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Mgr. Monika Uhlířová

Raný vývoj suchozemských rostlin v období siluru se speciálním zřetelem na pražskou pánev
(Barrandien, Česká republika)

Early evolution of land plants in the Silurian with special respect to the Prague Basin
(Barrandian area, Czech Republic)

Disertační práce

Vedoucí práce: RNDr. Josef Pšenička, Ph.D.

Konzultant: doc. RNDr. Jakub Sakala, Ph.D.

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Abstrakt

Předkládaná disertační práce je zaměřena na výzkum fosilních dokladů suchozemských rostlin v období siluru ze sedimentů pražské pánve, která v kontextu dokumentace vývoje rané flóry představuje lokalitu světového významu. Podstatnou část práce tvoří úvodní pojednání seznamující s daným tématem, na jehož závěru jsou shrnuty dosavadní výsledky studie ze čtyř recenzovaných publikací.

Vznik suchozemských rostlin představoval zásadní událost, která přispěla k utváření globálního ekosystému a umožnila rozvoj terestrických forem života. K přechodu rostlin na souš došlo s jistotou nejpozději v průběhu ordoviku, kdy si řasové předci vytvořily nezbytné adaptace, které jim umožnily úspěšnou kolonizaci pevniny. Jednotlivé etapy procesu terestrializace a vývoje této rané suchozemské flóry jsou rekonstruovány na základě dochovaného mikro- a makrofosilního záznamu. Nálezy makrofosilií z období siluru poskytují již jistou představu o podobě zástupců těchto rostlin, přičemž vůbec nejstarší pochází z paleontologicky významné oblasti pražské pánve. Předmětem této disertační práce je zmapování raných dokladů evoluce suchozemských rostlin prostřednictvím studia rostlinných makrofosilií ze silurských uloženin pražské pánve.

Předmětem tří publikovaných studií (Přílohy 2 až 4) jsou detailní morfologické popisy dvou významných makrofosilií rostlin ze sbírky Západočeského muzea v Plzni. Jednu z nich představuje typový materiál taxonu *Tichavekia grandis*, který se vyznačuje unikátní kombinací znaků směřující k bazálním plavuním, a především svou mimořádnou velikostí. U rostliny byla rovněž afinita k suchozemským rostlinám potvrzena jednou z provedených studií na základě izolace triletních spor *in situ*. Vzorek druhé rostlinné makrofosilie byl rovněž podroben detailnímu popisu, přičemž výsledkem srovnání s jinými taxony bylo stanovení nového rodu a druhu *Capesporangites petrkraftii*.

Čtvrtá ze zmíněných studií (Příloha 1) využila geochemická data, fosilní záznamy a analýzu spor s cílem lépe porozumět vývoji suchozemských rostlin a jejich reakcím na klimatické změny. Zjistilo se, že globální změny teploty a koncentrace kyslíku v atmosféře významně ovlivnily diverzitu a evoluční strategie rostlin. Kryptospory se ukázaly jako odolné vůči klimatickým výkyvům, zatímco diverzita triletních spor se v období glaciálů snižovala. S oteplením pak následoval prudký rozvoj rostlinných druhů, konkrétně producentů triletních spor.

Abstract

This dissertation focuses on the study of fossil evidence of terrestrial plants from the Silurian period, found in the sediments of the Prague Basin – a site of global significance for documenting the evolution of early flora. The work begins with an introductory section that provides an overview of the topic and summarizes the findings of four peer-reviewed publications.

The origin of land plants was a major event that shaped the global ecosystem and enabled the development of life on land. The transition of plants to terrestrial environment occurred no later than the Ordovician period, when their algal ancestors developed essential adaptations that allowed them to successfully colonize land. The various stages of this terrestrialization process and the evolution of early land flora can be reconstructed based on the preserved record of micro- and macrofossils. Silurian macrofossils offer valuable insight into the appearance of these plants, with the oldest known specimens being found in Prague Basin, considered as palaeontologically significant locality. The objective of this dissertation is to map the early evidence of land plant evolution in relation to the study of plant macrofossils from the Silurian deposits of the Prague Basin.

Three of the published studies (Appendices 2–4) focus on the detailed morphological descriptions of two significant plant macrofossils housed in the collections of the West Bohemian Museum in Pilsen. One of these consists of the type material of *Tichavekia grandis*, which is notable for its unique combination of traits indicative of basal lycophytes and, above all, its remarkable size. One of the studies confirmed its affinity with land plants via the isolation of *in situ* trilete spores. The second plant macrofossil was also subjected to a detailed description and comparisons with other taxa that led to the establishment of a new genus and species, *Capesporangites petrkraftii*.

