1991).

First remains of plants were described by Constantin von Ettingshausen in 1852. He erroneously correlated the sediments with the Wealden Periode (Lower Cretaceous). Dionys Stur studied the flora of Zöbing as well and extended and emended Ettingshausens work in 1870. He classified the sedimentary sequence into the Rotliegend (Vasícek 1991, Berger 1951).

Von Ettingshausen and Stur mention the following species: *Calamites sp., Hymenophyllites semialatus* GEIN., *Neuropteris linguata* NAUM., *N. pteroides* GÖPP., *Odontopteris obtusiloba* NAUM., *Walchia piniformis* (SCHLOTHEIM) STBG., *Walchia filiciformis* STBG., *Voltzia sp., Cordaites ottonis* GEIN., *Cordaites sp., Schützia anomala* (GEIN.) GÖPP., *Guilielmites permianus* GEIN. (Von Ettingshausen 1852, Stur 1870, Berger 1951, Vasícek 1991).

Further determinations of fossil plants were made by Berger (1951), who defined the following taxa: *Calamites* sp., *Pteridospermae* indet. div., *Samaropsis* sp., *Rhabdocarpus* sp., cf. *Cardiocarpus cordai* GEIN., *Carpolithus* sp. div., *Cordaites* cf. *palmaeformis* GOEPP., *Walchia piniformis* (SCHLOTHEIM) STBG., *W. filiciformis* STBG., *Gomphostrobus bifidus* (GEIN.) ZEILL. (Bachmayer & Vasícek 1967, Berger 1951).

Most recent studies on the flora were carried out by Werner Vasícek (Vasícek 1977, 1983, 1991; Vasícek & Steininger 1996). Since 1965, he has systematically searched for plant fossils. Extensive finds were made at several locations: At the Rockenbauer Keller, the Lauser Künette at the lower part of the Lauser Weg, at the surroundings of the Kampbrücke, in which a relatively large *Callipteris*-flora was found, and at the Leopoldacker, yielding the largest amount of plant fossils (Vasícek 1983).

Vasícek identified various fossil plants from the different localities (Table 1). Further, he did the most recent detailed mapping and published a precise lithological profile of the Zöbing Formation, identifying seven members, which he interpreted in a stratigraphic context (Fig. 5).

Age (Ma)	Period	Epoche/ Stage		Regional subdivision		Lithostratigraphy	
280 -			Artinskian			Geißberg Sandst. Mb Lamm Silst./Arkose Mb	
290 -	Permian	Cisuralian	Sakmarian	Rotliegend	Saxonian	Heiligenstein Arkose Mb with Heiligenstein Conglomerate Layers	ormation
			Asselian		Autunian	Kampbrücke Siltst. Mb Kalterbachgraben Sandst./Siltst. Mb Rockenbauer Sandst. Mb	Zöbing F
300 -	Carboni- ferous	Pennsyl- vanian	Gzhelian		Stefanian	Leopoldacker Siltstone Mb	
						Crystalline basement	

Fig. 5: Lithostratigraphic correlation of the Carboniferous and Permian sediments of the Zöbing Formation based on Vasícek, 1991; after Nehyba et al. (2012).

List of fossil plants from the Zöbing Formation identified by Werner Vasícek

KAMPBRÜCKE SILTSTONE MEMBER						
I Callipteris naumanni (GUTBIER) STERZEL Callipteris conferta (STERNBERG) BRONGNIART Callipteris nicklesi ZEILLER Callipteris bibractensis ZEILLER Reticulopteris germari (GIEBEL) GOTHAN Neuropteris cordata BRONGNIART Odontopteris lingulata GÖPPERT Calamites cisti BRONGNIART Annularia carinata GUTBIER (= A. mucronata SCHENK) Annularia stellata SCHLOTHEIM Calamostachys tuberculata STERNBERG Annularia spicata GUTBIER Asterophyllites dumasi ZEILLER Cordaites principalis GERMAR	II Ernestidendron (Walchia) filiciformis (SCHLOTHEIM) STERNBERG Lebachia (Walchia) speciosa FLORIN Gomphostrobus bifidus GEINITZ					
ROCKENBAUER SANDSTONE MEMBER						
Callipteris conferta (STERNBERG) BRONGNIART Odontopteris lingulata (GOEPPERT) SCHIMPER Odontopteris subcrenulata (ROST) ZEILLER Calamites gigas BRONGNIART Lebachia (Walchia) piniformis (SCHLOTHEIM) FLORIN Ernestidendron (Walchia) filiciformis (SCHLOTHEIM) STERNBERG						
LEOPOLDACKER SILTSTONE MEMBER						
Alethopteris zeilleri (RAGOT) WAGNER ("Alethopteris-grandini-zeilleri-Group") Neuropteris cordata BRONGNIART Reticulopteris (Barthelopteris) germari (GIEBEL) GOTHAN Callipteridium gigas (GUTBIER) WEISS Callipteridium rochei ZEILLER Odontopteris obtusa BRONGNIART Alethopteris cf. bohemica FRANKE						
Scolecopteris cyathea (SCHLOTHEIM) STUR Scolecopteris candolleana (BRONGNIART) STUR Scolecopteris arborescens (SCHLOTHEIM) STUR Scolecopteris hemitelioides (BRONGNIART) STUR Scolecopteris cf. permica (NEMEJC) BARTHEL Pecopteris dentata BRONGNIART Pecopteris plumosa (ARTIS) BRONGNIART Calamites sp. Annularia stellata (SCHLOTHEIM) WOOD Calamostachys tuberculata (STERNBERG) WEISS Asterophyllites equisetiformis (STERNBERG) BRONGNIART Sphenophyllum oblongifolium (GERMAR) KAULFUSS Walchia arnhardtii FLORIN Cordaites						

Table 1: Fossil plants from the different fossiliferous members of the Zöbing Formation (pteridosperms accentuated), named in Vasícek (1983, 1991) and Steininger & Vasícek (1996).

3.2 Lithostratigraphy

The whole succession of the Zöbing Formation is more than 1000 m thick and shows a lithological trisection (Vasícek 1983).

On top of the crystalline basement the Zöbing Formation starts with an about 300 m thick sedimentary succession, divided into four stratigraphic members (Fig. 6) (Vasícek 1991).

The basal **Leopoldacker Siltstone Member** mainly consists of fine-grained dark-grey laminated and layered silt- and sandstones. In the dark-grey siltstones, organic remains in form of coal seams, coal streaks and fusites can be found. Occasionally, grey to black carbonate nodules occur in the sediment. Basal layers contain well preserved plant remains (Vasícek 1991, Vasícek & Steininger 1996).

Above, thin-bedded ochre-brown coloured silt- and sandstones define the **Rockenbauer Sandstone Member**. These sediments partially contain carbonate and merge into varve-like shales (Brandschiefer) (Vasícek 1991, Nehyba et al. 2012). Therein, resedimented clay- and sandstone pebbles can be found, as well as a few conifer remains (Vasícek 1991).

The Kalterbachgraben Sandstone/Siltstone Member reflects a more episodic sedimentation, presumably sheetflood deposits, in form of massive alternating layers of sandstones and arkoses. Dark grey laminated limestones and a layer of reddish siltstones are intercalated (Vasícek 1991). The ultimate member of the first part, the Kampbrücke Siltstone Member, consists of layered siltstones, which are interrupted in longer intervals by layers of arkoses and sandstones. Further, two horizons occur within the siltstones bearing fossils and carbonaceous substances (Vasícek 1991, Nehyba et al. 2012).

The **Heiligenstein Arkose Member** initiates the second about 700 m thick part of the Zöbing Formation and comprises an alternation of bedded arkoses, sandstones and conglomerates of varying thickness. In the upper part of this member, the amount of crystalline pebbles (grainsize) increases towards the top and passes into the **Heiligenstein Conglomerate Layers** (Vasícek 1991, Nehyba et al. 2012).

A decline in coarse sediments characterises the third and about 400 m thick and uppermost section of the succession. The Lamm Siltstone/Arkose Member displays a sequence of reddish siltstones, sandstones and arkoses (due to reddish Potassium-Feldspar) alternating with red-brown siltstones. In finer sediments intercalations of SiO₂-rich, dark grey limestones occur.

The Zöbing succession is terminated by the **Geißberg Sandstone Member**, showing an alternating sequence of red and gray claystones, in which lenses of sandstones and arkoses are intercalated (Vasícek 1991).

14 Pub. Krahuletz-Ges. 2023/01

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Fig.6: Lithotratigraphic profile of the Zöbing Formation (plant bearing horizons marked with leaf); after Vasícek & Steininger 1996: 1 Leopoldacker Siltstone Member 2 Rockenbauer Sandstone Member 3 Kalterbachgraben Sandst./Siltst. Member

3a Sandstone and arkoses 3b reddish siltstones 3c dark laminated limestones

- 4 Kampbrücke Siltstone Member
- 5 Heiligenstein Arkose Member
- 6 Lamm Silstein/Arkose Member
- 7 Geißberg Sandstone Member

3.3 Flora & Biostratigraphy

In the coaly shales below and above a small coal seam within the **Leopoldacker Siltstone Member**, a fossil flora is preserved. This flora, generally containing pteridosperms, ferns, sphenophytes, conifers and cordaites, is dominated by the pteridosperm *Alethopteris zeilleri* and numerous pecopterids, whereas conifer remains are rare (Vasícek, 1991). Hence, Vasícek (1991) assigned this member to the Stephanian (Late Carboniferous). Furthermore, Flügel (1960) described freshwater bivalves found in the siltstones and Schindler & Hampe (1996) identified freshwater gastropods, ostracods and small fish teeth and scales.

The strata of the **Rockenbauer Sandstone Member** contain ostracodes, a fragment of an insect wing, teeth, scales and coprolites of fish (Schindler & Hampe 1996). Regarding floral fossils, mainly conifer remains occur in varve-like shales. Furthermore, *Callipteris conferta* (*= Autunia conferta*) is quite abundant. Therefore Vasícek assumed an Autunian age of this member (Vasicek 1991).

The fossils indentified by von Ettingshausen, Stur and Berger are part of this member as well (see above).

From the **Kalterbachgraben Sandstone/Siltstone Member** no plant fossils are preserved. Ostracode shells, fish teeth and scales are the only fossils that were found in a single limestone bed (Schindler & Hampe 1996).

The **Kampbrücke Siltstone Member** shows a richer fossil content in two fossiliferous horizons. While the lower horizon comprises a great number of pteridosperms, ferns and sphenophytes, in the upper horizon conifer remains, freshwater bivalves and the relic of an insect wing were found (Nehyba et al. 2012, Bachmayer & Vasícek, 1967, Vasícek, 1991). Due to the occurrence of various callipterids, particularly *Callipteris conferta* (= *Autunia conferta*), the seed *Samaropsis crampii* and the evidence of the fructification *Calamostachys dumasii*, Vasícek correlated this member with the Autunian as well (Vasícek 1991).

3.4 Palaeoecology

Some interpretations regarding the palaeoecologic conditions during the deposition of the basal parts of the Zöbing Formation were made by Schindler & Hampe (1996) and Vasícek (1983). The depositional environment was interpreted as either small shallow eutrophic lakes with rich vegetation in littoral zones, or as larger, temporarily stagnant oxbow lakes (Vasícek & Steininger 1996, Schindler & Hampe 1996). According to Vasícek (1983) the plants of the

Leopoldacker flora were deposited in warm and humid climatic conditions. The characteristics of the flora and the absence of freshwater bivalves, ostracods and specific brachiopods reflect largely anoxic conditions during deposition.

The ferns (pecopterids) found in these basal strata derive from a "flöznahe" flora, whereas most plants like alethopterids inhabited higher "flözferne" areas. The occurrence of fusite (charcoal) in the fossiliferous siltstones supports the evidence of drier habitats, due to their formation in connection with forest fires (Vasícek 1991).

