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Sphenopteridní typy pravých kapradin z karbonských pánví Českého masívu
Sphenopterid type of true ferns from the Carboniferous basins of Czech massive

Disertační práce

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Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze dne 10. září 2017

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Abstract

This thesis deals with the sphenopterid types of ferns from the Czech Carboniferous basins. Thesis is presented as a combination of two published papers in peer-reviewed journals, one manuscript in review and one manuscript ready for submission. The actual text of the thesis is a general introduction with introduction to the study subject of sphenopterid ferns, methodology, studied type collections, terminology and the result of my study. The introduction of the thesis provides a general overview of the ferns and history of their studies. All four papers presented here are focussed on modern redescription, redefinition, emendation and revision of genera *Boweria* Kidston, *Dendraena* Němejc, *Sturia* Němejc. Based on the revision of these genera, following two new genera were established: *Kidstoniopteris* gen.nov. and *Paraszea* gen.nov. A new species *Boweria nowarudensis* has been described during the course of this study. The “whole plant concept” was applied to all studied specimens, which allows to obtain as much information on the ferns morphology, anatomy, and reproductive organs as possible. This was combined with data on *in situ* spores as well as sedimentological and petrological analyses. The sporangial cells as annulus, stomium and apical cells and *in situ* spores were described for all genera and species for the first time. The new observations and researches allow a better integration of genera/species into the plant system. Reproductive organs analysis combined with *in situ* spores and anatomy researches enable more detailed systematic evaluation of the studied genera. This proved useful in palaeoenvironmental and palaeoecological interpretations as well, especially when combined with sedimentological analyses.

Abstrakt

Tato práce se zabývá sphenopteridními kapradinami z českých karbonských pánví. Práce je předkládaná jako kombinace dvou článků, které byly publikovány ve vědeckých recenzovaných časopisech, jeden článek je v recenzním řízení a poslední článek je připravený k odeslání. Text samotné práce je především úvod obsahující uvedení do problematiky sphenopteridních kapradin a jejich morfologie, dále obsahuje pasáže věnované metodice, studovaným typovým sbírkám, terminologii a výsledkům revize studovaných rodů. Úvod práce slouží jako obecný přehled fosilních kapradin a historie jejich výzkumu. Všechny čtyři články, zde prezentované, jsou zaměřeny na moderní popisy, emendování a revize rodů *Boweria* Kidston, *Dendraena* Němejc a *Sturia* Němejc. Na základě revizí těchto rodů byly popsány následující dva rody: *Kidstoniopteris* gen.nov. a *Paraszea* gen. nov. V rámci revize rodu *Boweria* byl také popsán nový druh *Boweria nowarudensis*. Pro všechny studované taxony byl použit „celostní přístup“, který umožňuje získat co nejvíce informací o kapradině, jak o její morfologii, anatomii, tak reprodukčních orgánech a *in situ* sporách. Informace o lokalitě a případné zahrnutí petrologických a sedimentárních analýz doplní tato data. Poprvé byly popsány sporangiální buňky jako je annulus, stomium, vrcholové buňky a *in situ* spory pro všechny studované rody a druhy. Nové poznatky a výzkumy umožňují lépe zařadit rody/druhy do rostlinného systému. Analýza reprodukčních orgánů s *in situ* spory a anatomii umožňuje přesné systematické zařazení studovaných rodů. Tyto výzkumy jsou užitečné v paleoekologických interpretacích a rekonstrukci paleoprostředí, zvláště v kombinaci se sedimentárními analýzami.

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Introduction

This PhD thesis is a taxonomical revision of five genera of true ferns with sphenopterid-type leaves from the Carboniferous Period using a “whole plant concept”. These genera comprise six species. Generally “sphenopteroid ferns” represent a common plant fossil from the Carboniferous–Permian Period (Taylor et al. 2009). Sphenopterids represents a large group of plants which includes true ferns (cryptogamic vascular plants) and pteridosperms (seed plants). Their classification can only be done on the basis of reproductive organs. Unfortunately, most of those are known only as sterile pinnae. Therefore, this thesis is focused on fertile samples that have been consequently compared to those sterile equivalents based on pinnae/pinnule morphology or cuticles (if possible).

True ferns with sphenopterid pinnules systematically belong to poorly studied group of plants. Their characteristic feature is segmented lobate pinnules sutured to the axis of the tapered base (Brongniart 1828). Specimens with sphenopterid type of pinnule are reported from almost all localities around the world from the Mississippian to Mesozoic Era (i.e. Brousmiche 1983, He et al. 2016). This type of ferns includes plants of various habits from lianas to herbaceous types. Nevertheless, the sphenopterid ferns has been until recently poorly understood since they had never been systematically studied using “whole plant concept”. For instance, only a few genera will be mentioned here including *Oligocarpia* (Abbott 1954, Pšenička and Bek 2001), *Discopteris* (Pfefferkorn 1978), *Renaultia*, *Sphenopteris* and others (Brousmiche 1983) or *Tenchovia* (Pšenička and Bek 2004), these mentioned works have been studied with the aim of “whole plant concept”.

One of the main aims of my research was the study of type collections housed in the National Museum, Prague, Czech Republic; Department of Palaeontology, Geological Survey, Vienna, Austria; the Palaeontology Unit, British Geological Survey, Keyworth, United Kingdom; the Museum für Naturkunde, Berlin, Germany; Muséum national d'histoire naturelle, Paris, France; Natural History Museum, London, United Kingdom collected by Stur, Kidston, Němejc, Sternberg, Brongniart and Renault. The main problem with these ferns is that many species with sphenopterid pinnules were established based on sterile specimens/parts. Only some authors attempted to match the fertile and sterile parts of one plant. Due to this fact many different combinations of “sphenopterid” ferns species were described (e.g. species *schatzlaensis*: *Boweria schatzlaensis* (Stur) Kidston, *Renaultia schatzlaensis* (Stur) Kidston, *Sphenopteris schatzlaensis* (Stur) Zeiller). This may have been caused by limited

knowledge of the type material, some studies may have only been based on illustrations in scientific publications. Another equally important issue is that many authors joined sterile and fertile fronds without the study of type collections and also did not sample and macerated specimens.

This research was based on modern research methods for the revision of Carboniferous sphenopterid true ferns, i.e. scanning electronic microscope in low-vacuum and high-vacuum, *camera lucida*, cross section, preparation of sporangia and *in situ* spores. The methodology of the research requires complete study of each specimen, i.e. details of the morphology and anatomy (if it is preserved), reproductive organs and *in situ* spores. The revision is based on the systematic study of frond and pinnule morphologies, rachial anatomy, cuticular analyses, sporangial analyses and *in situ* spores so-called “whole plant concept”. The fertile specimens, grouped sporangia into sorus, synangia or irregularly or ungrouped, cells of sporangia and *in situ* spores are characteristic features in modern botany and also in palaeobotany. Therefore my research focused on fertile specimens and their relation to sterile ones. The research was concentrated on revision of genera *Boweria* Kidston, *Kidstoniopteris* Frojdová et al., *Sturia* Němejc, *Dendraena* Němejc, *Zeillera* Kidston, *Discopteris* Stur, *Paraszea* gen.nov. complemented with palaeobotanical, palynological and sedimentological data. Results have been published in two peer-reviewed paper, one manuscript is in review and one ready for submission (see **Papers I-IV**).

List of papers

This thesis is based on four following papers, referred to in the text by Roman numerals:

I. **Frojdová, J.**, Pšenička, J., Bek, J., Cleal, J.C. 2017. Revision of the Pennsylvanian fern *Boweria* Kidston and the establishment of the new genus *Kidstoniopteris*, *Review of Palaeobotany and Palynology* 236, 33–58.

II. **Frojdová, J.**, Pšenička, J., Bek, J., Martínek, K. 2017. Revision of *Dendraena pinnatilobata* Němejc from the Pennsylvanian of the Czech Republic. *Bulletin of Geosciences* 92(1), 75–94.

III. **Frojdová, J.**, Pšenička, J., Bek, J., in review. Revision of Carboniferous sphenopteroid genus *Sturia* (Stur) emend. and its spores (Duckmantian of the Czech Republic). *Acta Palaeobotanica*.