The fourth study (Appendix 1) integrates geochemical data, fossil record, and plant spore analysis to gain a deeper understanding of the evolution of terrestrial plants and their responses to climate changes. The results indicate that global fluctuations in temperature and atmospheric oxygen concentration had a significant impact on plant diversity and evolutionary strategies. Cryptospores demonstrated resilience to climatic fluctuations, whereas the diversity of trilete spores declined during glacial periods. As temperatures rose, there was a rapid expansion of plant species, particularly those producing trilete spores, suggesting that warming played a key role in their evolutionary success.

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1 Introduction

1.1 Importance of the topic

Research on the oldest terrestrial plants provides answers to questions concerning the initial colonization of land, a process that was crucial to the evolution of terrestrial life forms and establishment of ecosystems as we currently find them. The fossil record provides a valuable insight into the process of terrestrialization and the evolution of terrestrial flora, enabling palaeobotanists to estimate the stages of the transition of plants to land and the subsequent development of early land plants. The microfossil record has been instrumental in establishing the existence of terrestrial flora probably as early as the Middle Ordovician (Vavrdová 1984; Strother et al., 1996; Rubinstein and Vajda, 2019). Later macrofossils from the Silurian (summarised in Wellman et al., 2014) reveal significant information regarding the morphology of this ancient vegetation. Notably, significant adaptations to terrestrial environments by these early plants are evident from Silurian macrofossil records, suggesting a well-developed capability for survival. Subsequent diversification of flora led to the emergence of diverse plant lineages (Capel et al., 2022). Consequently, studying the earliest land plants is fundamental to understanding their physiology, as well as the palaeoecological drivers that led to their diversification during the Early Paleozoic times, and resolving the evolutionary relationships among plant groups.

In this respect, the Prague Basin represents a globally significant site providing a fossil record of early land plants (Kraft et al., 2019). The area has also yielded some of the earliest dispersal spores, indicating the presence of land plants from the Ordovician period (Vavrdová 1984) along with the earliest plant macrofossils dating back to Wenlock (Libertín et al., 2018a). Recent studies have led to the discovery of numerous valuable Silurian plant macrofossils in this region. This underscores the significance for further research into the potential of localities within the Prague Basin in order to reveal more about the diversity of early plant communities and the terrestrial conditions prevailing during that period.

1.2 Brief overview of previous research

Research into early land plants began in the late 19th century with pioneering studies by Sir John William Dawson (1870, 1871). However, intensive study of these plants began in the early 20th century with the discovery of the Lower Devonian ecosystem of the Rhynie chert in Scotland (Garwood et al., 2020). This site, known as a Konservat-Lagerstätte, is characterised by an exceptional type of fossils preservation. The silicified three-dimensionally preserved fossil flora, as documented by Robert Kidston and William Henry Lang (1917, 1920a, b, 1921a, b), initially prompted astonishment among palaeobotanists given the remarkable preservation of anatomical structures, enabling observation at cellular detail. Notwithstanding the simplicity of body plan exhibited by this flora, the discovery was perceived as a significant milestone, as it facilitated the establishment of a comprehensive understanding of the early terrestrial flora and its significance for the evolution of terrestrial life. The well-known genera *Aglaophyton* Edwards, *Asteroxylon* Kidston et Lang, *Horneophyton* Barghoorn et Darrah and *Rhynia* Kidston et Lang were described from this locality. Another significant contribution to this field was made by Lang with his iconic publication entitled "*On the plant remains from the Downtonian of England and Wales*" (Lang, 1937), in which he provided a comprehensive description of valuable fossils of early land plants, algae and the so called "nematophytes". This work also led to the establishment of a new genus of early land plants, *Cooksonia* Lang, named after the botanist Isabel Clifton Cookson, who discovered the plant remains.

Harlan P. Banks is another notable palaeobotanist who made significant contributions to the expansion of knowledge about the early evolution of land plants. He devoted himself to the description of fossils of these plants (Banks, 1973; Banks et al., 1975; Edwards et al., 2004) and the process of terrestrialization (Banks, 1975a, b). Significantly, he introduced a fundamental classification system for these early land plants, which remained widely utilised for long (Banks, 1975c). Initially, only a limited number of localities had been documented as sources of early land flora. One such locality was the Barrandian area, from which early land plants were first described by Jiří Obrhel (1962).