The arkoses and conglomerates of the Kalterbachgraben Sandstone/Siltstone Member and the Heiligenstein Arkose Member on the contrary, were deposited as flash-floods in arid alluvial environments.

4 Material

4.1 Samples

During an excavation in 1977, numerous plant fossils have been exposed and collected at the Leopoldacker by Werner Vasícek, Fritz F. Steininger, F. Sattler and W. Simeth. Moreover, by digging a trench connecting the crystalline basement and the finding site at the northern margin of the Leopoldacker, the proximate sedimentary strata above the crystalline basement could be identified (Vasícek 1983, 1991).

Additional finds of fossil plants have been made by Vasícek (1977, 1983, 1991, Vasícek & Steininger 1996) at different sites in the Zöbing area (see above), covering several horizons of the Zöbing Formation and altogether resulting in a large fossil collection.

This collection is in possession of the Krahuletz Museum in Eggenburg, Lower Austria.

For adequate taxonomic studies, the collection was transported to the Forschungsstelle für Paläobotanik in Münster (Westfälische Wilhelms-Universität Münster) in October 2013.

The whole inventory of the collection transported to Münster comprises 56 boxes containing an estimated amount of 2000 specimens.

Due to the large extent of specimens in the collection, only a part, i.e. the pteridosperms from the Leopoldacker, are subject of this study.

4.2 Preservation

In Zöbing, a fossil flora is preserved in form of compressions and impressions, which is part of the collection of the Krahuletz Museum in Eggenburg (Lower Austria). In this collection a large amount of pteridosperm remains is available (mainly foliage), which are the subject of this study.

The plant remains from Zöbing are preserved as compression and impression fossils in grey to brownish siltstones and in rather small scale of pinnae of the ultimate, rarely penultimate order or as isolated pinnules.

Compressions are one of the most common types of plant fossils. In compressions, internal plant structures are usually obliterated due to flattening of the cells during compaction of the sediments enclosing the plant and only a carbonaceous film that conforms the original outline of the plant (organ) remains. However, depending on the grain size or matrix of the sediment burying the plant parts, more or less details are preserved. Often compressions even show surface details and overall morphology. Some of the most common plant parts found in compressions are leaves. Apart from characteristics like the leaf shape and the pattern of *Pub. Krahuletz-Ges. 2023/01*

venation, sometimes even the distribution of stomata in the leaf surface is identifiable (Taylor et al. 2009).

Impressions are the negative imprints of plants or plant parts, with little or no carbon adhering (counterpart to compressions). Imprints show the same surface details as the compression (e.g. leaf shape and venation), but there is no actual plant material. Hence, under normal circumstances cellular details cannot be seen on an impression (Taylor et al. 2009).

5 Methods

5.1 Decryption & Preparation

First, the entire collection of fossils was ordered according to the numbering established by Werner Vasícek. Unfortunately, a revealing record book is not available, so the locality data could not be reconstructed precisely for all specimens. At least the correlation of the fossils to stratigraphic horizons or finding sites based on Vasícek's numbering and his records was possible. Exact spots at a locality or precise horizons within a stratigraphic member could not be identified.

Accordingly, the largest amount of specimens (~ 1000), which are starting with the collection number 153, have been collected at the Leopoldacker and therefore belong to the **Leopoldacker Siltstone Member**.

Thereupon the collection of Leopoldacker fossils was scanned for specimens of pteridosperms, which were preserved well enough for further examinations.

Afterwards, the fossil specimens were cleaned for accurate studies, especially of the fine structures. Because of the prior studies and preparation by Werner Vasícek, no rough dirt, but only dust and, in a few cases, mould had to be removed.

5.2 Macrofossil analysis

To date, more than 1000 "species" of pteridosperms have been described based solely on impression and compression specimens of sterile foliage. The classification is based on an artificial system of morphotaxa considering only macromorphological features, disregarding phylogenetic relations (Krings et al. 2006).

Morphotaxa are based on morphological characteristics such as size, shape, venation pattern, and the attachment of the ultimate foliar segments to the axis (Taylor et al. 2009).

Depending on the state of preservation of a fossil, remains of different scale, e.g. whole fronds or only foliar segments like ultimate pinnae and pinnules, can be used for the differentiation and identification of pteridosperm taxa.

Typically, for an ideal identification, the single elements and features are described precisely. That includes:

- Size (length and/or width) of rachises, pinnae and pinnules;
- Overall shape of pinnae and pinnules (e.g. oval, linear, linguiform, triangular or lanceolate) and rachises (e.g. straight, undulating);
- Shape of segments like base, apex or margins;
- 20 Pub. Krahuletz-Ges. 2023/01

- Specific structures on the different elements are important characteristics (e.g. ridges or striae on rachises);
- Arrangement of pinnae and pinnules to the axis (e.g. alternate or oppositely; touching, overlapping or distantly spaced);
- Attachment of pinnae and pinnules to the rachis (e.g. single point or entire base, decurrent, conjoined by a rim) and angle of attachment;

Very important, especially for taxonomy on species level, is the venation pattern of the pinnules:

- Pinnate or reticulate venation (e.g. midvein with lateral veins or several equal veins or anastomosing veins; subsidiary veins);
- Intensity and the number ('denseness') of veins that attain the pinnule margins;
- Angles (e.g. between rachis and vein(s), mid- and lateral veins, lateral veins and margin).

Generally the fossil can be classified via combination of multiple characteristic features. In case that several plant specimens belong to one plant species, even the degree of variability can be determined (Taylor et al. 2009).

5.3 Limitations

The identification of taxa is mainly dependent on the fossil's state of preservation. Frequently, the venation is not preserved well enough to permit a distinct identification on species or genus level.

Moreover, the major intraspecific variability of the foliage (pinnules) complicates the identification, either due to the natural variation inherent in foliage from different parts of the same frond or by reason of ontogenetic development. Further different habitat conditions may be relevant or simply differences in the preservation (Krings et al. 2006, Taylor et al. 2009).

Furthermore, the existence of organ genera, based on the fact that organs like roots, leaves or reproductive structures are usually found separately, impedes the work on wholeplant reconstructions and phylogenetic relations (Stewart & Rothwell 1993). Therefore, some authors now use the generic name of the fructification instead of the name of sterile foliage, when both are found conjoined (Taylor et al. 2009).

5.4 Utensils

5.4.1 Stereo microscopy

For the taxonomic classification of the macrofossils, especially for the identification of fine structures and the venation pattern, a stereo microscope (Leica EZ4) with integrated LED illumination is used. The objective zoom magnification ranges from 8X to 35X and illumination settings allow the adjustment of the incident angle to provide high resolution images.

A light source at an oblique angle (sidelighting) often reveals or intensifies the finest structures and reliefs of a specimen by increasing the amount of contrast, especially when the matrix of the rock and the fossil have similar colour values (Taylor et al. 2009).

5.4.2 Images

In some cases photographs help to reveal details of features, that cannot (or poorly) be seen under the microscope.

Some techniques, e.g. the use of cross-polarisation or polarising filters over the camera lens can significantly enhance contrast (Taylor et al. 2009, Kerp & Bomfleur 2011).

Sometimes also sketches and drawings of plant organs and structures are useful to exemplify or emphasise features for a better understanding.

5.5 Documentation

Working on previously collected fossil material shows the importance of good documentary work. A structured and comprehensible documentation of field data, particularly concerning their precise stratigraphic and geographic context, simplifies further work and is of great scientific value.

Besides being an adjuvant device for species identification, an essential method for documenting and presenting results of palaeobotanical studies is the photography of fossils. The equipment required for this photographic documentation comprises an adequate DSLR Camera (Canon Eos 7D) with a macro lens and a polarising filter, that is attached to a horizontally adjustable repro stand with adjustable lights on two sides. Further, a light tent with frosted glass plates and a sandbag is deployed. The camera settings are externally controlled via computer and live view function.

Photographic techniques and tricks advised by Kerp and Bomfleur (2011) are applied in order to obtain high-quality pictures: The aperture diaphragm have to be closed (high *f*-number) to achieve the greatest possible depth of field (DOF). This requires long exposure times. Hence, the camera and the fossil are fixed in a stable position and the self-timer function is used to avoid shaking. The fossil is placed parallel to the plane of the object lens on the sand-filled bag. For the background, a neutral black velvet cloth is draped over the sandbag on which the specimen is placed, to avoid distraction and reflection.

With the help of two adjustable reflector lamps, the fossil is illuminated obliquely (angle about 45°) from one side, to enhance contrast and visualise the relief details and fine structures like the venation of pinnules. Hence, the fossil is orientated correctly towards the incident light to emphasise as many details as possible.

The light tent and a frosted glass plate are used as shown in Fig. 7, to generate diffuse lighting and to avoid too strong shadows. To compensate the overexposure of the side of the fossil facing the light source, the 'dodging and burning'-technique (described in Kerp & Bomfleur 2011) is applied. Before taking pictures, the white balance has to be adjusted to ensure that colours are rendered correctly.



Fig. 7: Setting used for the photography of the plant fossils from Zöbing: One-sided illumination (a) through a frosted glass plate (c), which is fixed by a light tent (b) (Kerp & Bomfleur 2011).

Afterwards the photographs are edited as far as necessary (e.g. background) using Eos Utility software and image processing programs like Adobe Photoshop or CorelDraw.

6 Results & Discussion

6.1 Elements of the flora

6.1.1 Alethopteris STERNBERG 1825

The foliage of the genus *Alethopteris* is characterised by asymmetric pinnules of variable shapes, which are decurrent at the basiscopic side of the pinna and pinnule bases are mostly conjoined by a rim. The acroscopic side is either decurrent, straight or slightly constricted (Wagner 1968). The pinnules are often relatively large, up to 5 cm in some species, and attached at an acute or wide angle at the ultimate order rachis (Taylor et al. 2009). Rachides usually show longitudinal striations (Wagner 1968).

The venation shows a well-marked midvein and numerous, one or more times forked lateral veins, which attain the pinnule margins at different angles depending on the species (Wagner 1968). In some species, subsidiary veins directly enter the decurrent base arising from a vascular bundle in the pinna rachis (Taylor et al. 2009).

Alethopteris fronds are bipartite, tri- or quadripinnate and attain considerable sizes (Laveine et al. 1993, Wagner 1968).

Alethopteris schneideri STERZEL (1881) 1918

Plate I, Figure 1-4

Synonymy: Barthel 1976a,b

Material (Table 4): Ultimate order pinna fragments.

Description: The rachis shows longitudinal striations. The pinnules are inserted obliquely at the rachis and are broadly attached. They are asymmetrically shaped. The margins are slightly convex.

The basiscopic side of the pinnule base is decurrent; the acroscopic side is deeply constricted, almost as far as the midvein. The pinnules are not confluent. Different types of pinnules can be observed:

A) Small pinnules of a maximum of 10 mm length and about 5 mm width; distantly spaced. These pinnules are roundish or tongue-shaped with broadly rounded apices.

B) Large and broad, tongue-shaped pinnules about 25 mm length and \sim 12 mm width. The apex is broadly rounded. Pinnules are overlapping in some specimens but they are not conjoined.

C) Large, elongate and narrow pinnules, which are about 20 to 25 mm long and 6 mm wide. Their apex is more acuminate but still blunt. The pinnules are distantly arranged in the present specimen.

The venation is pinnate, relatively dense and appears rather uniform (35+ marginal veins per 1 cm). The midvein is straight and prominent through almost the whole pinnule. Lateral veins arise at an acute angle from the midvein, bend over immediately and follow an almost straight course to the margin. They enter the margin at different angles: almost perpendicular in large pinnules and relatively oblique in small pinnules. They bifurcate once or twice close to the midvein. At the basiscopic side subsidiary veins arise directly from the rachis.