IV. **Frojdová, J.**, Pšenička, J., Bek, Wang, J. (before submitting). A new genus of gleicheniacean fern *Paraszea* gen.nov. from the Carboniferous-Permian boundary from Inner Mongolia, China. *Review of Palaeobotany and Palynology*

Remarks: The genera *Zeillera* Kidston, *Discopteris* Stur and species *Zeillera delicatula*, *Discopteris karwinensis*, *D. doubravensis* sp.nov. were preliminarily also studied during the course of this PhD research. However, the amount of material and the necessity to compare it with additional material means additional work is required before manuscript preparation. The genus of *Renaultia* Brongniart was not possible to study because the holotype *Renaultia chaerophylloides* was not found in the collections of Muséum national d'histoire naturelle in Paris due to the reconstruction works.

Aim of this thesis

This thesis is focused on revision of several genera of sphenopteroid ferns from the Carboniferous and the related species. Specifically, the main objectives of the thesis are as follows

1. A modern description based on „whole plants concept“ i.e. characteristic features of sterile fronds such as shape of pinnae, pinnules, rachises, rachial analyses complemented with cuticle analyses if preserved and also fertile fronds based on sporangial analyses and *in situ* spores, using appropriate imaging techniques (*camera lucida*, high resolution optical microscopy, scanning electron microscopy in low and high vacuum), maceration, statistical analysis of size of sporangia (**Papers I-III**).
2. Study of holotypes in type collections and comparison with other specimens previously described (**Papers I-IV**).
3. Based on “whole plants concept” is possible to redefine or emended particular genera and species from types collections, using new observations and techniques (mentioned above or in Chapter material and methods). This is the main topic of all referred **Papers I-IV**.
4. A discussion of plant ecology and life-strategy, based on morphology and anatomy, taphonomy and petrological analyses (partly studied in **Paper II**).

Introduction to the Carboniferous sphenopterid ferns

Ferns in geological history

Ferns have been significant and important part of biotopes during geological history. They occur in mountain, desert, water, open files and all types of forest habitats. The first fern or fern-like plants have been known since Devonian (Taylor et al. 2009) and today more than 10,000 species have been recognized in modern environments. They also appear in different growth forms. Nevertheless, this group maintains one significant character for the whole time span of their existence - planar fronds/pinnae with reproductive organs (sporangia) placed on the underside of the pinnules. This made them typical pioneering plants in terrestrial ecosystems. It means that they were successful in habitats where various environmental factors have limited the success of another plant species. Evaluation of fern role in terrestrial ecosystem evolution faces numerous problems such as incomplete fossil record during the geological time. The small segments of the branching system are known in large percentage of species and that it leads to complication of classification of ferns in fossil record. Due to this fact, an idea about fern evolution has been often changed in palaeobotany history.

Ferns can be characterized as megaphyllous plants with spore producing reproductive organs (sporangia) attached to the lower side of pinnules. Ferns can be divided into three groups: Early fern-like plants, eusporangiate and leptosporangiate ferns. Early fern-like plants come from Paleozoic and the characters (anatomy of stem/rachides or reproductive organs) show that can be placed among ferns. Nevertheless, their classification as eusporangiate or leptosporangiate ferns cannot be seriously done. Eusporangiate ferns are characterized by sporangial wall that develops from the periclinal division of group superficial initials. The sporangial wall consists of several cell layers with high number of spores. This type of ferns has large sporangia (sometimes grouped into synangia). Leptosporangiate ferns have sporangial wall developed from slightly oblique division of a single superficial initial cell. The sporangial wall consists of one cell layer with small number of spores. Sporangia are rather small in size. Ferns are characterized by alternating generations: Sporophyte (asexual phase) and Gametophyte (sexual phase). Gametophyte generation is generated by small tissue composed of prothallus, while sporophyte generation is characterized by large spores. The vast majority of ferns are isosporous, only small group of *Salviniaceae* is heterosporous. Species studied in this thesis belong to leptosporangiate ferns and show high variability of genera/species during Carboniferous and Permian periods when they represented an important

part of forest ecosystems. Leptosporangiate ferns are known from all phytoprovinces: Euroamerican and Cathaysian provinces were located in tropical zone areas, while Gondwanan and Angaran (Siberian) provinces were located in temperate areas (Kvaček et al. 2007; Zhang et al. 2007 and others). The high variability of leptosporangiate fern species can be observed in Euroamerican province. Humid and warm climate prevailed here and ferns with other types of plants formed mainly peat-type vegetation that is now found in coal seams and related sedimentary rocks. Later, during Permian Period occurred aridisation of the climate and ferns retreated to seed plants. However, the fern species revived in the Mesozoic Era and many fern genera thrive until today (Cobb et al. 2005).

History of research of sphenopterid ferns

The most important works are selected in this subchapter where the earlier authors tried to insert true fern to ready systematic position and coherence. Only selected works on leptosporangiate ferns from Euramerica and Gondwana flora and concerning their reproductive organs and systematic position are mentioned here. The Carboniferous–Permian flora from Cathaysian province has been not systematically studied, only a few systematic studies of leptosporangiate ferns have been published so far (see below).

First attempts on linkage of ancient and modern ferns were published by Schlotheim (1804) who grouped all fossil ferns under the name *Filicites*. Later, Count Kaspar M. von Sternberg (1820) published work which has become an important milestone of palaeobotany and specialisation palaeobotany was founded in 1820. Another important work was published by Brongniart (1822) who described genus *Sphenopteris*. Among other important papers we can mention Brongniart (1828), Goeppert (1836) and Zeiller (1883, 1888, 1899). Stur (1883, 1885) published one of the most important and extensive works entitled „Die Carbon-flora der Schatzlarer Schichten“. He defined numerous new genera/species (e.g. *Sphyropteris*, *Discopteris*, *Grand'-Eurya* or species as *Hapalopteris schatzlarensis*, *H. amoena*, *H. crépini*, *H. typica*, *H. Schwerini*, *H. bella*, *Senftenbergia stipulosa*, *Oligocarpia Brongniarti*, *O. pulcherrima*, *O. Discopteris karwinensis*, *D. schumanni* and others). Several of these species/genera have been revised in this thesis. Later, Kidston (1884, 1888, 1911, 1923) revised several genera and species with sphenopterid pinnules and defined new genera such as *Zeillera*, *Radstockia* and *Boweria*. Němejc (1928, 1937a,b, 1938, 1963) revised

Carboniferous–Permian flora from Central Bohemian Coal Basins. However, their systematic position was in many cases described inaccurately.

Abbott (1954) published an extensive revision of the Paleozoic fern genus *Oligocarpia*. Abbott (1954) emended its diagnosis and described nine new species in detail. Abbott (1954) emended two species *O. brongniarti* (Stur) and *O. missouriensis* (D. White) and she established two new combinations of species *O. capitata* (D. White) Abbott and *O. mixta* (Schimper) Abbott. She also described spores *in situ* that unfortunately have not been compared with the dispersed ones. Later Danzé (1956) described sphenopterid ferns from the Nord de la France and Pas-de-Calais basins. He also outlined a history of genus *Sphenopteris*. Sixty-seven genera such as *Discopteris*, *Myriotheca*, *Crossotheca*, *Oligocarpia*, *Renaultia*, *Dendraena* have been studied in his PhD thesis. Danzé (1956) newly established genus *Stellatheca* and thirteen species (e.g. *Renaultia acutiloba*, *Discopteris opulenta*, *Sphenopteris dentaefolia*) based on their detailed diagnoses and descriptions. Later, Brousmiche (1983) published the most important paper that deals with reproductive organs of sphenopterid ferns from Sarro-Lorain Coal Basin in detail. Brousmiche (1983) drew from work by Danzé (1956) but they did not deal with differentiation pollen organs versus sporangia. Consequently she did not solve the problem with differentiation of pollen and *in situ* spores (see her interpretation of the genus *Crossotheca*). A few selected works on leptosporangiate ferns were published from Cathaysian province. Regé (1920) established genus *Chansitheca* from Permian of China. Halle (1927) established species with sphenopterid pinnules *Oligocarpia gothanii* from Shanxi Province in China. Later Yao et Taylor (1988) defined the genus *Szea* belonging to leptosporangiate ferns but characterised by cladophlebid type of pinnules. These genera were later emended by Yang et al. (1997), Stevenson and Hilton (2009) and He et al. (2016). Another large work that deals with fossil flora with sphenopterid ferns from all provinces was published by Taylor and Taylor (1993), Taylor et al. (2009). They established (2009) *Sphenopteris*-type ferns with tripinnate frond, lobate pinnules, biseriate annulate sporangia grouped into sorus with five sporangia per group and with receptaculum. Most recent work on the Late Paleozoic filicalean ferns was published by Galtier and Phillips (2014).