The microfossil aspect has proven to be very beneficial in revealing the individual steps in the transition of plants to land. Initial research in this area was carried out by palynologists Jane Gray and John B. Richardson, who were able to advance the boundaries of current knowledge of early terrestrial flora by connecting both micro- and macrofossil record thanks to studies of *in situ* spores and also dispersed spores record in the context of tracing the process of plant

terrestrialization (Richardson and Lister, 1969; Richardson, 1985, 1992; Gray, 1993). In addition, Jane Gray encouraged the use of analogies with bryophytes to infer the possible physiology and paleoecology of early land plants (Gray and Boucot, 1977; Gray, 1985).

Nonetheless, the appearance of these plants can be reconstructed on the basis of observable morphological characteristics from plant macrofossils. Significant contributions to this field are attributed by Dianne Edwards, whose detailed morphological descriptions of Silurian-Devonian plant fossils have provided invaluable insights (e.g., Edwards 1968; Edwards and Feehan 1980; Edwards et al. 1983; Edwards and Richardson 2004). Her research also led to the establishment of new genera, *Steganotheca* Edwards and *Tortillicaulis* Edwards. D. Edwards and her colleagues Una Fanning and J. B. Richardson achieved a revolutionary discovery when they demonstrated the presence of stomata in anatomically preserved fossils of the genus *Cooksonia* (Edwards et al., 1986). This was followed by the confirmation of its vascularity by Edwards et al. (1992) when working alongside Kevin L. Davies and Lindsey Axe. Notable contributions have also been made in collaboration with Patricia G. Gensel (Gensel and Edwards, 2001) and Catherine W. Rogerson (Edwards and Rogerson, 1979; Rogerson et al., 1993; Rogerson et al., 2002). In addition, Patricia Gensel devoted a substantial number of works to the Paleozoic flora (Gensel, 1976, 1979; Kotyk et al., 2002; Gensel, 2008). Paul Genez and Philippe Gerienne further contributed to the field by proposing a modified definition and lectotypification of the genus *Cooksonia* (Genez and Gerienne, 2010a), and establishing a new genus, *Aberlemnia* Genez et Gerienne (Genez and Gerienne, 2010b).

Further studies of the Rhynie chert plant fossils (e.g., Remy, 1982; Edwards, 1986; Remy et al., 1993; Kerp et al., 2003; Kerp, 2018) were of equal importance, with reported interactions with fungal symbionts, which were mainly studied by Hans Kerp, Michael Krings, Winfried Remy, Thomas N. Taylor and Edith L. Taylor. (Taylor et al., 1992; Remy et al., 1994; Krings et al., 2007, 2014; Krings and Taylor, 2015).

Significant progress has been achieved in spore research, primarily due to intensive work by palynologists Philippe Steemans, Paul Strother and Charles Wellman. Their research on dispersed spores has yielded valuable insights into the transition of plants to land (Strother, 1991; Steemans, 2000; Wellman, 2004; Steemans and Wellman, 2018; Strother and Taylor, 2024) as well as further flora development (Steemans et al., 2009; Wellman et al., 2014; Strother and Taylor, 2018; Wellman et al., 2023).

Current research in molecular biology has repeatedly demonstrated its efficacy in estimating the origin of land plants and the divergence time of plant lineages (see Clarke et al., 2011; Cooper et al., 2012; Zhong et al., 2014; Bowels et al., 2023). Pioneering studies in molecular phylogenetics by Kenrick and Crane (1991, 1997) have provided insight into the relationships among different plant lineages. Since then, there has been rapid development in this field, particularly in relation to the origin of early land plants using molecular clocks. However, the estimates obtained from these studies vary considerably, ranging from the Precambrian to Cambrian interval (Clarke et al., 2011; Cooper et al., 2012; Zhong et al., 2014) or more probably in the Cambrian to Ordovician (Morris et al., 2018) as well as during the Ordovician (Sanderson, 2003; Smith et al., 2010). Phylogenetic studies by Morris et al. (2018) and Tomescu (2022) also address the relationships between plant lineages, especially between vascular plants and bryophytes, and refine estimates for the origin of land plants.

The establishing of a new plant group, eophytes, by Dianne Edwards and her colleagues (Edwards et al., 2022a, b, c), also previously called cryptophytes (Edwards et al., 2014) or cryptosporophytes (Wellman et Ball, 2021), has provided significant new information about the early evolution of land plants. As the eophytes combines features of both polysporangiophytes and bryophytes (Edwards et al., 2022b), it once again raises the question concerning the relationship between vascular plants and bryophytes, which are generally considered to be two distinct lineages. This subject has garnered significant attention among the plant evolution research community (Tomescu, 2022).