Discussion: These specimens can be easily identified by the unusually deep constricted acroscopic side, the decurrent basiscopic side and the non-confluent pinnules. The only similar species, *Alethopteris sullivanti* (LESQUEREUX) SCHIMPER shows less constriction on the acroscopic side and generally more oblique lateral veins.

A great variability of this species can be seen in terms of pinnule size, outline, venation and distance of the pinnules. Barthel (1976a,b) gave a detailed description of this species and provided a compilation of different pinnule types. He also noticed a swift transition to unipinnate apical frond parts. Hence, according to Barthel, the variability of pinnule types mainly depends on their position in the frond: Small pinnules belong to bipinnate frond parts, whereas large or oblong pinnules are elements of unipinnate parts.

While Barthel (1976a,b) mentions in his descriptions that lateral veins attain the pinnule margins almost perpendicular, the specimens from Zöbing featuring small pinnules show quite oblique angles between laterals and the margins, like described by Šimůnek (1989).

Remarks: Specimen 153 414 exhibits small oval-shaped insect-eggs on the surface of the pinnules.

Alethopteris zeilleri (RAGOT) WAGNER 1958

Plate II, Figure 1-4; Plate III, Figure 1-2

Synonymy: Wagner 1968

Material (Table 4): Last order pinna fragments.

Description: Ultimate pinnae are usually almost linear. The rachides of the last order show longitudinal striae and are about 1 to 1.5 mm wide. The pinnules are inserted alternately at a right angle or slightly oblique. In some specimens pinnules are closer to each other, but usually not touching.

Pub. Krahuletz-Ges. 2023/01

The pinnules are relatively symmetrical, roundish or rather tongue-shaped with broadly rounded apices. They are 5 to 20 mm long and 4 to 9 mm wide (in the middle of the pinnule). They are broadly attached by their entire base to the rachis. The basiscopic sides can be more or less decurrent (sometimes too closely spaced), the acroscopic sides are straight. The pinnules are mostly conjoined by a rim of 0.5 to 2 mm width. The pinnule margins are parallel or subparallel, occasionally even lobate. This species shows certain variability in pinnule (or ultimate pinna) morphology. Two general types of pinnule shapes can be observed:

(A) Broad shape: The pinnules are rather wide and up to 2 cm long. The apex is broadly rounded and pinnules are closely spaced on the supporting rachis.

(B) Narrow shape: The pinnules are longer, more elongate, almost linear, often less closely spaced and show less broadly rounded apices.

The pinnules at apical frond parts ("young" pinnules) exhibit small, short, broad and roundish or sometimes slightly triangular shapes. Terminal pinnules are short and triangularroundish. Larger pinnules show undulating margins.

The venation is pinnate and rather thin showing about 30 to 42 veins per 1 cm pinnule margin. The midvein is usually strong, sometimes minimally decurrent and follows a relatively straight course through around 3/4 or more of the pinnule. Lateral veins depart at acute angles from the midvein and attain the pinnule borders nearly perpendicular. They are a little bent near the midvein, apart from that rather straight and bifurcate one or two times. At the decurrent base/rim, subsidiary veins directly arise from the rachis.

Discussion: *Alethopteris zeilleri* is represented by a great amount of specimens, which can be identified by their rather large pinnules and characteristically broadly rounded apices. The described variability can also be seen between specimens described and pictured by Doubinger et al. 1995, Šimůnek 1989 and Wagner 1968. First remarks regarding variability have been made by Zodrow (2007), who described *Alethopteris zeilleri* from the basal Cantabrian coal seam of the Sydney Coalfield of Nova Scotia in Canada and separated two major architectural groups of ultimate pinna, the first showing near-linear, narrow pinna with basally confluent pinnules and the second showing wider pinna with longer pinnules, which are inserted more loosely. The variability is further discussed in the following (6.4).

Cf. Alethopteris zeilleri (RAGOT) WAGNER 1958

Plate III, Figure 3-4

Material (153 1207; 1209; 1513): Last order pinna fragments.

Description: The rachis is about 2 mm wide and longitudinally striated. The pinnules are inserted perpendicular or in wide angles. They are attached with their whole base, which appears a little constricted in some pinnules, whereas others seem to be conjoined by a diminutive rim. The pinnules are alternately arranged, and they are generally closely spaced or overlapping. The pinnules are elongate, ribbon-like, about 30 to 35 mm in length and 7 or 8 mm in width. Lateral pinnule margins vary from parallel to lobate. The pinnule surface appears somewhat undulating. Towards the rounded apex the pinnules are slightly tapering.

The midvein is strongly marked and continues through 5/6 of the pinnule. Slightly flexuous lateral veins depart from the midvein obliquely and are up to three times bifurcated. They attain the pinnule border almost perpendicular. The venation is not very dense (~ 35 veins per 1 cm pinnule margin).

Discussion: Disregarding their length, these specimens share most characteristics of *Alethopteris zeilleri* (RAGOT) WAGNER. They are similar in the width of the pinnules and the venation. The undulating appearance and apex shape resembles those of large *Alethopteris zeilleri* pinnules, so probably these are even longer ones.

Zodrow (2007) also described pinnules of *Alethopteris zeilleri* of lengths up to 34 mm, which show lobate margins quite similar to these specimens.

Another genus showing long ribbon-like pinnules, *Desmopteris* STUR can be excluded through the following characteristics: Representatives of this taxon never show conjoined pinnules and exhibit rather thin and sinuous rachides. The pinnules are often distantly spaced and the venation is wider (cf. Doubinger & Germer 1984, Crookall 1955, Vetter 1968).

Alethopteris sp.1

Plate IV, Figure 1

Material (153 85a/b; Table 4): Ultimate order pinna fragments.

Description: The rachis is rather thin. Pinnules are closely spaced, some are minimally overlapping. They are about 20 mm long and about 6 mm wide in the middle (= broadest part). Their shape is oval, showing greatest width in the middle. Convex margins converge towards the rounded apex. The base of the pinnules is decurrent at the basiscopic side and a little constricted at the acroscopic side. Pinnules are conjoined by a narrow rim.

The venation is pinnate. A well-marked, almost straight or slightly curved and a little decurrent midvein runs through almost the whole pinnule. Lateral veins are once or twice

bifurcated and relative closely spaced (~ 35 veins per 1 cm pinnule margin). They attain the pinnule border nearly perpendicular. Subsidiary veins are visible on the basiscopic side.

Discussion: The specimens show a fairly large affinity to *Alethopteris zeilleri* (RAGOT) WAGNER regarding pinnule size and venation. However, a divergent pinnule shape, showing little acroscopic constriction and a broadened middle part of the pinnules, bears more resemblance to the species *Alethopteris serlii* (BRONGNIART) GOEPPERT. However, *Alethopteris serlii* usually does not exhibit these clearly rounded apices and shows a more regular lateral venation. Though, these specimens may possibly be a variability of *Alethopteris serlii*.

Furthermore, Zodrow (2007) described different architectural categories of *Alethopteris zeilleri*, in which one "parallels the architecture observed in ultimate pinnae of *Alethopteris serlii*". Accordingly, the specimens may also represent another pinnule type of *Alethopteris zeilleri*.

Alethopteris sp.2

Plate IV, Figure 2

Material (153 322): Ultimate order pinna fragments.

Description: The rachis is about 1 mm wide and longitudinally striated. The pinnules are large, but comparatively short, 13 to 16 mm in length and 6 to 8 mm in width. They are attached alternately and are oblique to the rachis. Bases are decurrent at the basiscopic side and conjoined by a rim of 1 to 2 mm width. The pinnules are asymmetrical and conically shaped, margins are slightly curved, and apices rounded.

The venation is pinnate and exhibits a rather straight definite midvein, which proceeds almost to the pinnules apex. Lateral veins depart from the midvein obliquely. They are forked once or twice and attain the margin obliquely (acroscopic side) or almost perpendicular (basiscopic side). The venation appears denser and more uniform at the acroscopic side of the pinnule.

Discussion: The specimen shows little characteristics of *Alethopteris bohemica* FRANKE, like the general pinnule shape and the long midvein, which proceeds almost to the apex of the pinnule. However, *Alethopteris bohemica* shows a denser, finer and more regular lateral venation and pinnules appear thicker or more vaulted. In contrast to *Alethopteris zeilleri*, the pinnules of this specimen are attached more oblique and the pinnule outline is more tapering with a much less rounded apex. The pinnules of *A. schneideri* differ in the deep acroscopic constricted bases and non-confluent attachment of pinnules.
Alethopteris cf. barruelensis WAGNER 1967

Plate IV, Figure 3

Synonymy: Wagner 1968

Material (153 561; 589): Last order pinna fragments; no terminal pinnules.

Description: The rachis of the last order is relatively robust and $\sim 1 \text{ mm}$ wide. It shows fine longitudinal striations.

The pinnules are 12 to 15 mm long and 5 to 6 mm wide. The pinnule shape is linear and slightly tapering towards the apex. Borders are slightly convex and the apex is blunt. The pinnules are inserted suboppositely and they are attached almost perpendicular or oblique ($\sim 60^{\circ}$). They are distant, not touching. The bases are faintly decurrent on the basiscopic side and confluent (rim). The venation is pinnate. A quite strong midvein continues almost to the apex. Lateral veins are relatively dense, ~ 40 veins per 1 cm of the pinnule margin, fork one to three times and attain the pinnule border at right or oblique angles.

Discussion: The specimens resemble the narrow types of *Alethopteris zeilleri* due to the slender pinnules of similar size. However, the pinnule insertion and the pinnule shape differ slightly. Also the rachis appears comparatively thicker. *Alethopteris zeilleri* shows more parallel margins and more rounded pinnule apices. Also the venation of these specimens rather resembles *Alethopteris barruelensis*, which shows finer and somewhat more flexuous veins.

Alethopteris sp.3

Plate IV, Figure 4

Material (153 217): Ultimate order pinna fragment; no terminal.

Description: The rachis is about 1 mm wide and shows longitudinal striations. The pinnules are attached perpendicular or somewhat oblique and are distantly spaced. Bases are confluent. The pinnules are rather small, 6 to 10 mm long and 4 to 5 mm wide. They are linguiform, slightly tapering, but the apices are rounded.

The midvein is strong, straight or somewhat decurrent, continuing through about 3/4 of the pinnules. Lateral veins depart from the midvein only slightly oblique, follow a straight course and attain the margin mostly perpendicular. They are once or twice bifurcated. Subsidiary veins enter the pinnule directly from the rachis.

Discussion: The specimens differ significantly from *Alethopteris schneideri*. *Alethopteris zeilleri* exhibits comparatively larger and broader pinnules with more broadly rounded apices. Also the midvein is thinner in relation to the pinnule width. Furthermore this specimen exhibits more distantly spaced pinnules.

The available specimens rather show similarities to *Alethopteris ambigua* (LESQUEREUX) WHITE or *Alethopteris lesquereuxi* WAGNER. However, *Alethopteris ambigua* usually shows less confluent pinnules and a wider venation, and *Alethopteris lesquereuxi* exhibits more oblique lateral veins (cf. Wagner 1968).

6.1.2 Callipteridium WEISS 1870

The genus *Callipteridium* is similar to *Alethopteris*, but the pinnules are generally smaller, slightly confluent and inserted at almost right angles to the pinna rachis. They are attached with their entire base. The basiscopic side of the pinnules is usually less decurrent than in *Alethopteris* (Taylor et al. 2009, Wagner 1965). A single midvein enters the pinnule straight and perpendicular and becomes less distinct near the apex (Wagner 1965, Taylor et al 2009). Lateral veins, departing from the midvein, follow a course oblique to the pinnule border and fork usually either once or twice at irregular intervals (Wagner 1965).

Subsidiary veins may enter the base of the pinnule directly from the rachis (Taylor et al. 2009).

Callipteridium gigas (GUTBIER) WEISS 1877

Plate V, Figure 1

Synonymy: Excerpt in Barthel 1976b.