Material, methods and terminology

Methods

Type specimens from original collections have been evaluated in this study. In total, 126 specimens of Stur, Němejc, Brongniart, Kidston and Sternberg collections have been studied. All studied specimens are preserved as compression in greyish claystone, siltstone, volcanoclastic rock, with the coal component of variable degrees of coalification. Some specimens (e.g. *Dendraena*, *Boweria nowarudensis*, *Zeilleria delicatula*) are badly damaged by weathering and limonitisation. Both destructive and non-destructive methods have been applied for detailed study.

1) Non-destructive methods:

Camera Lucida: The first non-destructive method included drawing of the fossils using Camera Lucida equipment (attached to a binocular microscope OLYMPUS SZX12). This method is useful for punctual graphical representation of frond, pinnules and rachises with venation shape and also for position of grouped sporangia (**Paper I-IV**).

Scanning electronic microscope Low-vacuum (SEM: Hitachi S-3700N, Tescan VEGA3 XMU) method for observing plant morphology. (**Paper I**). This non-destructive method enabled a precise description of pinnule and rachial morphology, including the attachment pattern of the sporangium.

2) Destructive methods

Some specimens were mechanically selected from specimens, golden-plated and observed under the high vacuum SEM. (**Paper IV**). This method is used only for material newly obtained from excavations; it cannot be applied to type collections. This method is helpful in observation of sporangia cells in high detail, especially in of specimens badly damaged by weathering or maceration.

Some specimens were mechanically selected from specimens and macerated. Maceration proceeded has several important steps which each step bring different informational aspects for reproductive organs, pinnules and cuticles.

First step: Some samples with sporangia were mechanically selected from the fertile specimens. If the specimens contain a carbonate, the samples were placed into 35 per cent hydrochloric acid for 3–12 hours, at first **(Papers I-IV)**.

Subsequently, the samples were placed in 35–40 per cent hydrofluoric acid for 6–24 hours and then washed in distilled water. Some of these sporangia and cuticle were examined under binocular microscope (Olympus BX51) and under the scanning electronic microscope (SEM). The sporangia treated in HF showed position of sporangia on pinnules lobe, whole sorus, cells of sporangia, pedicel.

Second step: Some sporangia and pinnules were additionally macerated in Schulze's solution. Schulze's solution is supersaturated solution of potassium chlorate in nitric acid (concentration of nitric acid is 65 per cent). Maceration in Schulze's solution takes 10–40 minutes, depending on degree of coalification and on the saturation of the solution, following by treatment by 10% potassium hydroxide or technical ethanol in order to remove oxidation products and washed in distilled water. In case of highly coalified specimens second step using only 65 per cent nitric acid for 6-24 hours and washed in distilled water several times because Schulze's solution would have been too reactive. Macerated and selected sporangia with *in situ* spores were sputtercoated with gold for examination under SEM and some sporangia and *in situ* spores were mounted in glycerine jelly or entellan for direct light microscopic examination. This step after Schulze's solution showed clearly cells of annulus, stomium and *in situ* spores which enabled observation on the variability, ontogenic stages and number of *in situ* spores filling a single sporangium **(Papers I-IV)**.

Third step: Selected sporangia and *in situ* spores were mounted in glycerine jelly or entellan slides and they were observed under Nomarski phase-contrast using microscope OLYMPUS BX51 for detailed observations of sporangia cells or exines of spores **(Papers I-IV)**.

Fourth step: Some *in situ* spores were recovered from fertile fronds by dissolving sporangia in the Schulze's solution or nitric acid and subsequently in KOH for several minutes and washed in distiller water. *In situ* spores were mounted in glycerine jelly or entellan for direct light microscopic examination and observed in details and compared with dispersed spores **(Papers I-IV)**.

Following facilities have been used in this study: electronic microscope for low-vacuum and high-vacuum including JEOL 6380LV (Institute of Geology and Palaeontology, Faculty of

Sciences, Charles University, Prague), Tescan VEGA3 XMU (Institute of Geology of the Czech Academy of Sciences, v.v.i., Prague) and Hitachi S-3700N (National Museum, Prague).

Rachial anatomy (**Paper II**) was performed on specimens mechanically selected from the studied material, fixed in a resin, cutting (cross section), fixed on glass slides and subsequently polished on DISCOPLAN-TS. Thin sections with rachides were examined under OLYMPUS BX51 microscope. Rachial anatomy is important for exact taxonomical classification (**Paper II**).

Petrological and mineralogical study (**Paper II**): Polished thin sections were used for transmission light microscopy to examine the host rock. The composition and microstructures were studied using standard petrological optical microscopy in transmitted light with semiquantitative estimates of each component. An electron microprobe was used to understand the mineralogy and microstructures of the host rock. An X-ray powder diffraction investigation of sample was carried out with a Bruker D8 Discover diffractometer (analyst A. Kallistová, Department of Analytical Methods, Institute of Geology of the Czech Academy of Sciences, v.v.i.) equipped with a silicon-strip linear LynxEye detector and a germanium primary monochromator providing $\text{CuK}\alpha 1$ radiation ($\lambda = 1.54056 \text{ \AA}$). Data were collected in the 2Θ range of $3\text{--}70^\circ$ with a step size of 0.017 and a counting time of 1 second at each step. The phase analysis was performed with the analytical computer program Diffract.

Material

Studied specimens come from the following type collections: Stur's, Němejc's, Sternberg's, Kidston's, Brongniart's housed in different institutions in Prague, Vienna, Berlin, Paris, London, Keyworth and China.

Národní muzeum (National Museum), Departement of Palaeontology, Prague, Czech Republic:

Specimens were studied in National Museum in Prague from two collections, collection of Němejc and Sternberg, genera *Dendraena* Němejc, *Sturia* Němejc and *Zeillera delicatula* Sternberg. Němejc's collection comprises the genera *Dendraena* and *Sturia* and species *Dendraena pinnatilobata* and *Sturia amoena*. It was studied twenty-eight fertile specimens of *Dendraena pinnatilobata* from Stradonice locality and thirty-one specimens from Štílec locality which were originally named as *Dendraena pinnatilobata* but after detailed study,

these specimens were transferred to a new species and genus from Štílec locality. Two specimens (sterile and fertile) of *Sturia amoena* were studied, macerated and prepared and consequently compared with sterile holotype (originally named *Hapalopteris amoena*). Stenberg's collection comprises the species *Zeilleria delicatula* (originally named as *Sphenopteris delicatula*). *Zeilleria delicatula* contains only the type specimen.

Geologische Bundesanstalt, (Geological Survey) Vienna, Austria

Specimens were studied in the Geologische Bundesanstalt in Vienna from Stur's collection which comprises the genera originally ranked under the genus *Hapalopteris*. Following species have been studied in details: one specimen of *Boweria nowarudensis* (originally named *Hapalopteris schatzlarensis*), 3 specimens of *Zeilleria delicatula* (originally named *Hapalopteris schatzlarensis*), one specimen of *Sturia amoena* (originally named *Hapalopteris amoena*), 3 specimens of *Discopteris karwinensis*.

Museum für Naturkunde, Berlin, Germany

Specimens were studied in the Museum für Naturkunde in Berlin from Stur's collection. Following species were studied in detail: 2 specimens of *Boweria schatzlarensis* (originally named *Hapalopteris (Sphenopteris) schatzlarensis*), 8 specimens of *Discopteris karwinensis*, one specimen of *Oligocarpia brongniartii*, 5 specimens of *Zeilleria delicatula* (originally named as *Sphenopteris (Zeilleria) delicatula*).

Palaeontology Unit, British Geological Survey, Keyworth, UK

Specimens were studied in the British Geological Survey in Keyworth from Kidston's collection, 3 specimens of *Boweria schatzlarensis* and 6 specimens of *Kidstoniopteris minor* (originally named as *Boweria minor*).