1.3 Aim of the thesis

This PhD thesis is focused on the analysis of the fossil record of early terrestrial plants from the Silurian age, with a particular emphasis on those from the Barrandian area. The fossilized plant material is described using morphological characteristics and, based on these features, are systematically classified and discussed within the context of their potential physiology and the palaeoecological conditions under which they may have prospered. In consideration of macrofossil preservation of early land plants being rare, the present study focuses on the acquisition of comprehensive data set from each specimen. The primary contribution of this study is the documentation of significant plant macrofossils from the Silurian sediments of the Prague Basin. The detailed morphological descriptions provided may be useful for future

research by palaeobotanists, contributing to current knowledge of their morphology, evolutionary development and palaeoecology.

2 Materials and methods

Throughout my Ph.D. study I have been researching the whole spectrum of Lower Paleozoic fossils of plant affinity. Most of my work has focused on the fossil remains of the early terrestrial plants, including the study of macrofossils (Uhlířová et al., 2022; Uhlířová et al., 2024a, in prep. b) and the use of maceration methods to isolate plant mesofossils and spores (Bek et al., 2024). In addition to land plants, I have also studied macroalgal remains and fossils of prasinophyte algae of the genus *Tasmanites* Newton (Uhlířová et al. in prep. a) and have described enigmatic fossils of the *Pachythea* Hooker and *Prototaxites* Dawson genera (Pšenička et al., 2021; Uhlířová et al. in prep. c).

The studied specimens are from the collections of public institutions (West Bohemian Museum in Pilsen, the National Museum, the Institute of Geology and Palaeontology - Faculty of Science of the Charles University), as well as from my own collections. The fieldwork involved sampling and collecting new palaeontological material and the documentation of selected geological sections.

The fossils were described on the basis of morphological characteristics and, for the genera *Pachythea* and *Prototaxites*, the internal ultrastructure was also examined. A comprehensive observational approach was undertaken for the study of macrofossils. This methodical process involved the utilisation of the stereomicroscope (Olympus SZX12) and the Keyence microscope (VHX-7000) with immersion of the fossils in alcohol to enhance visual contrast, in addition to their examination in a dry state. The use of a scanning electron microscope (JEOL JSM-6380LV) in a low vacuum mode further facilitated the study. Fossils were evaluated and described precisely based on their morphological characteristics. The use of a camera lucida device enabled the creation of line drawings of the plant macrofossil specimens. Based on the observations, presumed reconstructions of the studied plants were also created. In order to obtain possible microfossil contents from macrofossils, the maceration technique was implemented (maceration process in Uhlířová et al., 2022).

3 Terrestrialization and early evolution of plants

The transition of plants to terrestrial environments has resulted in significant changes in ecosystem evolution and climatic conditions, which have facilitated the dynamic development of life on land (Beerling, 2007; Wellman et al., 2023). In response to changing environmental conditions, diverse habitats arose, leading to the diversification of early flora and fauna, the development of interactions among living beings, and the influence of natural processes. This transformation is attributed to ancestors of terrestrial plants seeking to occupy available ecological niches.

3.1 The process of plants transition and adaptation to land

Terrestrial plants (embryophytes) represent a diverse group of eukaryotic organisms that have adapted to life on land, forming a key component of terrestrial ecosystems. They are characterised by a multicellular sporophyte, a cuticle to reduce water loss, sporopollenin in the spore wall (Donoghue et al., 2021) and development of functional conducting tissue (Woudenberg et al., 2022). Embryophytes are divided into two evolutionary lineages: the clade Polysporangiophyta and the group of bryophytes (Bryophyta s.l.). Polysporangiophyta includes all vascular plants (Tracheophyta) and several basal members without true vascular tissue (Kenrick and Crane, 1997). A distinctive trait of this group is a branched sporophyte able to produce multiple sporangia, facilitating more efficient reproduction (Kenrick and Crane, 1997). By contrast, bryophytes (which include liverworts, mosses, and hornworts) possess a dominant gametophyte phase in their life cycle, with their sporophyte unbranched and dependent on the gametophyte (Ligrone et al., 2012). This disparity in the organization amongst the sporophyte and gametophyte represents a substantial evolutionary innovation that distinguishes vascular plants from bryophytes thus enabling vascular plants to undergo greater diversification. From an evolutionary perspective, embryophytes are classified as part of the broader group Streptophyta, which also encompasses the charophyte algae, which are divided into six distinct classes (Bowles et al., 2023).