Material (153 111): Last order pinna fragment.

Description: The rachis is about 1.5 mm wide and shows fine longitudinal striations. The pinnules are inserted perpendicular and subopposite. They are closely spaced and their margins are touching. The entire pinnule base is attached to the rachis, sometimes the bases even are a little confluent. The pinnules are 16 to 17 mm long and 6 to 7 mm wide, broadly linear with a broadly rounded apex.

The venation is rather fine. A midvein is marked through about 3/4 of the pinnule. Lateral veins depart obliquely from the midvein and follow an arcuate course to the margin, which is

attained rather obliquely. They are at least once forked (hard to see due to state of preservation).

Discussion: *Callipteridium gigas* differs from other *Callipteridium* species in showing more parallel-sided pinnules that are never triangular and exhibit clearly rounded apices. Furthermore, the thin and dense venation is quite characteristic (Barthel 2006). This also distinguishes the specimen from *Alethopteris zeilleri*, which generally exhibits pinnules of similar shape. However, *Alethopteris zeilleri* also shows differences in pinnule insertion and pinnule distance.

Callipteridium cf. pteridium SCHLOTHEIM EX ZEILLER 1888

Plate V, Figure 2

Synonymy: Castro (2005).

Material (153 1003): Ultimate order pinna fragment.

Description: The rachis is proportionally wide ($\sim 1.5 \text{ mm}$) and shows fine longitudinal striations. Pinnules are attached at right angles or slightly oblique and suboppositely. They are about 13 to 15 mm long and 4 to 5 mm wide at the base (= broadest part). Pinnules are narrow and elongate. They are minimally curved upwards with the acroscopic margin being almost straight and the basiscopic margin being a little convex. They are tapering towards a blunt apex. The pinnules are touching at the base and partly confluent.

The midvein is well-marked through more than three-quarters of the pinnule. Relatively straight running lateral veins branch off from the midvein acute-angled and attain the margin obliquely. Venation appears rather loose, but an exact number of veins or furcation cannot be determined in the available specimen due to its state of preservation.

Discussion: This specimen shows characteristics of *Callipteridium* like perpendicular pinnule insertion and the slightly confluent pinnule shape. It differs from *Callipteridium gigas* in the triangular pinnule shape and the less dense arrangement of the pinnules.

It can also be distinguished from *Callipteridium costei* (ZEILLER) WAGNER and *Callipteridium trigonum* FRANKE by the narrower pinnules, and from the latter by the less dense venation (cf. Vetter (1968), Knight (1983) and Wagner & Álvarez-Vázquez (2010a).

Regarding size and shape this specimen is most similar to *Callipteridium pteridium* (SCHLOTHEIM) ZEILLER, although pinnules of this species are generally more vaulted (cf. Doubinger 1956, Castro 2005).

Callipteridium sp.

Plate V, Figure 3

Material (153 650): One ultimate order pinna fragment.

Description: The last order rachis is robust in comparison to the pinnules and shows fine longitudinal striations. Pinnules are alternate and inserted at more or less right angles. They are attached by the entire base and slightly confluent. Margins are not touching. The pinnules are rather small, about 4 to 6 mm long and \sim 3 mm wide in their middle. The pinnule shape is subtriangular with apices quite rounded and slightly bent upwards.

The midvein is well-marked for over three-quarters of the pinnule and a little arcuate.

Lateral veins arise at an acute angle from the midvein and attain the border obliquely. They are at least forked once. Venation appears rather wide.

Discussion: This specimen exhibits some characeristics of *Callipteridium zeilleri* WAGNER and *Callipteridium rochei* ZEILLER like rather small subtriangular-shaped pinnules and wide venation, which differs from those of the more parallel-sided and more densly veined species *Callipteridium gigas*. *Callipteridium trigonum* FRANKE also exhibits a rather triangular pinnule shape, but shows a different, more oblique venation (cf. Remy & Remy 1959) and as well *Callipteridium striatum* WAGNER, differs with a much denser venation (cf. Wagner 1965). In general it is difficult to distinguish between the two first mentioned species. *Callipteridium zeilleri* exhibits the less extreme triangular shape and *Callipteridium rochei* shows the more rounded apex, which both match this specimen.

According to Castro (2005) the species *Callipteridium striatum* and *Callipteridium zeilleri* are local variations of the species *Callipteridium pteridium*. Therefore, this fossil may represent either another differently shaped specimen of *Callipteridium pteridium* (var. *zeilleri*) or of *Callipteridium rochei*.

Cf. Callipteridium

Plate V, Figure 4

Material (153 429): Ultimate order pinna fragment; Pinnules only on one side.

Description: The rachis is relatively wide. The pinnules are inserted at right angles and close to each other, but margins are not touching. They are attached by their entire base. The pinnules are 22 to 24 mm long and about 8 mm wide, linear-linguiform with a broadly rounded apex.

The midvein is strong and runs through about 5/6 of the pinnule. It is straight and inserted perpendicular. Lateral veins depart from the midvein slightly oblique and attain the margin perpendicular. They bifurcate up to three times.

Discussion: Concerning the insertion of the pinnules an affinity to *Callipteridium* can be seen. The shape of the pinnules roughly resembles *Callipteridium gigas*, but this genus generally exhibits smaller pinnules and a less strong midvein. Though, the lateral veins are relatively dense and similar to those of *Callipteridium gigas*.

Regarding the midvein and the broadly rounded pinnule apices, also a resemblance to *Alethopteris zeilleri* may be assumed. However, pinnules are a bit broader, especially with regard to their length. Furthermore, long pinnules of *Alethopteris zeilleri* generally show less straight margins and a wider venation.

Thus, a definite conclusion is difficult. An explicit classification would provide the presence of intercalated pinnules, which cannot be seen in this specimen.

6.1.3 Neuropteris sensu lato (BRONGNIART) STERNBERG 1825

The morpho-genus *Neuropteris* (*sensu lato*), as initially established by BRONGNIART, describes compound leaves or fronds, whose pinnules have a constricted or cordate base, rounded or pointed tips, and a non-anastomosing venation (Cleal & Shute 1995, Taylor et al. 2009).

Because of the fact that several genera are included in this definition of *Neuropteris* regarding their general appearance and pinnule shape, although displaying deviations from *Neuropteris sensu stricto*, a synoptical evaluation based on both frond/leaf architecture and cuticular features has resulted in a generic reclassification. Nine more defined and homogenous morphogenera were established: *Laveinopteris, Macroneuropteris, Margaritopteris, Neurolottopteris, Neurolottopteris, Neurolottopteris, Neurolottopteris, Neurolottopteris, Neurolottopteris, Neuropteris sensu stricto, Paripteris and Sphenoneuropteris (Cleal & Shute 1995, Taylor et al. 2009).*

The pinnules of *Neuropteris sensu stricto* are often partly fused to the pinna axis and have a relatively weak midvein (Taylor et al. 2009).

Neurocallipteris shows small pinnules (< 2 cm long), which are attached to the rachis by a minimum of $\frac{1}{4}$ of their base. Larger pinnules are more constricted (Cleal et al. 1990). The venation ranges from neuropteroid to callipteroid to odontopteroid (Barthel 2006).

Neuropteris cordata BRONGNIART 1830

Plate VI, Figure 1-3; Plate VII, Figure 1-2

Synonymy: e.g. Barthel (1976b).

Material (Table 4): Last order pinna fragments; One specimen with terminal pinnule.

Description: The rachis is rather strong, about 2 mm wide and shows longitudinal striae. Pinnules are alternate, inserted obliquely (40° to 80°) and are punctually attached to the rachis.

A great range in the shape of the pinnules can be observed:

Large pinnules, about 50 mm long and 15 mm wide, are elongate tongue-shaped, a little tapering, slightly arcuate and have a rounded apex. The base is cordate and partially overlaps the rachis.

The venation is well-marked, but rather wide. A thin midvein is visible through almost the whole pinnule (5/6). Lateral veins branch off at an acute angle. They are uniformly arcuate, up to three, or possibly four times bifurcated and enter the margin obliquely.

Shorter pinnules, 10 to 12 mm long, 7 to 10 mm wide, show a less cordate base. The acroscopic side is still constricted, the basiscopic side is more broadly attached. The outline is either more roundish or more conical or sloping-rectangular linguiform, the apex is still rounded. The venation is a little denser and the midvein less distinctive and shorter. Lateral veins are up to four times bifurcated and sometimes flexuous. In the basal part some secondary veins arise from the base or rachis.

The pinnules in apical parts are attached with their entire base and slightly decurrent. Their midvein is indistinct, short and decurrent as well.

Some specimens show tiny nodular features, between their veins, which are more crowded near the midvein and become less numerous towards the margin.

Discussion: The observed variability in pinnule shape is consistent with those described by Barthel (1976b) and allows a reliable identification.

The nodular features on the pinnule surface are possibly trichomes or hair bases. According to Krings (2004), pinnules and pinnule rachides of Neuropteris *cordata* were densely covered with multi-cellular hair, which probably constituted a protective mechanism (barrier) against small insects.

Plate VII, Figure 3-4

Synonymy: Cleal et al. (1990).

Material (153 940, 153 832): Last order pinna fragments; no terminals.

Description: The rachis is about 1 mm wide and shows fine longitudinal striations. The pinna fragment is relatively linear shaped. The pinnules are closely spaced and overlapping. They are attached somewhat obliquely and alternate. The outline is shortly tongue-shaped and has a general neuropteroid character. The base is a little constricted and a bit lobed at the basiscopic side, but the attachment to the rachis is still relatively broad. The pinnules are small, about 6 mm long and 3 to 4 mm wide.

The venation is rather odontopteroid. Fan-like veins mainly arise from a central point at the rachis and are a bit compacted in the slightly depressed middle part of the pinnule. They fork at least one or two times and attain the pinnule margin obliquely.

Discussion: The relatively wide rachis, pinnule size, roundish shape and the more or less odontopteroid venation resemble *Odontopteris subcrenulata* ROST, but pinnules as well as the main veins of this species are usually decurrent, pinnules even confluent (Doubinger & Germer 1971). The linear pinna with small, regular neuropteroid shaped pinnules and venation are rather characteristic for *Neurocallipteris neuropteroides*, which generally exhibits neuropteroid pinnules in basal regions and more odontopteroid pinnules in apical regions (Barthel 2006, Kogan et al. 2008). Small similar shaped pinnules of *Neuropteris ovata* HOFFMANN differ in the more constricted base and the venation, which shows a strongly decurrent midvein (Cleal & Zodrow 1989).

6.1.4 Odontopteris (BRONGNIART) STERNBERG 1825

This genus is characterised by pinnules, whose base is completely adherent to the rachis, and in which the venation lacks a midvein or shows a main vein ("midvein") restricted to the lowermost (usually < 1/4) pinnule part. Instead it shows one or more steeply ascending veins that enter the pinnule base directly from the rachis and fork at irregular intervals (Knight 1983, Šimůnek & Cleal 2004). Two morphological 'sub-groups' of *Odontopteris* can be distinguished. The first group features elongate, asymmetrically triangular pinnules, and the second group rounded pinnules (Taylor et al. 2009).

Fronds are relatively small, typically maximally 1 m long (Šimůnek & Cleal 2004).

Odontopteris brardii BRONGNIART 1825

Plate VIII, Figure 1-2

Synonymy: Knight (1983).

Material (153 309): Small last order pinna fragment. No terminal pinnule.

Description: Rhachis is longitudinally striated. The pinnules are attached by their entire base and at an oblique angle. They are closely spaced. The pinnules are about 11 mm long and 6 mm wide, the margins are parallel and the apex is asymmetrically triangular, but rounded.

The venation shows no midvein, but a lot equally fine veins depart from the rachis and dichotomise during their course to the margin, which is attained obliquely. Veins are a little compacted in the middle of the pinnule. A "Doppelkontur" as described by Barthel (2006) can be seen in this impression specimen.