Natural History Museum, London, UK

Specimens were studied in the Natural History Museum in London from Kidston's collection of genus *Zeilleria*: 18 specimens of *Zeilleria delicatula* (originally named as *Zeilleria meifolia*).

Muséum national d'histoire naturelle, Paris, France

Specimens were studied in the Muséum national d'histoire naturelle in Paris from Brongniart's and Renault's collections. 6 specimens of *Zeilleria delicatula* (originally named

as *Sphenopteris (Zeilleria) moravica*) and 3 specimens of *Oligocarpia crépinii* and 4 specimens of *Oligocarpia similis*.

Chinese Academy of Sciences, Nanjing Institute of Geology and Palaeontology, China.

The specimens of *Paraszea* gen.nov. were collected during excavations in the Wuda coalfield, Inner Mongolia, China in 2016. These specimens (Nos. PB22602 – PB22603) are stored in the Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences in China.

Remarks: Genera *Dendraena* and *Sturia* was selected from the Czech Carboniferous localities. For another revision of species it was needed to observe type collections and only afterwards selected significant species. For other revisions it was needed to explore type collection at the first, because the specimens are often from different locations. Therefore type specimens have to be observed at the first and after that can be compared with Czech material. It was important compared also stratigraphic positions all of them (**Papers I-III**).

Terminology

Terminology of pinnae or pinnule, rachial anatomy and cuticle

The shape of pinnule is an important characteristic for fern describing. However, in many features the described species and genera of the sphenopterids ferns show such similarity to one another that the classification of them presents difficulties to the systematic. This opinion was already mentioned by Bower (1900). The sphenopterid ferns have several main types of pinnules: deeply lobate (*Boweria*), narrowly lobate (*Kidstoniopteris*), deeply laminar lobate (*Dendraena*) (see Figure 1). Nevertheless the shape can be amended by some ecological role when the fern had difficult environmental conditions. The fossil fern fragments usually represent plants growing in different biotopes, an effect that is also known today (Lehnert 2007; Lehnert and Weigand 2013). Therefore, the not only shape of fronds/pinnae/pinnules but also rachial anatomy or cuticle, if preserved, must be taken into consideration. Fern fragments anatomy may be preserved in three dimensions in special circumstances such as burial in volcanoclastic rocks/tuffites, coal-balls of permineralised nodules (**Paper II**). Compression specimens can be compared with specimens from coal-balls or from permineralisation. The permineralised specimens have beautifully preserved anatomy of stem, of rachises, and also reproductive organs (e.g. Galtier and Phillips 2014). The connection of permineralized rachises is not often visible, what is the problem.

Terminology of Brousmiche (1983, p. 50) was adopted in this study combined with adjectives as ultimate, penultimate and antepenultimate rachis/pinna (**Paper I**, Fig. 7A and here Figure 3) used e.g. in Pšenička and Bek (2004). The terminology of ultimate pinna and pinnules was adopted from Boersma (1972, Text-fig. 2). This terminology was used in all **Papers I-IV**.

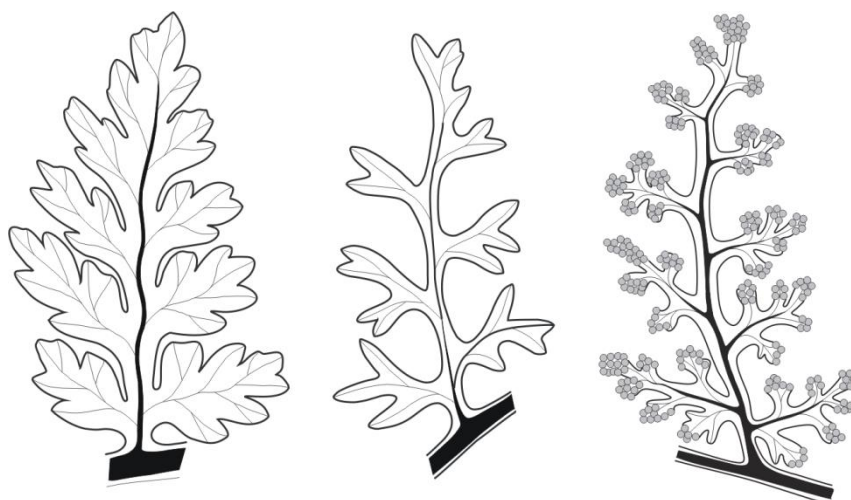


Figure 1. Three main types of pinnules (from the left): very deeply lobate (*Boweria*), narrowly lobate (*Kidstoniopteris*), deeply laminar lobate (*Dendraena*)

Epidermal structure: Cuticle is a layer positioned on the outer epidermal cell wall of a plant. Cuticle is often not preserved on fragments of true ferns. Some pteridosperms have fernlike, sphenopterid type of pinnule, which certainly complicates their systematic classification. Therefore, study of reproductive organs and/or cuticles has been used for distinction between true ferns and pteridosperms. However, it is very difficult to obtain cuticle from true ferns because this cuticle is very thin, against pteridosperms have strong cuticle. Occasionally the epidermal structure was observed under the scanning electronic microscope in low-vacuum (**Paper I**). Terminology for the epidermal structures followed Van Cotthem (1970), Frys-Claessens and Van Cotthem (1973) and Sen and De (1992).

Terminology and characteristic features of reproduction organs and *in situ* spores

Reproductive organs, such as grouped sporangia, individual cells of sporangia (annulus, stomium) and *in situ* spores from fertile fragments are the most characteristic diagnostic features of true ferns. Already Bower (1900) mentioned the frequent disregard and undervalued of a several features which are: the relative time of occurrence of sporangia of the same sorus, the structure of individual sporangium, the orientation of the sporangia relatively to the whole sorus and the potential productiveness as estimated by the number of

spore and extent to which this is realised in the output of mature spores. This unfortunately still holds true but the earlier systematic works in the middle of 19th century could not see great details due the technical limitations. However, some earlier systematic works omitted the structure of sorus or sporangial group (it means irregular group of sporangia, **Paper I-III**), sporangial cells and *in situ* spores. Poorly preserved fragments of fertile certainly complicate observations of detailed structure of sporangia and therefore their systematic evaluation (**Paper I**, *B.nowarudensis*).

In following lines it could be find the differences between the leptosporangiate and eusporangiate ferns, the characteristic features of each group of sporangia, and then the detail of the sporangial cells. It exist two basic type of sporangial structure from fossil-record to recent: eusporangiate and leptosporangiate fern (Taylor et al. 2009, p. 385, fig. 11.3). Eusporangiate ferns have pecopterid type of pinnule, sporangial wall consists of several layers of sporangial cells. On the other hand, leptosporangiate ferns have sphenopterid type of pinnules, sporangial wall consists of one layer of sporangial cells. In some cases, it is possible to distinguish transitional type which is referred to as proleptosporangiate ferns. There is some improvement in evolutionary development of sporangia. Primitive type of ferns, eusporangiate group, possess large sporangia, their wall is composed of several cell layers. This type of sporangia split by apical pore, they typically lack annulus. Evolutionarily more complex sporangia split by dehiscence area or sporangia had hint of annulus or primitive annulus (e.g. *Corynepteris*). The most advanced types, leptosporangiate, have smaller sporangia with one reduced layer of walls (Brousmiche 1983). One of the principal characteristic features of reproduction organs is the grouping of sporangia. Explanation of differences among sorus, synangia, free sporangia and irregularly grouped sporangia are in following lines. At first it is mentioned synangium. Sporangia grouped in synangia (typically with 4 to 5 sporangia per group) are characterised by presence of one initiating cell that produced the whole group of sporangia. Synangia are typical of “pecopterid” ferns (e.g. *Scolecopteris* Zenker). Sporangia grouped in sorus represent another types of reproductive organ arrangement characterised by presence of one initiating cell for every sporangium in group. It is possible to distinguish two types of grouping in sorus. At first the regularly group is mentioned where sporangia create an oval to circle shape of sorus (e.g. *Oligocarpia*, *Chansitheca*, *Discopteris*). One characteristic feature of sorus is presence of central sporangium in regularly grouped sporangia into sorus or without central sporangium in sorus (Figure 2).