The most recent genome-sequencing analyses (Wodniok et al., 2011; Zhong et al., 2014, 2015) have identified the Zygnematophyceae as the closest sister group of terrestrial plants in the streptophyte algal lineage. Zygnematophyceae present a series of significant characteristics associated with land plants (Feng et al., 2024). Genome studies of Zygnematophyceae have

identified genes associated with stress tolerance, including desiccation resistance (Cheng et al., 2019; Rieseberg et al., 2023). Some species have developed various stress tolerance mechanisms similar to those found in terrestrial plants, including mucilage osmolytes production to cope with desiccation and also UV protection substances against intense radiation (Holzinger and Pichrtová, 2016). Additionally, Zygnematophyceae cell walls contain pectin homogalacturonan, which aids in water retention and is essential for terrestrial adaptation (Herburger et al., 2019). These features shared between Zygnematophyceae and land plants are believed to have been contributing in the successful colonization of terrestrial habitats by land plants (Žárský et al., 2022).

The transition of plants to terrestrial environments required a series of evolutionary steps. Initially, the transition involved a shift from the marine environment to fresh waters (de Vries and Archibald, 2018), as evidenced by zygnematophyte algae, which are predominantly freshwater species (Hall and McCourt, 2017). Subsequently, further adaptations were necessary to ensure the survival and success of plants on land (de Vries et al., 2018). These plants had to deal with stress factors such as ultraviolet radiation, insufficient water, nutrient intake changes and modified reproductive strategies (Taylor et al. 2009). While water partially serves as a protective filter against UV radiation for algae in aquatic environments), terrestrial plants were required to form a cuticle to protect their aerial parts (Taylor et al., 2009; Puginier et al., 2022). Similarly, it was also necessary for plants to adapt their nutrient intake (Puginier et al., 2022). All these plants had no roots, but they are thought to have been attached to the substrate by rhizoid-like structures. However, some basal holdfast-like structures (see Gerrienne et al., 2006) or root-like structures (see Edwards et al., 2004) have been reported. An exception is found in the plant fossils from Rhynie chert, where unicellular rhizoids are captured in minute detail in *Nothia aphylla* Lyon (see Edwards, 2003; Kerp, 2018).

Plant pioneers in the early stages of the transition to land faced the disadvantage of having inadequate or insufficiently developed mechanical tissues resulted in limited opportunity for growth (Boyce, 2008) and their upright growth mostly ensured by internal pressure (turgor) (Speck and Vogellehner, 1988). It is noteworthy that some plants (e.g., *Asteroxylon*) from Rhynie chert, which were noticeably more complex compared to Silurian plants, possessed a well-developed internal stele with mechanical tissues (Trewin and Kerp, 2017). However, some of them (e.g., *Aglaophyton*) were also dependent on turgor for their upright growth allowing them to reach a height of slightly over ten centimetres (Bateman et al., 1998), then bend their axes towards the ground, where they were attached by rhizoids (Kerp, 2018).

The subsequent development of mechanical tissues, leading to the evolution of tracheids, enabled plants attain larger forms (Decombeix et al., 2019; Woudenberg et al., 2022). Furthermore, plant organs had to be equipped with stomata (Clark et al., 2022), facilitating the process of photosynthesis to ensure the exchange of gases (Edwards et al., 1986). Additionally, plants had to adapt their reproduction mechanisms to the new environment, relying primarily on wind and water for spore spreading (Wellman et al., 2023). These spores were produced inside the sporangium of the sporophyte, from which they were released at maturity (Shute and Edwards, 1989). As early colonizers, the r-strategy was an effective approach for the initial land plants, involving the rapid propagation and development of the population. Representatives of these plants produced a substantial quantity of small spores, facilitating their transportation over long distances and rapid growth of the plant population (Gray, 1985). This strategy is further substantiated by the fossil record, which documents the cosmopolitan dispersal of these spores during the Ordovician and Silurian periods (Wellman et al., 2023). The aforementioned properties are indicative of pioneering organisms, for which the primary objective constitutes the expeditious colonization of unoccupied habitats.