Discussion: The specimen exhibits the general shape and characteristics of *Odontopteris brardii* BRONGNIART. The general shape of this specimen also resembles *Odontopteris minor* BRONGNIART, which is assumed to be a synonym of *Odontopteris brardii* by many authors (Barthel 2006). However otherwise it could be differentiated due to its larger pinnule size (Doubinger 1956).

Remarks: Another specimen was found in bed 148 (= unknown finding site, but must be a proximate 'younger' fossiliferous bed). This specimen exhibits slightly more rectangular pinnules and the venation appears wider.

Odontopteris cf. nemejcii ŠIMŮNEK & CLEAL 2004

Plate VIII, Figure 3-4

Synonymy: Šimůnek & Cleal (2004).

Material (153 780): Penultimate order pinna fragment; no terminal pinnules.

Description: The Length of the whole pinna is unknown, the width is about 10 to 12 mm. Penultimate and ultimate rachides show longitudinal striations. The pinna and the pinnules are inserted somewhat oblique. The pinnules are attached alternate and by their entire base. They are minimally decurrent on the basiscopic side. The pinnules are small, 6 mm in length and 2 to 3 mm in width, and linguiform with relatively straight and parallel margins. The apex is broadly rounded.

The venation lacks a midvein. However a few veins enter the pinnule apparently direct from the rachis, basally bunched in the middle, which appears a little sunken as well. They continue

fan-like, dichotomising at least once, and curve toward the margin which is attained slightly oblique. The venation is rather wide.

Discussion: This specimen shows a great affinity to those of *Odontopteris nemejcii* described by Šimůnek & Cleal (2004). They are especially similar in size and venation, though the latter cannot be observed that detailed in the available specimen. Merely the outline of the pinnules is explicitly linguiform, not triangular, and appears more symmetrical than those pictured by Šimůnek & Cleal (2004). The pinnules are also more closely spaced and less obliquely inserted.

The specimen differs from small forms of *Odontopteris brardii* in having more symmetrical pinnules with rounded apices. *Odontopteris brardii* in contrast shows more rhomboidal pinnules and also a slightly denser venation (Šimůnek & Cleal 2004).

Based on the size and oblong-oval shaped pinnules with rounded apices and the venation, the specimen resembles *Odontopteris obtusa* BRONGNIART, but it differs clearly in the attachment of pinnules. *Odontopteris obtusa* shows more constricted bases and less uniformly shaped pinnules. *Odontopteris subrenulata* ROST var. *elongata* DOUBINGER & VETTER differs primarily in the size of pinnules (Vetter 1968).

6.1.5 Dicksonites STERZEL 1881

The genus *Dicksonites* is characterised by broadly attached triangular or elongate-triangular pinnules, which are generally lobed. The venation shows a slightly flexuous midvein and departing lateral veins, which bifurcate on their course to the lobes and margin (Taylor et al. 2009). The rachides are longitudinally striated and may show intervallic transversal bars. Relatively wide bipartite fronds are born by long and slender stems with long internodes (Vetter 1968, Galtier & Béthoux 2002).

Dicksonites cf. pluckenetii (SCHLOTHEIM EX BRONGNIART) STERZEL 1881

Plate IX, Figure 1

Synonymy: Selected synonymy in Knight (1983).

Material (153 382a): Ultimate order pinna fragment; rather poorly preserved.

Description: The ultimate rachis is robust and broad (~ 2 mm) and shows weak longitudinal striation. The pinnules are about 15 mm long and 4 to 5 mm wide near the base and arise from

the rachis alternately and in wide angles. Their attachment is not visible. They are elongate, slightly triangular and divided into small, thickened knobbly lobes.

The midvein is strong and runs up to the apex. Lateral veins are not preserved in this specimen.

Discussion: The lobed pinnules are characteristic for *Dicksonites*. Due to the state of preservation it is difficult to identify the species of this specimen. *Dicksonites pluckenetii* (SCHLOTHEIM EX BRONGNIART) STERZEL and *Dicksonites sterzelii* (ZEILLER) DANZÉ-CORSIN have to be considered both.

The similarity of these species was discussed by several authors. Some propose the synonymy of both species, whereas others differentiate between them. According to Doubinger et al. (1995) both species vary in terms of pinnule insertion, which is more oblique in *Dicksonites sterzelii*, and the pinnule shape. *Dicksonites pluckenetii* exhibits elongated pinnules with round lobed margins and characteristically thick "bloated" lamina, whereas pinnules of *Dicksonites sterzelii* are rather thin and triangularly to trapezoidally shaped. They also mention that due to the bloated lamina the venation can hardly be seen in *Dicksonites pluckenetii*.

Galtier & Béthoux (2002) support the distinction of the species as they found out that *Dicksonites sterzelii* exhibits more robust fronds and broader pinnules, which feature "distinctive secretory glands which are absent in *Dicksonites pluckenetii*".

In this specimen, the aspect of thickened knobbly lobes and the visual absence of lateral veins favour its identification as *Dicksonites pluckenetii*.

6.1.6 Pseudomariopteris DANZÉ-CORSIN 1953

Specimens of *Pseudomariopteris* have pinnules of variable shape and size. They are tongueshaped or triangular, generally broadly attached acroscopically constricted, and often decurrent. In lowermost pinna parts pinnules often exhibit a basal lobe. The rachises are smooth or show weak longitudinal striae. The pinnae are often shorter on the interior frond sides. On the pinna apices either single small apical pinnules or hook-like prolongations can be found. The fronds are small, bipartite and bipinnate (Krings & Kerp 2000).

Pseudomariopteris cordato-ovata (WEISS) GILLESPIE, CLENDENING & PFEFFERKORN ex KRINGS & KERP 2000

Plate IX, Figure 2

Synonymy: Krings & Kerp (2000).

Material (153 663): A pinna fragment with only one complete pinnule.

Description: The rachis is about 1 mm wide, a structure on it is not discernible. The pinnules are attached broadly and only slightly oblique to the rachis. They are about 8 mm long and 4 to 5 mm wide and appear rather thick and vaulted. Their outline is a little triangular, tongue-shaped with a basal lobe. The basal acroscopic side seems to be constricted. The apex is rounded. The pinnules are touching at the base. The midvein is prominent, somewhat sunken and runs almost straight through about three-quarters of the pinnule length. The lateral veins are not visible.

Discussion: This specimen shows a prominent midvein and pinnules with a basal lobe, which are characteristics for *Pseudomariopteris cordato-ovata*.

6.1.7 Sphenopteris (BRONGNIART) STERNBERG 1825

Sphenopterids (*Sphenopteris sensu lato*) represent a very heterogeneous group of uppermost Devonian to Permian foliage types of often unknown systematic relation. They are associated with several true ferns, as well as pteridosperms. The pinnules usually exhibit a constricted base and are generally decurrent. Their shapes range from oval and almost entire margined, to lobed or toothed. The venation is pinnate. Lateral veins depart at an acute angle from a straight or flexuous midvein. Either one or a few laterals run toward the margin of each lobe. Until now this group is not totally understood. *Sphenopteris sensu stricto* was defined to describe species to which specific gymnospermous reproductive structures could be assigned (Taylor et al. 2009).

Sphenopteris cf. mathetii ZEILLER 1888

Plate IX, Figure 3-5

Synonymy: Brousmiche (1983).

Material (153 378, cf. 388): Penultimate order pinna fragments.

Description: The rachis of the penultimate order shows coarse longitudinal striae, rachises of the last order show fine longitudinal striations.

Pub. Krahuletz-Ges. 2023/01

Last order pinnae are inserted obliquely to almost perpendicular at the axis. The pinnules are attached slightly oblique to the rachis and are conjoined by a narrow rim. Pinnules are generally oval or slightly triangular and show lobed margins. Some pinnules appear vaulted. They are 3 to 7 mm long and 2 to 4 mm wide near the base. Their base is a little contracted, sometimes decurrent. Small pinnules show fewer lobes than the larger pinnules. The number of lobes ranges from 3 to 7, possibly 9. Lobes are generally rounded.

The venation is wide. A slightly decurrent midvein runs through the whole length of the pinnule. One lateral vein per lobe departs from the midvein at an acute angle and sometimes bifurcates one or two times before reaching the margin.

Discussion: The pinnules are typically sphenopteroid and the shape of pinnules and lobes mostly resembles *Sphenopteris mathetii*. However, the pinnules are partly a bit larger than mostly described (cf. Doubinger et al. 1995, Langiaux 1984).

6.1.8 Foliage of unknown affinity

A: Plate X, Figure 1

Material (153 650): Impression of an ultimate order pinna fragment; no terminal.

Description: The rachis of the ultimate order is fine and arcuate. The pinna of the last order is roughly triangular, but lacks the apical part. The pinnules are distant. Attachment appears pecopteroid or alethopteroid and a little decurrent. The pinnules are inserted almost perpendicular. They are elongate and slender, 5 to 10 mm long and about 2 mm wide, straight or somewhat bent, slightly tapering towards a rounded apex (rotundity even more distinct in smaller pinnules).

The venation is poorly preserved. A distinctive midvein follows a straight or slightly arcuate (like the pinnule itself) course through the pinnule. The lateral veins are not visible.

Discussion: Due to its poor state of preservation, especially of the venation, this specimen cannot be identified adequately. Therefore, the following assumptions are purely speculative. The outline of the pinnules first reminds of taxa of *Neuralethopteris*, but the attachment of the pinnules bears more resemblance to pecopterids or alethopterids. The apparently minimally decurrent bases favour the correlation to the genus *Alethopteris*.

The specimen roughly resembles a rather long-pinnuled form of Alethopteris leonensis WAGNER. Alethopteris bohemica FRANKE diverges regarding the width of pinnules and

Alethopteris moravica AUGUSTA (1927) shows more biconvex pinnules than the specimen at hand (Wagner & Álvarez-Vázquez 2010a).

B: Plate X, Figure 2

Material (153 304): Ultimate order pinna fragments; only one complete pinnule preserved. **Description:** The rachis is hardly preserved. The pinnule is attached broadly and decurrent at the basiscopic side. The acroscopic side appears slightly constricted. The pinnule is small, 11 mm long and 6 mm wide and oval to tongue-shaped with a broadly rounded apex.

The venation is rather wide. A thin midvein runs about half of the pinnule length and then bifurcates at least twice. Lateral veins depart from the base rather than the midvein. They fork up to three or four(?) times and attain the margin obliquely.

Discussion: This specimen shows affinity to Neuropteris sensu lato.

C: Plate X, Figure 3

Material (153 183): Isolated pinnule fragment (no apex).

Description: This pinnule exhibits a neuropteroid shape with a cordate base. The pinnule is 8 mm in width, however its length cannot be measured because its apical part is missing, but its general shape is elongate with parallel margins. The venation is reticulate, showing a clearly marked midvein and anastomosing lateral veins.

Discussion: An identification of this specimen is not possible, due to its incomplete preservation. In general, pinnules of the taxa *Linopteris, Reticulopteris* and *Barthelopteris* share all characteristics of *Neuropteris sensu lato* except for the pattern of the lateral venation, which is reticulate and shows anastomosing lateral veins (Taylor et al. 2009, Zodrow & Cleal 1993). Therefore, this species probably belongs to one of these genera.

D: Plate X, Figure 4

Material (153 689): Tip of an ultimate order pinna fragment with terminal pinnule.

Description: The specimen shows a rather thin rachis at which pinnules are inserted obliquely and suboppositely. They are distantly spaced. The terminal is oblong and rather slender (10 x 3 mm). The pinnules are small, 5 mm long, 3 mm wide and roundish. They are broadly attached and a little decurrent.

The venation lacks a midvein. Several veins enter the pinnule directly from the rachis and continue fan-like and more or less arcuate through the pinnule. They attain the margin at different angles and are forked at least once.