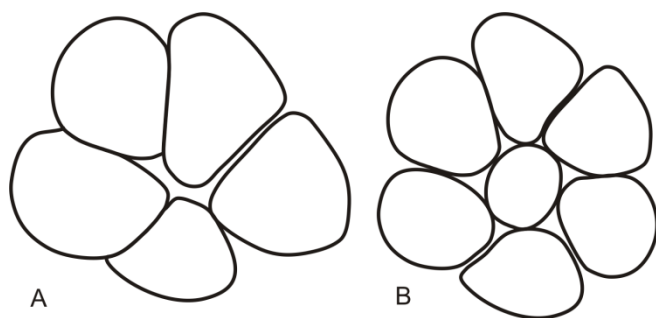


Figure 2. Sketch of sporangia regularly

grouped into sori A) without central sporangium B) with central sporangium

Some authors (He et al. 2016) define it as an important feature but may have seen that the genus *Paraszea* has the central sporangium in sorus and also sorus without the central sporangium (**Paper IV**). This is probably not a primary characteristic feature as the shape of the sorus mentioned below. There is one difference between *Chansitheca* and *Oligocarpia* for the genus which is the oval or circle shape of sorus. It has been observed in the genus *Paraszea*, where a circular sorus is in larger numbers than oval sorus. The opposite to *Paraszea* is genus *Chansitheca* where oval sorus is major and circular sorus is minority (He et al. 2016, p. 203, fig. D). Probably this feature is not characteristic, it is possible that shape is influence by preservation and it cannot be perceived as a distinctive feature between genera. Therefore it suggests newly genus *Chansitheca* replaced under the new species of *Oligocarpia*. Second type of sorus is formed by sporangia irregularly grouped together, forming undefinable shape of sorus and often covering the entire pinnule lamina (*Kidstoniopteris*, *Dendraena*, *Sturia*, **Paper I-III**). Finally free sporangia are sporangia which are not grouped into sorus or synangium (*Boweria*, **Paper I**). This terminology is used in **papers I-IV**.

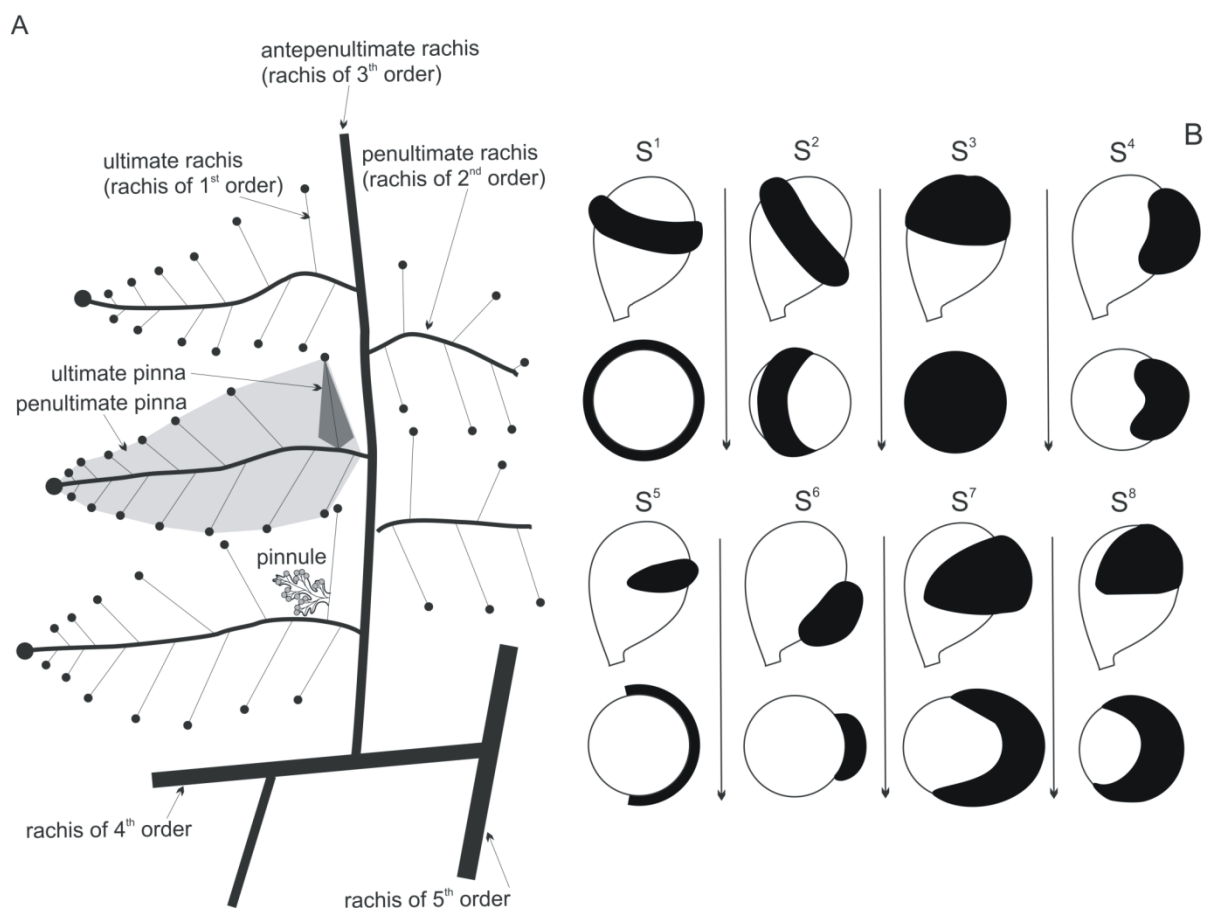


Figure 3. A) Schematical drawing of a description of pinna/rachis structures; B) types of annulus - terminology: S1 equatorial annulus; S2 oblique annulus; S3 apical annulus; S4 bean-lateralequatorial annulus; S5 semi- equatorial annulus; S6 bean-lateral-lower annulus; S7 shield-lateral annulus; S8 semi-apical annulus.

The surface of the sporangia is composed of several cell types that are specific for each genera/species. Four types of sporangial cells can be observed: cells of annulus, stomium, apical cells and ordinary cells. Every type of cells has its specific functions. Annulus is a ring or band of thickened specialised cells characteristic for each genus. These cells form one or more rows of annulate cells which help the stomium to split off or dehiscence after their shrink. The stomium consists of several rows of thick walls cells. The stomium is located on the opposite side of the annulus. Stomium or dehiscence is place where the sporangium burst and spores are dispersed into environment. Apical cell is formed of one or more thick walled cells positioned on the apex of sporangium. Finally it is mentioned ordinary cells which are thin walled cells usually cover the remains of sporangium.

Standard terminology (**Papers I-IV**) is used for the description of sporangial structures (e.g. Bower 1923; Tryon and Tryon 1982). Leptosporangiate/sphenopteroid ferns produce a large variety of annulus types during their evolution. The earlier systematics work have established three terms for the description of annulus (lateral, oblique and apical annulus). For this moment, it exist eight main types of annulus which are described and illustrated in **Paper I** (Fig. 3B and Figure 3). But types of form for annulus are much more diversified than in mentioned list. It can be seen in another manuscript (**Paper II**) which combines terms of type of annulus from the first manuscript with new knowledge. Annulus is characteristic feature for all sphenopteroid ferns.

Each sporangium contains a large amount of *in situ* spores. One of the interesting considerations is the ontogenetic stages of *in situ* spores. The ontogenetic stages of *in situ* spores can be determined in some macerated specimens (**Papers I-III**). In my opinion, the ontogenetic stadia's are the cause of preservation. If the ferns were living when came to fast burial and the ferns had not all spores mature in this time of burial, it is obviously preserved as immature so mature *in situ* spores (**Papers I-III**). Descriptive terms for the spores follow the latest edition of the Glossary of Pollen and Spore Terminology (Punt et al. 2007). Spores are classified according to the system of dispersed spores suggested by Potonié and Kremp (1954, 1955), Dettmann (1963) and Smith and Butterworth (1967). *In situ* spores were directly compared with the original diagnoses, type specimens, descriptions, and illustrations of dispersed spore species. Species determinations are solely based on the original diagnoses, and not on the interpretations of subsequent authors.