These plants were also minute in size, and exhibited structural features which, from the perspective of successful adaptation, were simple yet functionally effective. Fossil evidence indicates that their diploid generations (sporophytes) typically exhibited dichotomously branched leafless axes, which were terminated by reproductive organs (sporangia) (Gerrienne and Genez, 2011). However, Boyce (2010) suggested that the fossilization potential of the two phases differed, with the gametophyte being less likely to be preserved. In contrast, according to Kenrick (2018), both life stages had roughly the same chance of being fossilized. The life cycle of these oldest plants remains a subject of discussion, with two theories proposing characteristics of the alternating generations (Blackwell, 2003). The first of these is the homologous theory, which suggests that the haploid phase (gametophyte) and the diploid phase (sporophyte) were initially indistinguishable and underwent gradual differentiation over time (Strother and Taylor, 2018). In contrast, the antithetic theory (Bower's theory) assumes an initial pronounced dominance of the gametophyte over the sporophyte, followed by a delay in the mitotic division of the zygote, that results in the sporophyte increasing in size and complexity (Strother and Taylor, 2018, McCourt et al., 2023). This theory is currently widely supported (Blackwell, 2003), but still many questions remain (Žárský, 2021). The primary argument is predicated on the apparent evolution of the sporophyte towards larger and more complex forms

in more derived groups of terrestrial plants, with an evident trend towards its increasing dominance as seen in the most modern plant groups (Gerrienne and Gonez, 2011).

The Lagerstätte Rhynie chert in Scotland presents a unique Lower Devonian ecosystem (Trewin and Kerp, 2017), comprising silicified plant fossils, which offers insight into the appearance of the life cycle of the earliest plants (Remy, 1982; Remy et al., 1993; Kerp, 2018). These fossils exhibit both sporophytic and, for certain taxa, also gametophytic generations, showing comparable morphology and size. The gametophytes consist of axes that are either recumbent or erect terminating in gametangia (sexual organs) and similarly sporophytes are terminated by sporangia (reproductive organs) (Gerrienne and Gonez, 2011).

Inside silicified axes of Rhynie chert plants, fungal hyphae in the form of arbuscular mycorrhiza were also detected (Remy et al., 1994; Taylor et al., 1995). As in the present day, the plant probably provided organic compounds to its fungal partner and received minerals and water as a return (Puginier et al., 2022). The symbiosis with fungi is hypothesised to have been an essential factor in the process of plant terrestrialisation (Puginier et al., 2022). The earliest fossil evidence of fungi has been identified in the Proterozoic (Loron et al., 2019; Bonneville et al., 2020). These organisms were, however, initially restricted to the marine environment, and it is possible that their transition to land was initially allowed through the symbiosis with photobionts (Lutzoni et al., 2018).

As well as streptophytes, green algae from the Chlorophyta lineage had the capacity to become established on land independently (Puginier et al., 2022). This is clearly evident when considering that almost every Chlorophyta group comprises recent representatives of algae adapted to life on land, including the Ulvophyceae and Trebouxiophyceae classes (Puginier et al., 2022; McCourt et al., 2023). It may also be concluded that microorganisms colonised land considerably earlier than plants (Tomescu et al., 2006). These microbial biofilms have likely been present on substrate surfaces since the Proterozoic (Edwards and Selden, 1992; Wellman and Strother, 2015) and thus have contributed to the formation of palaeosols for future plant colonisers (Wellman et al., 2023).

3.2 Fossil record as a source of data of transition to land

The fossil record, encompassing microfossils and macrofossils, provides substantial evidence for the evolution of terrestrial flora. Plant microfossils are represented mostly by dispersed spores (Wellman and Gray, 2000). Notably, these spores appear significantly earlier in the Middle Ordovician (see Vavrdová 1984; Strother et al. 1996) than macrofossils dating to Wenlock (see Libertín et al., 2018a). It should be noted that recently Xu et al. (2022) has discovered promising mesofossils from the Upper Ordovician represented by three-dimensionally preserved fragments including internal anatomy with tracheids. It would therefore probably represent the very oldest fossil evidence of vascular plants. This delay could be attributed to the absence of recalcitrant plant tissues and the paucity of Ordovician terrestrial deposits as well (Wellman et al., 2023). In contrast, spores of terrestrial plants contain a biopolymer called sporopollenin in their cell walls, which has a high potential for fossilisation (Wellman, 2003).

The oldest spore-like microfossils occurring in the fossil record since the Cambrian are known as cryptospores (Richardson et al. 1984). The term cryptospores has been defined in two different ways. According to Strother and Beck (2000), cryptospores encompass all spore-like palynomorphs of non-marine origin, including non-embryophytes, which likely originated from algal ancestors and contain sporopollenin in their spore walls. In contrast, Steemans (2000) defines cryptospores more specifically as propagules of the earliest embryophytes. Cryptospores differ from later land plant spores primarily in their smaller size. In addition, some of them may be enclosed inside an outer envelope with surface ornamentation becoming less distinct in younger geological periods (Steemans et al., 2012). Fossil evidence suggests that cryptospores of land plant affinity first appeared in the Middle Ordovician (summarized in Wellman et al., 2023). However, true trilete spores, which are characteristic for tracheophytes, do not emerge until the Upper Ordovician (Steemans et al., 1996). Nevertheless, it should be noted that some species of liverworts produce spores that bear trilete mark as well (Gray, 1985).