Discussion: This apical pinna fragment exhibits a rather odontopteroid shape and venation. It clearly differs from the species identified as *Neurocallipteris neuropterides* and from the specimen 153 663 (see above), regarding pinnule (and terminal pinnule) shape and venation. Furthermore the pinnules are rather distantly spaced.

This specimen may represent a species of Odontopteris or Neuropteris sensu lato.

E: Plate X, Figure 5

Material (153 663): Last order pinna fragment with terminal pinnule.

Description: The ultimate pinna is of triangular shape. The terminal pinnule is rather short and broad. The rachis shows fine longitudinal striations. Pinnules are densely spaced and touching, but not overlapping. The attachment is oblique and alternate. Pinnules are tongue-shaped, almost parallel sided and exhibit broadly rounded apices. The base is a little constricted and a small auricle formed on the basiscopic side. Pinnules are rather small, 6 to 10 mm in length and 4 mm in width.

The venation is fan-like, very fine and rather dense. A centred aggregation of slightly decurrent veins gives the impression of a short midvein. These main veins are decurrent. The arcuate extending veins fork several times.

Discussion: This specimen exhibits a neuropteroid shape and generally a similar size to that of *Neurocallipteris neuropteroides*, but in comparison to the specimens described above this one exhibits a rather triangular than linear pinna fragment. Moreover, the venation is denser. The identification of this specimen is problematic, because apical pinnules generally may be quite similar in several species and genera of *Neuropteris sensu lato* and *Odontopteris* (cf. Barthel 2006). Therefore, this specimen may be a potential representative of a neuropteroid or odontopteroid species. Possibly it may be linked to the genera *Neurodontopteris* or *Mixoneura*.

6.2 Quantitative analysis

The following species from the Leopoldacker collection could be identified:

Taxon	Quantity
Alethopteris schneideri	9
Alethopteris zeilleri	49
Cf. Alethopteris zeilleri	3
Alethopteris sp.1	5
Alethopteris sp.2	1
Alethopteris cf. barruelensis	2
Alethopteris sp.3	1
Callipteridium gigas	1
Callipteridium cf. pteridium	1
Callipteridium sp.	1
Cf. Callipteridium	1
Neuropteris cordata	9
Neurocallipteris neuropteroides	2
Odontopteris brardii	1
Odontopteris cf. nemejcii	1
Dicksonites cf. pluckenetii	1
Pseudomariopteris cordato-ovata	1
Sphenopteris cf. mathetii	3
Unknown affinity	5

Table 2: List of pteridosperms from the Leopoldacker and number of identified specimens.

The results extend the list of fossils from the Leopoldacker by several taxa (Table 2). However, only three of Vasícek's identifications, i.e. *Alethopteris zeilleri, Neuropteris cordata* and *Callipteridium gigas* could be confirmed. The fact that some of the previously mentioned taxa could not be identified may have different reasons. Primarily, it is difficult to understand all of Vasícek's identifications, as most of them were not recorded in descriptions or refer to specific specimens (= inventory numbers). Furthermore, these specimens may be missing in the present collection or simply have been overlooked.

Alethopteris zeilleri is the most abundant pteridosperm species from the Leopoldacker and comprises about 50 % of the identified taxa (Table 2). Some species are represented by several specimens, like *Neuropteris cordata or Alethopteris schneideri*, but most of the taxa occur only once or twice in this collection (Table 2).

However, these data are only roughly significant, due to their dependence on factors like preservation potential, fossil size (completeness) and sampling bias.

6.3 Systematics

The above-named species of the genera *Alethopteris, Neuropteris, Odontopteris, Neurocallipteris and Callipteridium* (6.1.1 - 6.1.4) are included in the order Medullosales, one of the three pteridosperm groups that are known from the Late Pennsylvanian and Early Permian of Europe and North America (DiMichele et al. 2006).

Medullosales were a successful pteridosperm group including many species, especially in the Pennsylvanian. They are known from the Late Mississippian and became extinct during the Permian (Stidd 1981).

Medullosans are generally reconstructed as small trees and comprised the largest representatives of seed ferns. However, other growth habits (leaners, vines, or lianas, e.g. *Laveinopteris* (*Neuropteris*) *attenuata*) are known as well (Barthel 2006, Taylor et al. 2009).

Arborescent representatives feature thick stems with complex steles (e.g. *Medullosa*) and large multipinnate planar fronds. Seeds vary in size but are typically large, acupulate, radial in transverse section and mostly triangular. The pollen organs are tubular and synangiate (Barthel 2006, Taylor et al. 2009).

Medullosales can be subdivided further into four families regarding characteristics of frond architecture, foliage and associated dispersed organs (DiMichele et al. 2006, Cleal & Shute 2003, Laveine 1997). *Alethopteris* belongs, amongst *Lonchopteris*, *Neuralethopteris*, *Cardioneuropteris*, and possibly *Neurocardiopteris* and *Lonchopteridium*, which were not found at the Leopoldacker, to the family Neuralethopteridaceae. This family is characterised by bifurcate pinnate fronds, which have a naked petiole and can reach large sizes. Known pollen organs are *Aulacotheca-Whittleseya* and seeds belong to the genus *Trigonocarpus* (DiMichele et al. 2006). *Alethopteris zeilleri*, for example, was reconstructed as a small 5 to 7 m high tree with relatively large fronds that bore both *Pachytesta incrassata* ovules and *Dolerotheca*-type fructifications (Zodrow 2007).

In the family Neurodontopteridaceae the genera *Neuropteris*, *Odontopteris*, *Reticulopteris*, and *Macroneuropteris* are included. Perhaps *Neurocallipteris*, *Neurodontopteris*, and *Barthelopteris* are comprised within this family as well (DiMichele et al. 2006, Zodrow and Cleal 1998).

Callipteridium, *Laveineopteris* and *Margaritopteris* are members of the family Cyclopteridaceae (Cleal & Shute 2003, DiMichele et al. 2006).

Genera of both families are characterised by bifurcate, semi-pinnate fronds, which are imparipinnate and may exhibit intercalary ultimate pinnae. Cyclopteridaceae bear true cyclopterid pinnules in contrast to Neurodontopteridaceae, which show large lateral pinnules below the main fork of the frond (Cleal & Shute 2003, DiMichele et al. 2006).

The family Parispermaceae, including the genera *Paripteris* and *Linopteris*, that have "pseudopinnate" compound fronds with paripinnate foliage (DiMichele et al. 2006), is not represented in the collection of Leopoldacker fossils.

The species *Pseudomariopteris cordato-ovata* and *Dicksonites pluckenetii* belong to the Order Callistophytales (Taylor et al. 2009).

This group existed in the Late Palaeozoic from the Late Westphalian to the Rotliegend/ Autunian (Kerp et al. 2007). Callistophytales have pinnately compound fronds and pinnules of characteristically pecopteroid-sphenopteroid shape, which bear reproductive organs on the abaxial pinnule side (Barthel 2006, Rothwell 1981). The pollen organs are synangiate with small and saccate pollen. The seeds are also relatively small, slightly flattened and noncupulate (Taylor et al. 2009).

Callistophytales mainly had scrambling and climbing growth habits characterised by fine axes, profuse branching, adventitious roots and in some cases features like climbing hooks (Barthel 2008, Kerp et al. 2007, Krings & Kerp 2000, Rothwell 1981).

Pseudomariopteris cordato-ovata belongs to the family Mariopteridaceae (DiMichele et al. 2006). Because of specialized plant parts like paired climber hooks, its growth habit could be identified as vine-like climber or thicketformer (Krings & Kerp 2000).

Dicksonites pluckenetii, a member of the family Callistophytaceae (DiMichele et al. 2006), was a scrambling or climbing plant, which could form dense stands (Galtier & Béthoux 2002).

No representatives of the order Peltaspermales could be identified in the collection of Leopoldacker fossils.

Until now, *Sphenopteris mathetii* is a pteridophyll of unknown affinity. No evidence for its classification as a pteridosperm could be found. Some specimens, e.g. from French basins, indicate a shrub-like habit with large rigid fronds. However, basal aphleboid pinnae rather favour its relation to ferns (Barthel 2006).

6.4 Plant architecture and development

The state of preservation of the Leopoldacker fossils permits no conclusions regarding the reconstruction of fronds or whole plants. However, these reconstructions are a primary goal in the study of pteridosperm foliage due to the use for analyses of phylogenetic relations among *Pub. Krahuletz-Ges. 2023/01 Berkholz/Zöbing* 45

the seed ferns (Krings et al. 2006). The collection lacks large frond specimens, or foliage attached to reproductive structures or other organs, which would be necessary for an expedient interpretation.

Merely the high amount of *Alethopteris zeilleri* specimens demonstrates a great variability of its foliage.

Zodrow (2007) already documented the variability of this species and compared specimens of *Alethopteris zeilleri* from different localities (Table 3).

Compared with his data, the specimens from Zöbing share a similar range in pinnule length as those from Canada, provided that the long-pinnuled specimens (Cf. *Alethopteris zeilleri*) are included. They show even the largest range of all documented specimens (Table 3).

The variety of pinnule width is rather small and lies close to but within the data of the Czech specimens, as well as the vein density. Apparently, the specimens from Zöbing may show one lateral vein dichotomy more than those from Canada, France and the Czech Republic (Table 3).

In general, the shape and variability of pinnules depends on their position in the frond and developmental degree of the frond.

According to Zodrow (2007), the wide range in pinnule length reflects the pinnule-growth pattern observed in other *Alethopteris* species, in which growth is typically characterised by apical pinnule development at a relatively constant pinnule width (Zodrow & Cleal 1998).

Origin of data	Pinnule length (mm)	Pinnule width (mm)	Midvein	Marginal vein density (/cm)	Lateral vein dichotomies	Subsidiary veins	Margin of larger pinnules
Holotype ^a : Czech ^b : French ^c : Canadian ^d :	15-25 6-24.5 15-17 6-34	6-8 4-11 5-7 4-7	Non-decurrent Non-decurrent Non-decurrent Non-decurrent; slightly decurrent in undifferentiated ultimate pinnae of penultimate pinna	30-35 28-43 - 26-36 ^e	1 or 2 1 or 2 - 1 or 2	Bifurcated Bifurcated - Bifurcated	Lobed - - Lobed
Zöbing:	5-20 Cf. A. zeilleri: 30-35	5-9 7-8	Non-decurrent or minimally decurrent	30-42 ~ 35	1 to 3 1 to 3	Bifurcated Not existent	Lobed Lobed

^a Wagner (1968, p. 160).

^b Šimůnek (1989).

^c Doubinger and Grauvogel-Stamm (1970, pl. 1, Fig. 1).

^d Zodrow (2007).

^e Measured as 18 per 5-mm length of margin on a 7-mm long pinnule.

Table 3: Gross-morphological comparison of the holotype of *Alethopteris zeilleri* with Canadian, French and Czech specimens of the same species (Zodrow 2007), extended by data from Zöbing.

6.5 Palaeoecology

The habitats of pteridosperms have been subject of prior discussions and speculations.

Due to the fact that seed ferns are a more tradition-based, heterogeneous group, than a well circumscribed phylogenetic order, they represent a wide range of ecological roles, for which reason they are valuable for ecological inferences (DiMichele et al. 2006).

Primarily, pteridosperms are elements of wetlands or wetter zones of seasonally dry environments. Furthermore, the different pteridosperm groups are adapted to different habitats: The Medullosales are commonly known from clastic wet floodplain (non-swamp) habitats. The Callistophytales densely inhabited wetland landscapes, but also occurred in areas prone to fires (DiMichele et al. 2006, Taylor et al. 2009).

Also the individual species indicate special conditions.

Most of the Leopoldacker species have been described as elements of hygrophilous to mesophilous floras, e.g. *Odontopteris brardii*, *Neurocallipteris neuropteroides*, *Dicksonites pluckenetii*, *Pseudomariopteris cordato-ovata*, *Callipteridium pteridium and Sphenopteris mathetii* (Barthel 2006, Kerp & Krings 2003).