Result of individual revised genera

The theme for these manuscripts was chosen base on the most problematic genus/species. The first species named as “*schatzlarensis*”. There were detected taxonomical and nomenclatural problems which were solved at the end. Although this species had been redefined several times, the newly introduced names remained often unpublished. This caused serious problem in identification of the original specimens in the type collections. This group of ferns was not studied for many years. It was not easy to find specimens that are stored in museums around world. Finally, all specimens coming from the type collections were reported in **Papers I-III**.

The first manuscript (**Paper I**) solve the problem with one of the most commonly used combination of name “*schatzlarensis*”. Results of this study indicate that the name *schatzlarensis* belongs to the genus *Boweria* according to ICN. Following **Paper II** and **Paper III** incoherently continue to the first manuscript for precise classification. Already systematic studies of Němejc (1934) compared genus *Boweria*, *Sturia* and *Dendraena* and it was necessarily continue in his work and make a revision of these genera firstly. Species/genera of leptosporangiate ferns from the Cathaysian flora (**Paper IV**) had been only poorly described so far. These had to be revised firstly before subsequent studies on Late Palaeozoic ferns from the Czech Republic. The genus *Paraszea* (**Paper IV**) belongs to the leptosporangiate ferns with similarity of its reproductive organs and *in situ* spores to “oligocarpoid” type of ferns. Although *Paraszea* does not possesses the same type of pinnules, it has been included in this study (refer to a detailed comparison of genera *Oligocarpia*, *Chansitheca* and *Szea* in **Papers IV**). Summary of all genera characteristics are summarized below (**Paper I-IV**).

Table 1. Overview of studied genera/species with reference to the papers by author.

Studied genera/species	
<i>Boweria schatzlarensis</i> (Stur) Kidston	Paper I
<i>Boweria nowarudensis</i> Frojdová et al.	Paper I
<i>Kidstoniopteris minor</i> (Kidston) Frojdová et al.	Paper I
<i>Dendraena pinnatilobata</i> Němejc	Paper II
<i>Sturia amoena</i> (Stur) Němejc)	Paper III in review
<i>Paraszea wangii</i> gen.et sp.nov.	Paper IV before submitted
<i>Zeilleria delicatula</i> (Sternberg) Kidston	preliminary result
<i>Discopteris karwinensis</i> Stur	preliminary result
<i>Renaultia chaerophylloides</i> (Brongniart) Zeiller	holotype not found

1. Genus *Boweria* Kidston, 1911

Revision of this genus was started by revisiting of species originally described as “*Haplopteris schatzlarensis*”. Its systematic revision was published in **Paper I** (Review of Palaeobotany and Palynology). Several taxonomical and nomenclatural issues have been faced during the course of this study. Diagnosis of *Boweria schatzlarensis* (Stur) Kidston was subsequently emended and a new species *Boweria nowarudensis* was established. This emendation of *B. schatzlarensis* was very important for tidiness in taxonomy because this epithet was often used in combination with many different genera (e.g. *Boweria schatzlarensis*, *Renaultia schatzlarensis*, *Sphenopteris schatzlarensis*). It was established lectotype according to the ICN code (McNeill et al., 2012). Using the above mentioned method not only reproductive organs but also cuticle was described for this species, and clearly connection between sterile and fertile specimens was established. The Stur and Kidston specimens of *B. schatzlarensis* agree in 13 features. The most important characters unifying the sterile and fertile parts are: all rachises of the same order are more or less of the same width, straight or slightly sinusoidal, and markedly winged; ultimate pinnae are triangular in shape and gradually taper distally; pinnules are ovoid-elongate with a deeply lobate margin, adjacent lobes separated by a blunt sinus; pinnule midvein is sinusoidal; basal acroscopic pinnules with more veins (**Paper I**, Fig. 15A–D); lateral veins are simple or once dichotomised. The sterile parts are larger than the fertile pinnules (**Paper I**, Tab. 2) because they had a different function on the plant (Lehnert 2007). The epidermal structures of the sterile specimen were observed under the SEM without maceration. Epidermal cells are differentiated into two types of costal cells and one type of intercostal cells. Anomocytic stomata were observed only in intercostal fields (**Paper I**). Fertile pinnules mainly functioned to bear and protect the reproductive organs and so required less photosynthetic surface. Alternatively, Stur and Kidston specimens (Figure 4) represent plants growing in different biotopes, an effect that is also known today (Lehnert 2007; Lehnert and Weigand 2013). It should be mentioned that the sporangia were very nicely preserved. The sporangia are free, shortly stalked, ovoid-shaped with 350–530 µm in diameter (**Paper I**, Plate V). Four types of sporangia cells have been distinguished: cells of the annulus, the stomium, apical cells and ordinary cells. The annulus can be classified as a lateral shield-like annulus, stomium is pentaserial and one rounded apical cells. The *in situ* spores have two types, the first are *Granulatisporites microgranifer* and second relatively immature are *Leiotriletes* type (**Paper I**).

New species *Boweria nowarudensis* (originally named *Hapalopteris schatzlarensis* Stur, 1885) was established based on one poorly preserved fertile specimen from Stur's collection. The annulate sporangia are free, rounded or elliptical, with a 350–500 µm in diameter, with *Granulatisporites minutus* type of *in situ* spores (**Paper I**, Plate VII). A lateral shield-like annulus is known from both *Boweria* and *Sonapteris* (and in some species of *Botryopteris*) but *Boweria* and *Sonapteris* have a different sporangium organisation. The extensive comparison (**Paper I**, Tab. 3) shows that *Boweria* clearly differs from other genera of fossil ferns.

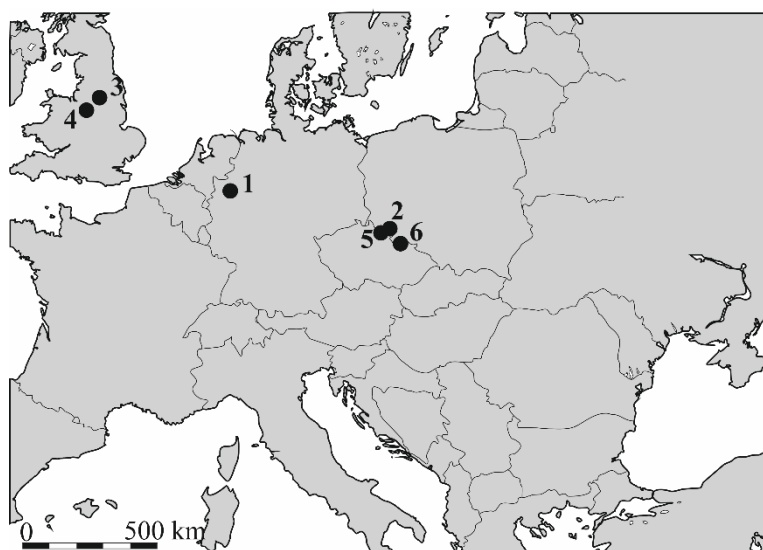


Figure 4. Map of occurrence of studied specimens from **Paper I**; localities: 1. Gelsenkirchen, 2. Boguszów-Gorce, 3. Barnsley, 4. Fenton, 5. Ťaclěj, 6. Nowa Ruda

2. Genus *Kidstoniopteris* Frojdová et al., 2017

A new genus *Kidstoniopteris* gen.nov. is defined also in paper mentioned above (**Paper I**). The type species of new genus *Kidstoniopteris* was originally named *Boweria minor* Kidston. Based on new observations, many characters appear to be significantly different from those of *Boweria* including the rachial system, pinnule morphology, sporangial structures and the type of *in situ* spores. It was necessary to establish a new fossil-genus. It was observed aplebiae, sterile and fertile part of pinnae with complicated rachial system and with sporangia and *in situ* spores. It was observed annulate sporangia which are solitary or clustered into groups of 5–7 sporangia, free, shortly stalked, ovoid shaped with 230–450 µm in diameter. Four types of cells have been distinguished: cells of the annulus, stomium, apical part and ordinary cells.

The annulus can be classified as a semi-equatorial annulus, stomium is quadri- or pentaserial and rounded apical cell. *In situ* spores are classified as *Granulatisporites-Apiculatisporites-Leiotriletes* type (**Paper I**).