The origin of the cryptospores remains unknown, so their producers are named as “cryptophytes” sensu Edwards et al. (2014) or newly named “eophytes” sensu Edwards et al. (2022b). These are considered to be early representatives of terrestrial plants that exhibited miniature axes of simple morphology (dichotomously branched, bearing sporangia) and internal structure (Edwards et al., 2022b). The occurrence of cryptospores is continuous from the Middle Ordovician to the Early Devonian (Wellman and Gray, 2000), and then their number

and diversity decrease. In contrary, the abundance of trilete spores increases from the lower Silurian and becoming dominant in the upper Silurian (Wellman and Gray, 2000; Wellman et al., 2023). The earliest spores that can confidently be attributed to terrestrial plants were identified from the Middle Ordovician (Vavrdová 1984; Strother et al. 1996; Rubinstein and Vajda, 2019). Also, the Upper Ordovician mesofossils containing tracheids (Xu et al., 2022) would suggest the presence of vascular plants at this time. In addition to this, significant plant mesofossils, represented by sporangia with a mass of *in situ* spores, are known from the Upper Ordovician of Oman and Saudi Arabia (Wellman et al., 2003). This finding is remarkable in that it provides the first evidence linking the microfossil and macrofossil records of these earliest plants, as it shows the reproductive organ of a plant producer, encompassing propagules.

The Ordovician period was marked by the occurrence of diverse types of micro- and mesofossils, some of which are believed to have originated from algae or perhaps even land plants (Wellman and Gray, 2000). Nevertheless, their affinity remains undetermined. These include resistant tubular structures and cuticle fragments (Edwards and Wellman, 2001). Although the tubes might resemble conductive elements of vascular plants, they lack the characteristic thickening patterns observed in tracheophytes. Consequently, their affiliation to other groups, such as nematophytes, cannot be excluded. Additionally, abundant ornamented cuticle fragments lacking stomata are commonly classified as *Cosmochlaina* Edwards (1986) and it is assumed that their producers could also be representatives of algae.

The first macrofossils that resemble remains of terrestrial plants were reported from the Upper Ordovician (Hirnantian) of Holly Cross Mountains in Poland by Salamon (2018). Only small fragments often without sporangia are described by the authors. Some terminal sporangia-like structures are indeed visible on some axial tips. However, given the poor preservation of these specimens, their unambiguous assignment is still controversial (Gerrienne et al., 2020). From the lower Silurian (Llandovery), Maine, USA, a fossil of *Eohostimella heathana* Schopf has also been described by Schopf et al. (1966), but these are only axial fragments and do not suggest an affinity for terrestrial plants. The oldest confirmed macrofossil of a land plant is dated to the Wenlock, the Sheinwoodian stage (Bek et al., 2022), and comes from the Loděnice locality in the Prague Basin of the Czech Republic. Represented by the species *Cooksonia barrandei* Libertín et al., this fossil demonstrates an affinity for terrestrial plants, evidenced by the presence of *in situ* trilete spores (Libertín et al., 2018a). Another plant fossil of *Cooksonia*-type of Wenlock age was reported from Ireland, county Tipperary (Edwards et al., 1983) Based on the features present, these specimens may represent either *Cooksonia pertoni* Lang,

Cooksonia hemisphaerica Lang and/or *Cooksonia cambrensis* Edwards (Edwards et al., 1983). In contrast to *Cooksonia barrandei*, the record from Ireland (Edwards et al., 1983) come from younger sediments corresponding to the Homeric stage.

Since Silurian period, there has been an increase in the number and diversity of plant macrofossils as evidenced by the fossil record (summarised in Wellman et al., 2014; Pšenička et al., 2021). The rise in trilete spores observed during this time corresponds well with the increase of plant macrofossils (Steevens et al., 2012). Preservation of these fossil remains is predominantly in the form of coalified compressions, which limits our ability to analyse them with regard to internal anatomy. Notably, the exceptional preservation of fossils from Shropshire, UK, as charcoals (Edwards et al., 2014, 2022a, b, c) comes from the Lower Devonian strata and presents a notable exception to this pattern. These plant fossils display three-dimensional preservation, including anatomical structures and fine detail, and thus provide data on the physiology of the plants of that time.