Ecological adaptions of some plants (or the presence of species lacking ecological adaptions) indicate wet habitat conditions: Firstly, almost all identified taxa exhibit a non-anastomosing venation. Only one neuropteroid shaped specimen, showing reticulate venation was found in this collection. Reticulate venation is suggested to have developed in Medullosan pteridosperms due to increased physiological stress with the onset of long-term drier tropical conditions. The change of the venation to increasing flexuousness and finally to anastomousing veins is interpreted as a method to enhance physiological functioning under water-limited conditions (Zodrow & Cleal 1993, DiMichele et al. 2006).

Furthermore, based on cuticular studies by Kerp & Krings (2003), hydathodes, special leaf structures, which permit the excretion of excess water, were found in *Odontopteris brardii* (DiMichele et al. 2006).

Odontopteris nemejcii however lacks hydathodes and shows a lower vein density than *Odontopteris brardii*, which is rather characteristic for drier habitat conditions or lower ambient temperatures (DiMichele et al. 2006, Šimůnek & Cleal 2004). In general, it is assumed that specimens of *Odontopteris nemejcii* occupied higher altitudes with lower levels of atmospheric humidity than *Odontopteris brardii*, but until now evidence is equivocal (Šimůnek & Cleal 2004). Therefore, the coexistence may simply reflect different habitat conditions.

Also *Callipteridium gigas* is probably adapted to drier conditions, because of findings among extrabasinal elements like conifers and cordaites in the Erzgebirge-Basin (Barthel 2006).

According to Šimůnek (1989), cuticles of *Alethopteris zeilleri* show mesomorphic features. *Alethopteris zeilleri* and *Alethopteris schneideri* are mainly found close to coal seams (Barthel 1976b, Šimůnek 1989). Both are mesophilous species that probably grew close to coal swamps on the margin of organic accumulating areas (Barthel 1976b, Martín-Closas & Martínez-Roig 2007).

The pteridosperms from the Leopoldacker were deposited along with a large number of ferns, several remains of calamites and cordaites, and a few relics of conifers.

Hence, this flora is clearly dominated by elements of wetter habitats like ferns, sphenophytes and most pteridosperms. Though, *Callipteridium gigas* and *Odontopteris nemejcii* may be adapted to drier conditions than indicated by the other species. The conifer and cordaite remnants indicate the coexistence of drier conditions, while modern pteridosperm taxa adapted to drier conditions, like callipterids, are absent. Plants of the drier extrabasinal habitats are usually rarely preserved, due to their larger distance to basinal depositional areas. Besides, the occurrence of fusites in the fossiliferous sediments is an evidence for (seasonally) drier conditions.

Most remains are very fragmented, in cm- to dm-scale or even smaller plant shreds. Large coherent frond fragments or attached reproductive structures are not available.

Furthermore, the fossils were deposited disorderly, which favours burial under steady conditions like available in stagnant waters. A depositional environment like small eutrophic shallow lakes or temporally stagnant oxbow lakes as previously assumed is possible (cf. Chapter 3.5).

However, the fragmented condition of the fossils indicates a rather long transport distance or a turbulent flow during fluvial transport. Small fragments of cm-size or smaller (like single pteridosperm pinnules) may also be aeolian deposits, but larger fragments rather point to fluvial transport. An allochthonous deposition would explain the presence of the different plant groups, which represent different habitats.

Accordingly, there may have existed a "less allochthonous" community of hygrophilous to mesophilous pteridosperms and possibly also rather hygrophilous ferns, which presumably grew on mineral habitats on margins or sandbanks of lakes or at the lower course of rivers, e.g. on alluvial plains (cf. Nehyba et al. 2012). A second assemblage of mesophilous to xerophilous elements, such as conifers, cordaites and other seed plants inhabited distal extrabasinal regions (cf. Barthel & Rößler 2012). Remains of both

communities, primarily those of the proximal hygrophilous-mesophilous community, then would have been transported fluvially to the depositional area.

Due to the fact that plants of both plant communities show a similar degree of fractionation, there could not have been a great distance between both habitats.

6.6 Biostratigraphy

While previous palaeontological data suggest an early Permian age of the floras from the **Rockenbauer Sandstone Member** and the **Kampbrücke Silstone Member** of the Zöbing-Formation, a late Stephanian age was assumed for the lowermost **Leopoldacker Siltstone Member**, which is based on biostratigraphic data, precisely on the mass occurrence of *Alethopteris zeilleri* (Vasícek 1983, 1991). Schindler and Hampe (1996) assumed a Stephanian C to Rotliegend age for this Member, because of the similarity of the strata to limestone and coal bearing profiles from the Saar-Nahe-Basin.

For reliable stratigraphic correlations the analysis of entire floras is important. Thus, the significance of one plant group or even of single pteridosperm species is rather limited.

Nevertheless, some Late Palaeozoic species have been used successfully as biostratigraphic markers for biozonation in the Carboniferous. Either single species or particular assemblages of species may indicate specific stratigraphic units (Taylor et al. 2009).

Though, validity is restricted by the some facts: Firstly several identified taxa are represented by only one specimen; furthermore fossils show differences in the state of preservation and therefore cannot be identified definitely; and moreover, important data of exact finding sites/horizons cannot be reconstructed.

However, some predications or speculations can be made regarding the Leopoldacker flora based on the current state of knowledge.

Both represented pteridosperm groups, the Medullosales and the Callistophytales, are generally known from the Stephanian and Rotliegend/Autunian. Representatives of the Peltaspermales, rarely occurring in the Pennsylvanian and becoming more common in the Permian, are absent though.

Most species are hardly usable for stratigraphic purposes. Taxa like *Callipteridium* gigas, *Pseudomariopteris cordato-ovata, Dicksonites pluckenetii, Sphenopteris mathetii, Neurocallipteris neuropteroides* and *Neuropteris cordata* are generally known from the Stephanian and the Rotliegend. However, their abundance is considerably larger in Stephanian floras (Barthel 2006, Wagner & Álvarez-Vázquez 2010b).

Pub. Krahuletz-Ges. 2023/01

Especially species of *Odontopteris* whose pinnules show a rather loose venation with only few veins, like *Odontopteris brardii* and probably also *Odontopteris nemejcii* are typical Stephanian elements (Kerp 2000).

Alethopteris zeilleri, the most common fossil from the Leopoldacker, is common in the Stephanian and rarely appears in the Stephanian C and Rotliegend (Šimůnek 1989, DiMichele et al. 2006).

The unconfidently identified taxa *Alethopteris barruelensis* and *Callipteridium pteridium* are typical elements of Stephanian floras and only known until the Stephanian B or C (Wagner 1968, Barthel 2006).

Therefore, these taxa rather represent a Stephanian plant assemblage.

However, according to Barthel (1976a/b, 2006, Barthel & Rößler 2012), *Alethopteris schneideri* is restricted to the Rotliegend of the Central European Lower Permian depression and therefore stratigraphically significant. Also, *Neuropteris cordata* and *Neurocallipteris neuropteroides* are known from many Rotliegend basins (Barthel 1976a, Kogan et al. 2008). According to Barthel (1976a), further the lack of the typical Permian callipterids in Rotliegend strata is possible in restricted outcrops or small finding sites.

In general, hygrophilous floras from the Rotliegend often comprise "Durchläuferformen" from the Stephanian as archaic components and therefore show similarities to typical Stephanian assemblages (Kerp 1996b, Kerp et al. 2007).

On the other hand, also late Stephanian strata occasionally comprise "Permian-type" plants, because drier habitats already existed, due to the beginning of seasonality.

This reflects the general problem that plants in Stephanian and Rotliegend strata are facies controlled: They derive from different types of depositional environment dependent on differences in climatic and ecologic conditions (Kerp 1996b, DiMichele et al. 2009). Therefore, the biostratigraphic significance of plants is limited at the Stephanian-Autunian boundary due to this "apparent lateral coexistence of environmentally determined "Stephanian-type" and "Autunian-type" plant assemblages" (Kerp 1996b).

Consequently, it can be certainly said that the fossils from the Leopoldacker derive from the transitional phase between both stages due to the coexistence of Stephanian and Rotliegend characteristics. An unambiguous correlation is difficult.

However, it is more likely that the flora reflects the late Stephanian, due to the high abundance of *Alethopteris zeilleri* and the general dominance of hygrophilous and mesophilous species, which are rather abundant in Stephanian assemblages. Also, the absence of callipterids is more likely in Stephanian strata, as well as the existence of coal seams. The

minor occurrence of dry-type elements, like conifers, cordaites and other seed plants marks the beginning of seasonality in the latest Pennsylvanian, induced by the tectonic and climatic changes.

Hence, these potential first findings of *Alethopteris schneideri* in Stephanian strata question its status as index fossil or indicate that the stratigraphic significance may only apply for different regions in Europe (e.g. Germany). Alternatively, this significance could be newly defined, based on the quantity of the occurrence of *Alethopteris schneideri* in specific strata.

7 Conclusions

The collection of the fossil flora from the Leopoldacker in Zöbing yields a high abundance of pteridosperms.

During this study three pteridosperm species previously identified by Werner Vasícek could be confirmed, i.e. *Alethopteris zeilleri, Neuropteris cordata* and *Callipteridium gigas*. Furthermore, the list of pteridosperms was extended by several new taxa, i.e. *Alethopteris schneideri, Alethopteris* cf. *barruelensis, Alethopteris* sp.1, *Alethopteris* sp.2, *Alethopteris* sp.3, *Callipteridium* cf. *pteridium, Callipteridium* sp., Cf. *Callipteridium, Neurocallipteris neuropteroides, Odontopteris brardii, Odontopteris* cf. *nemejcii, Dicksonites* cf. *pluckenetii, Pseudomariopteris cordato-ovata* and the rather fern-related *Sphenopteris* cf. *mathetii.*

Among these taxa, *Alethopteris zeilleri* is the considerably most abundant fossil, exhibiting a wide range of pinnule variability. Especially, the wide range in pinnule length displays the growth pattern of alethopterids (cf. Zodrow 2007).

Two orders of pteridosperms are represented by the identified taxa, the Medullosales and the Callistophytales, both typical groups of Late Palaeozoic environments.

The available species are hygrophilous to mesophilous and therefore attributed to a rather wet non-swamp habitat, like the marginal area of a lake or of the lower course of a river.

The degree of fragmentation of the fossils indicates mainly fluvial transport and an allochthonous deposition. Rather stagnant conditions can be assumed for the deposition, considering the irregular order of the deposited fossils in the sediments. The depositional environment like described by Schindler & Hampe (1996) as a shallow eutrophic lake or stagnating oxbow lake is quite plausible.

Furthermore, the taphocoenosis reveals a few plant remains of conifers and cordaites, which indicate the coexistence of a drier habitat. Callipterids, pteridosperm taxa, which are more adapted to aridity and commonly occur in Rotliegend communities, are absent. Instead, most of the identified species are generally abundant in Stephanian strata and only in minor extent occur in Lower Permian (Rotliegend) sediments.

The plants of drier habitats indicate the beginning of seasonality.

In this context, the development of facies in intramontane basins around the Carboniferous-Permian boundary complicates a correlation of floras from this interval to a specific time unit. Nevertheless, a late Stephanian age (Stephanian C) is presumed for this flora, based on the dominance of rather typically Stephanian pteridosperms and prevailing hygrophilous and mesophilous plants, also represented by ferns and sphenophytes. The minor existence of dry "Hinterland" elements is already known from Stephanian (even Westphalian) strata, due to the onset of seasonality.

However, according to this correlation, *Alethopteris schneideri*, which is only known from the Rotliegend (e.g. Barthel 1976a,b), would lose its presumed status as an index fossil, or at least this status would be restricted to different regions. Alternatively, the stratigraphic significance of this species may rather be defined by the quantity of its occurrence.