Genus *Kidstoniopteris* has a more complicated rachis system, laminar lobate pinnules, and grouped sporangia with a semi-equatorial annulus and smaller sporangia compared to genus *Boweria*. These significant differences substantiated introduction of the new genus. The comparison with other species with incomplete oblique annulus (see in **Paper I**, Tab. 4) shows that *Kidstoniopteris* clearly differs from other genera of fossil ferns.

3. Genus *Dendraena* Němejc, 1934

Paper II published in Bulletin of Geosciences deals with revision of genus *Dendraena*. Studied specimens of *Dendraena* come from Stradonice near Beroun locality from the Radnice Member (Figures 5, 6). *Dendraena* was preserved in the Whetstone Horizon and the detailed study from this locality and the profile was described with continuation to Šiftancová (2005) at first time.

Specimens of *Dendraena* are stored in National Museum in Prague collections. Nevertheless we tried to find the place where was found these specimens of *Dendraena* in the northern valley from where Němejc (1930, 1953) described abundant flora in volcanoclastic type of deposits (**Paper II**, Fig. 2). We studied three newly measured sections at this site in detail (**Paper II**, Fig. 1B). Thirty samples have been collected from Sections 1,2,3 in Stradonice locality (Figure 6). These samples were macerated for study of fossil flora or disperse spores of *Microreticulatisporites* type.

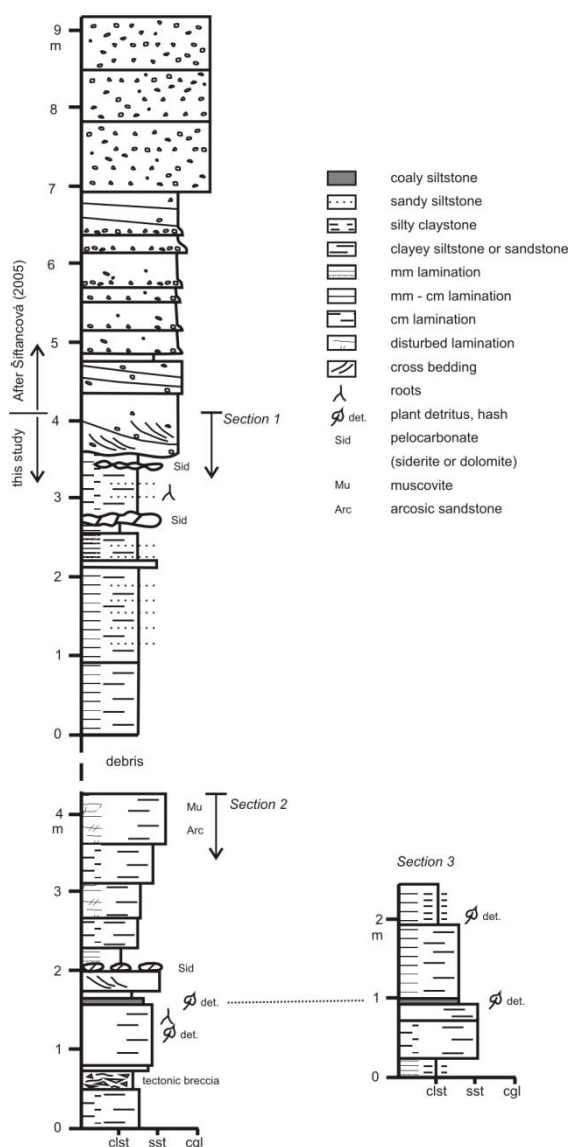


Figure 5. Lithological sections of the Stradonice locality (in the northern valley (*sensu* Šiftancová 2005).

Two important root horizons have been identified (**Paper II**, Fig. 2). First horizon is situated below several centimetres thick bed of carbonaceous siltstone representing short episode of vegetation development. Plant detritus commonly several millimetres in diameter was identified both in root horizon and overlying siltstone. Larger fossil plant fragments were not found, however. Second horizon underlies sandstone beds, roots penetrate laminated clayey siltstone and sandstones (**Paper II**, Fig. 2). However, the stratigraphical position of Němejc's (1934) specimens remains unknown.

Combination of several above mentioned methods was used for classification of plant remains. It was based on study of reproductive organs, *in situ* spores and rachial anatomy observed in thin sections. Studies on anatomy enabled precise systematic classification of this genus. Pinnae of *D. pinnatilobata* with reproductive organs are organically connected on the rachis of the *Anachoropteris* type. *Dendraena pinnatilobata* has also well-preserved

reproductive organs including rare type of *in situ* spores. *Dendraena* has sessile free sporangia, irregularly grouped, 190–494 µm in diameter, ovoid-shaped with band-lateral-upper annulus, which consists of three rows of thick-walled cells. It was obtained *in situ* spores of *Microreticulatisporites harrisonii*. Several fossil-genera of true ferns with lateral annuli are known, but *Microreticulatisporites* is the only taxon known from *in situ* spores. These *in situ* spores are attached to *Radiitheca dobranyana* (Brousmiche et al. 1985) from the Pilsen Basin, Dobře Štěstí locality, Moscovian (Asturian). Nevertheless *Radiitheca* has pectopterid type of pinnules and sporangia grouped into sori with apical annuli. Based on new observations of rachial anatomy, *Dendraena* was possible precisely systematic inclusion into *Anachoropteridaceae* family. Another interesting phenomenon all of the *Dendraena* samples from the Whetstone Horizon is whitish rim surrounding the plant. According to our petrology analyses was suggest that *Dendraena pinnatilobata* grew in close proximity to the riverside or peatland margins and preferred mineral (clastic) substrates (**Paper II**).

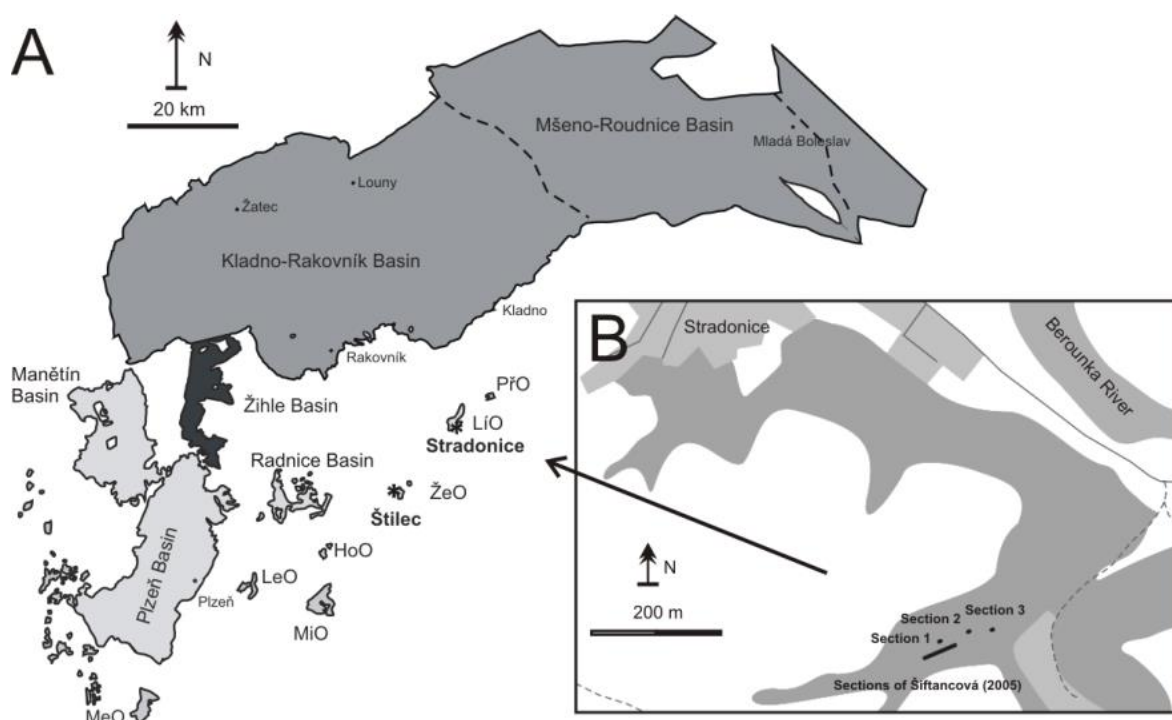


Figure 6. A) Map of occurrence of studied specimens from **Paper II**. B) Location of studied sections.