Eventually, for a better evaluation and the comprehension of the entire flora, a detailed taxonomic examination of the other available plant groups is required.

Though, more specific predications regarding the stratigraphic correlation would provide other stratigraphic markers like radiometric dates (DiMichele et al. 2009).

Furthermore a revision of the floras from the **Rockenbauer Sandstone Member** and the **Kampbrücke Siltstone Member** is important and interesting for the floral succession and a more accurate stratigraphic correlation of the strata. More precise sedimentological studies would allow a better definition of the palaeoenvironment.

Plates

Plate I

Alethopteris schneideri

[Scale = 10 mm]

- Figure 1: (153 414); Specimen shows large pinnules with broadly rounded apices and deeply constricted acroscopic and strongly decurrent basiscopic bases.Small insect eggs can be seen on the upper left pinnule.
- Figure 2: (153 415); Specimen with rather large elongate pinnules.
- Figure 3: (153 100); Specimen with small pinnules, revealing rather oblique lateral venation (cf. Šimůnek 1989).
- Figure 4: (153 1174); Specimen displays two pinnule types: Shorter broadly rounded pinnules in the lower part and narrower linear pinnules with less broadly rounded apices in the upper part.

Plate I



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Plate II

Alethopteris zeilleri

[Scale = 10 mm]

- Figure 1: (153 407); Specimen with rather broad pinnules (type A).
- Figure 2: (153 428); Specimen with slender, more distant pinnules (type B)
- Figure 3: (153 403); Specimen with short and broad pinnules (type A).
- Figure 4: (153 1613); Specimen with slender, more irregular shaped pinnules and less confluent bases (type B).

Plate II



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Plate III

Alethopteris

[Scale = 10 mm]

- Figure 1: *Alethopteris zeilleri* (153 226); specimen with long pinnules; pinnule margins slightly undulating; bases only partly confluent.
- Figure 2: *Alethopteris zeilleri* (153 218); apical pinna fragment exhibits bipinnate part with small roundish broadly confluent pinnules and unipinnate part with long and slender pinnules; furthermore a small and short triangular terminal pinnule can be seen.
- Figure 3+4: Cf. *Alethopteris zeilleri* (153 1207, 153 1209); specimens with very long pinnules, which show large similarity to *Alethopteris zeilleri* exhibit rounded apices, a similar venation and undulating margins; pinnule attachment rather pecopteroid, non-confluent and non-decurrent.

Plate III



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Plate IV

Alethopteris

[Scale = 10 mm]

- Figure 1: *Alethopteris* sp.1 (153 85a); specimen with combined characteristics of *Alethopteris zeilleri*, like venation and rounded apices, and *Alethopteris serlii*, like slightly constricted acroscopic base and pinnules, which are broadened in the middle part.
- Figure 2: *Alethopteris* sp.2 (153 322); very broad, but rather short confluent pinnules.
- Figure 3: *Alethopteris* cf. *barruelensis* (153 561); relatively broad rhachis, slightly tapering pinnules with blunt apices; venation thinner than in *Alethopteris zeilleri*.
- Figure 4: *Alethopteris* sp.3 (153 217); rather small, distant, and confluent pinnules; midveins are strong and rather straight.

Plate IV



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Plate V

Callipteridium

[Scale = 10 mm]

- Figure 1: *Callipteridium gigas* (153 111); pinnules attached perpendicular to the rachis; closely spaced; apices apices; venation thin.
- Figure 2: *Callipteridium* cf. *pteridium* (153 1003); pinnules attached perpendicular, triangular shaped and tapering towards blunt apex.
- Figure 3: *Callipteridium* sp. (153 650); small subtriangular pinnules; attached perpendicular; apices rounded.
- Figure 4: Cf. *Callipteridium* (153 429); large pinnules; attached perpendicular; strong midvein.
Plate V



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Plate VI

Neuropteris cordata

[Scale = 10 mm]

- Figure 1: (153 284); Specimen with large and elongate pinnules; cordate base, wide venation.
- Figure 2: (153 947); Specimen with rather slender terminal pinnule; apical pinnules broadly attached and rather short.
- Figure 3: (153 286); Specimen with tongue-shaped pinnules; base slightly constricted.





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Plate VII

Neuropteris, Neurocallipteris

[Scale = 5 mm]

- Figure 1+2: *Neuropteris cordata* (1 = 153 947, 2 = 153 519); pinnules show dot-like structures between venation pattern.
- Figure 3+4: *Neurocallipteris neuropterides* (1 = 153 940, 2 = 153 832); small neuropteroid shaped pinnules with rather odontopteroid venation.

Plate VII



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Plate VIII

Odontopteris

[Scale = 10 mm]

Figure 1:	<i>Odontopteris brardii</i> (153 309); roughly rectangular pinnules with rounded apices; broadly attached with odontopteroid venation.
Figure 2:	<i>Odontopteris brardii</i> (148 II 29); specimen from proximate unidentified bed 148 with more pronounced rectangular pinnules.
Figure 3:	<i>Odontopteris</i> cf. <i>nemejcii</i> (153 780); small pinnules; broadly rounded apices; slightly decurrent.
Figure 4:	Odontopteris cf. nemejcii; enlargement of Figure 3.

Plate VIII



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Plate IX

Dicksonites, Pseudomariopteris, Sphenopteris [Scale = 5 mm]

- Figure 1: Dicksonites cf. pluckenetii (153 382a); specimen with lobed pinnules.
- Figure 2: *Pseudomariopteris cordato-ovata* (153 663); fleshy pinnule with basal lobe and strong sunken midvein.
- Figure 3: Sphenopteris cf. mathetii (153 378); specimen with very small, lobed pinnules.
- Figure 4: *Sphenopteris* cf. *mathetii*; enlargement of figure 3.
- Figure 5: Sphenopteris cf. mathetii (153 388); specimen with little larger, lobed pinnules.

Plate IX



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Plate X

Foliage of unknown affinity

[Scale = 10 mm]

- Figure 1: (153 650); Specimen with long and slender pinnules; venation not preserved.
- Figure 2: (153 304a); Broadly attached pinnule of rather neuropterid shape; very thin midvein runs through $\sim 1/2$ of the pinnule.
- Figure 3: (153 183); Poorly preserved pinnule fragment with cordate base and reticulate venation.
- Figure 4: (153 689); Apical pinna fragment with rather slender terminal pinnule; small and roundish apical pinnules; fan-like rather wide venation.
- Figure 5: (153 663); Apical pinna fragment with rather broad and short terminal pinnule; apical pinnules neuropteroid shaped; bases slightly constricted; venation dense, fine and fan-like.

Plate X



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Appendix

Table 4: List of identified pteridosperm specimens

Inv. No. (153-)	Genus	Species	Notes
33 a	Alethopteris	zeilleri	
47	Alethopteris	cf. <i>zeilleri</i>	
52	Alethopteris	zeilleri	
66	Alethopteris	zeilleri	
83 a	Alethopteris	zeilleri	
84	Alethopteris	zeilleri	
85 a+b	Alethopteris	sp.1	aff. A. zeilleri/serlii
88	Alethopteris	zeilleri	
90 a+b	Alethopteris	zeilleri	
100	Alethopteris	schneideri	
105	Alethopteris	schneideri	
106	Alethopteris	sp.1	aff. A. zeilleri/serlii
111	Callipteridium	gigas	
134	Alethopteris	zeilleri	
134	Alethopteris	zeilleri	
138	Alethopteris	zeilleri	
141	Neuropteris	cf. cordata	
148	Alethopteris	zeilleri	
183	Unknown affinity		reticulate venation
214	Alethopteris	cf. <i>zeilleri</i>	
217 a+b	Alethopteris	sp.3	possibly another specimen without number
218	Alethopteris	zeilleri	
226	Alethopteris	zeilleri	
227	Neuropteris	cordata	
239	Alethopteris	zeilleri	
269	Alethopteris	zeilleri	
269	Alethopteris	zeilleri	
278	Alethopteris	cf. <i>zeilleri</i>	
284	Neuropteris	cordata	cf. Vasícek 1983
286	Neuropteris	cordata	
287 b	Alethopteris	sp.1	aff. A. zeilleri/serlii
304 a	Unknown affinity		neuropteroid
309	Odontopteris	brardii	another specimen in bed 148 (148 II 29)
322	Alethopteris	sp.2	

349	Neuropteris	cordata	
378	Sphenopteris	cf. mathetii	
382 a	Alethopteris	cf. <i>zeilleri</i>	
382 a	Dicksonites	cf. pluckenetii	
384	Sphenopteris	cf. mathetii	
388	Sphenopteris	cf. mathetii	
403	Alethopteris	zeilleri	
407	Alethopteris	zeilleri	
410 a+b	Alethopteris	cf. <i>zeilleri</i>	
412	Alethopteris	zeilleri	
414	Alethopteris	schneideri	
415	Alethopteris	schneideri	
428	Alethopteris	zeilleri	
428	Alethopteris	zeilleri	
429	Cf. Callipteridium		
433	Alethopteris	zeilleri	
440	Alethopteris	zeilleri	
444	Alethopteris	sp.1	aff. A. zeilleri/serlii
448	Alethopteris	zeilleri	
449	Alethopteris	zeilleri	
460	Alethopteris	schneideri	
464	Alethopteris	schneideri	
519	Neuropteris	cordata	
528	Alethopteris	zeilleri	
561	Alethopteris	cf. barruelensis	
567	Alethopteris	zeilleri	
576	Alethopteris	zeilleri	negative of 577
577	Alethopteris	zeilleri	positive of 576
578	Alethopteris	zeillleri	
589	Alethopteris	cf. barruelensis	
611	Alethopteris	zeilleri	
650	Unknown affinity		aff. Alethopteris?
650	Callipteridium	sp.	
663	Alethopteris	zeilleri	
663	Unknown affinity		neuropteroid-odontopteroid
663	Pseudomariopteris	cordato-ovata	
678	Alethopteris	cf. <i>zeilleri</i>	
689	Unknown affinity		neuropteroid-odontopteroid
699	Alethopteris	zeilleri	
775	Alethopteris	sp.1	aff. A. zeilleri/serlii

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780	Odontopteris	cf. <i>nemejcii</i>				
794	Alethopteris	zeilleri				
807	Neuropteris	cordata				
832	Neurocallipteris	neuropteroides				
940	Neurocallipteris	neuropteroides				
947	Neuropteris	cordata				
969	Alethopteris	cf. schneideri				
1003	Callipteridium	cf. pteridium				
1174 .2	Alethopteris	schneideri				
1207	Cf. Alethopteris	zeilleri				
1209	Cf. Alethopteris	zeilleri				
1315	Neuropteris	cordata	negative of 1332			
1332	Neuropteris	cordata	positive of 1315			
1343	Alethopteris	cf. schneideri	venation poorly preserved			
1386	Alethopteris	zeilleri				
1513	Cf. Alethopteris	zeilleri				
1517	Alethopteris	zeilleri				
1529	Cf. Alethopteris	zeilleri				
1553	Alethopteris	zeilleri				
1563	Alethopteris	zeilleri				
1583	Alethopteris	zeilleri				
1613	Alethopteris	zeilleri				
1644	Alethopteris	zeilleri				
1673	Alethopteris	zeilleri				
Specimens documented by Vasícek:						
45	Reticulopteris	germari	Vasícek 1983			
149	Alethopteris	cf. bohemica	Vasícek 1983			
225	Alethopteris	zeilleri	Vasícek 1983			
284	Neuropteris	cordata	Vasícek 1983			
326	Alethopteris	zeilleri	Vasícek 1983			
343	Alethopteris	zeilleri	Vasícek 1983			
384	Alethopteris	zeilleri	Vasícek 1983			
384	Alethopteris	zeilleri	Vasícek 1983			