4. Genus *Sturia* Němejc, 1934

Third manuscript (**Paper III**) deals with revision of the genus *Sturia*. Manuscript (**Paper III**) is currently in review in *Acta Palaeobotanica*. Pennsylvanian true fern *Sturia amoena* is known from the Charbonnière de Belle et Bonne, Belgium and Radnice and Kladno-Rakovník basins, Czech Republic (Figure 7). Based on new observations, using above mentioned destructive and non-destructive methods, this fern has a unique position among leptosporangiate ferns although the preservation of these specimens were not so good as in before mentioned genera. According to detailed observations and studied of pinnules morphology it was possible to confirm Němejc's joining of sterile and fertile specimens. Although the specimens come from different localities, they belong to the same stratigraphic levels (Duckmantian). Based on characteristic features such as shape of pinnae and measurement of rachises and pinnules (**Paper III**, Tab. 1), it can be safely proven that Stur's and Němejc's specimens belong to the same species. The characteristic shape of annulus of sporangia and other cells of sporangia such as stomium and apical cell and *in situ* spores were observed in details and described for the first time. *Sturia amoena* has sporangia irregularly grouped, free, sessile, ovoid-shaped, 300-375 µm in diameter with equatorial annulus, which is formed from two-three rows of thick-walled cells. It was obtained *in situ* spores of *Punctatisporites* and *Apiculatisporites* type. According to our observations and comparison this type of annulus is unique and this species of fern is unchallenged (viz. discussion **Paper III**).

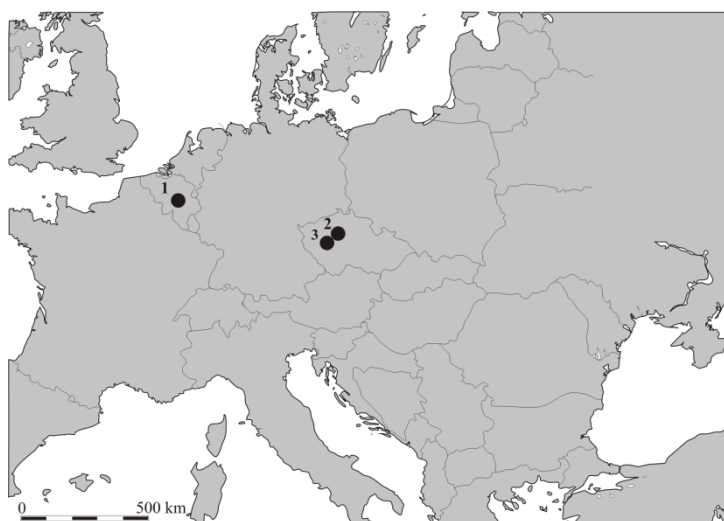


Figure 7. Map of occurrence of studied specimens from **Paper III**; localities: 1. Charbonnière de Belle et Bonne, Avaleresse Mine, Belgium; 2. Motyčín, Kladno-Rakovník Basins, Czech Republic; 3. Břasy locality, Radnice Basin, Czech Republic

5. Genus *Paraszea* gen.nov.

The fourth manuscript (**Paper IV**) describes new fern *Paraszea* gen.nov. This paper is ready for submission to Review of Palaeobotany and Palynology.

Large number of fossil fern fragments including fertile ones were discovered in Wuda, Inner Mongolia, China during excavation season in 2016 (Figure 8). Many fertile fossil fern remains from those specimens are similar to *Oligocarpia*, this interpretation is based on shape of sorus and shape and organization of their sporangia. The “oligocarpoid” type of ferns pertains to leptosporangiate gleicheniaceus ferns as well as to the new genus *Paraszea*. This manuscript presents important data for future revisions of genus *Oligocarpia*. For this reason, the study ferns from Euroameric and Cathaysian province was incorporated to my PhD thesis. A detailed research of this material shows a well preserved sorus and individual sporangia including annulus, stomium and apical cell and also *in situ* spores. It was found numerous similarities to *Szea* (Yao and Taylor 1988; Yang et al. 1997). However after difficult observation and study of differences of sorus and sporangia among *Szea*, *Chansitheca* and *Oligocarpia* it is established that the specimens from Wuda locality is defined to as the new genus *Paraszea* with type species *Paraszea wangii* sp.nov. The genus *Paraszea* has cladophleboid type of pinnules, sporangia grouped into sorus which is circle or oval shaped. The sporangia are oval to pyriform in shape, 270-420 µm in diameter, with mono- or biseriate oblique annulus of thick wall cells and it was observed stomium, apical cell and ordinary cells and *in situ* spores. It was obtained the smallest *in situ* record of *Granulatisporites* type of spores.

The genera *Paraszea* and *Szea* differ in their *in situ* spores type. The species of *Szea cinensis* (Yao and Taylor 1988) and *Szea hananense* (Yang et al. 1997) have the same *Triquitrites* type of *in situ* spores. Genus *Paraszea* has *Granulatisporites* type of *in situ* spores. And therefore from the palynological point of view, it is impossible to put these species together. The differences between *Paraszea* and *Oligocarpia* and *Chansitheca* are based on the type of pinnules. *Oligocarpia* and *Chansitheca* are very similar genera that differ only by the shape of sorus. *Oligocarpia* has circle-shaped sorus and *Chansitheca* has oval-shaped sorus. Their detailed comparison indicates that *Chansitheca* belongs to *Oligocarpia* since they exhibit only minor differences in sorus shape, which is usually circular to oval. Genus *Paraszea* has two types of sorus shape, circular and oval. However, in my opinion this may have originated from different fossilization process, not from its original morphology. Despite the above

mentioned differences, the genus *Paraszea* has cladophleboid type of pinnules, which does not allow to classify this genus as *Oligocarpia* or *Chansitheca*. *Oligocarpia* (Abbott 1954) was originally assigned to the Gleicheniaceae, but later *Oligocarpia* reinterpreted as a compressed specimen of *Sermaya* (Eggert and Delevoryas 1967; Pšenička and Bek 2001).

Genus *Paraszea* belongs to gleicheniaceous ferns together with genera *Oligocarpia* (earlier) and *Chansitheca* (Taylor et al. 2009). For this reason, **Paper IV** was incorporated to my PhD thesis although this fern does not have sphenopteroid type of pinnules (**Paper IV**).



Figure. 8. Maps of occurrence of studied specimens from **Paper IV**. Wuda locality, Inner Mongolia, China

Conclusions and future directions of the study

The main conclusions of this thesis can be summarized as follows:

1. One of the most important aims was clarification of the systematic position of “*schatzlaensis*” (**Paper I**). It was established to *Boweria schatzlaensis* according to ICN. New species *Boweria nowarudensis* was established based on new observations (**Paper I**). The genus *Kidstoniopteris* was differentiated from the genus *Boweria* based on differences of their characteristic features.
2. The genus *Dendraena* was revised and emended with rare type of *in situ* spores *Microreticulatisporites harrisonii*. Based on its rachial anatomy *Dendraena* was reliably classified to the Family *Anachoropteridaceae*. Based on taphonomy and petrological analyses

was suggested that *Dendraena* grew in close proximity to the riverside or peatland margins and preferred mineral (clastic) substrates. The Stradonice locality was profiled at first time (**Paper II**).

3. The genus *Sturia* was revised and emended. Its *in situ* spores, *Punctatisporites* and *Apiculatisporites* type, and equatorial annulus and others sporangial cells were described for the first time (**Paper III**).

4. New genus *Paraszea* was described from Wuda locality. This study presents comparison of *Szea*, *Chansithea*, *Oligocarpia* and *Paraszea* genera. Cladophlebid type of pinnules with annulate sporangia grouped into sorus and type of *in situ Granulatisporites* type of spores was observed (**Paper IV**).

Research on the present topic has numerous future perspectives. Currently, a paper about revision of species *Zeilleria delicatula* is in progress. Another paper which has preliminary result which is in progress is about revision of genus *Discopteris* and revision of species *Discopteris karwinensis* and established new species *Discopteris doubravensis*. This paper is being prepared. I want to continue to review the other broadly used genera in the future. The whole genus *Zeilleria*, *Oligocarpia*, *Renaultia* and *Myriotheca* must be reviewed at first and then continue to revise of other genera and species.

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