3.3 Early land plants and their classification

The discovery of plant fossils from Rhynie chert (Kidston and Lang, 1917, 1920a, b, 1921a, b), also brought with it the need to classify this extinct group of plants, which did not fit into the categories of either vascular plants or bryophytes. The name Psilophyta was therefore adopted for them by Kidston and Lang (1917). “Psilophytic plants” were defined as those possessing a simple morphology without leaves and roots (Němejc, 1960). Nevertheless, this group remained conceptually diverse and heterogeneous in characteristics of the representatives. This heterogeneity encompassed variations in branching patterns of leafless axes with or without enations, and different types of sporangia and their arrangement. In an attempt to address this heterogeneity, a further division into the orders Psilophytales and Rhyniales was proposed by Höeg (1967). However, this additional division was not sufficient to fully resolve the observed diversity, which still persisted. Subsequent to this, Banks (1975 c) proposed a new classification system that incorporated these features, establishing three subdivisions: Rhyniophytina, Zosterophyllophytina and Trimerophytina. Despite its simplicity, this classification persisted as the prevailing method for categorising these earliest plants for long time.

The study of phylogenetic relationships between plant groups marked a significant shift in the field. Kenrick and Crane (1991) proposed a classification of plant groups based on cladistic

studies, which continues to serve as a foundational framework for understanding the position and evolution of plants (see Kenrick and Crane, 1991, 1997). The clade Polysporangiophyta was created to provide a collective designation for plants that possess a branched sporophyte bearing sporangia. This clade encompasses all land plants, with the exception of bryophytes and includes vascular plants (Tracheophyta) as well as a group of extinct non-vascular land plants known as Protracheophyta (containing *Aglaophyton*). Within the Tracheophyta, a further distinction is made between the "true" vascular plants, termed Eutracheophyta, which possess a lignified tracheid wall, and their sister group, the Rhyniopsida, or newly as Paratracheophytes according to Gerrienne et al. (2006), which includes Devonian genera including *Rhynia*. The Eutracheophyta are further divided into two large plant groups showing more derived traits: the group Lycophytina, which includes lycophytes, and the extinct group Zosterophyllophytina; and the large group Euphyllophytina, which includes ferns, horsetails, progymnosperms and seed plants (Kenrick and Crane, 1997).

4 The Prague Basin in the context of Silurian flora research

One of the most important geological and palaeontological sites in the world, the Barrandian area. It was named in honour of Joachim Barrande, a French palaeontologist who studied the rich fossil fauna of the area in the 19th century. He summarised his findings in more than twenty scientific volumes in a monumental work entitled "*Système silurien du centre de la Bohême*". This area is a source of valuable data on the development of life and sedimentation during the Early Paleozoic in the the Bohemian Massif.

The Prague Basin (Fig. 1), a part of the Barrandian area, has been defined by Havlíček (1981) as an elongated rift depression extending from Starý Plzenec to Brandýs nad Labem. It is a significant sedimentary area with a continuous sequence of marine deposits from the Lower Ordovician (Tremadocian) to the Middle Devonian (Givetian) (Štorch, 1994). The development of the basin was influenced by periodic fluctuations in sea level and volcanic activity. At the onset of the Ordovician period, the area underwent a transformation, marked by the extension and subsequent subsidence of the region, driven by the expansion of the Rheic Ocean (Žák et al., 2023). Subsequently, the area underwent uplift during the Variscan orogeny from the Middle

Devonian onwards, resulting in the complete cessation of the sedimentary area (Kukal and Jaeger, 1988; Chlupáč et al., 1998).

The Prague Basin has attracted considerable interest among palaeobotanists, particularly in relation to research on the early development of terrestrial flora. A substantial number of fossils of plant affinities, including algae, dispersed spores and macrofossils of early terrestrial plants, have been documented from this region, underscoring the significance of the site in understanding the evolution of early terrestrial ecosystems. Palaeobotanists J. Obrhel (1962) and H.-J. Schweitzer (1980) initiated their research in Silurian deposits of the Prague Basin. Among the remarkable specimens are the one of the oldest records of dispersed spores belonging to land plants (Vavrdová, 1984) and the oldest land plant macrofossil (Libertín et al., 2018a) from this area. In addition, a diverse early land plant assemblages (e.g., Kraft et al., 2019) have been recorded.

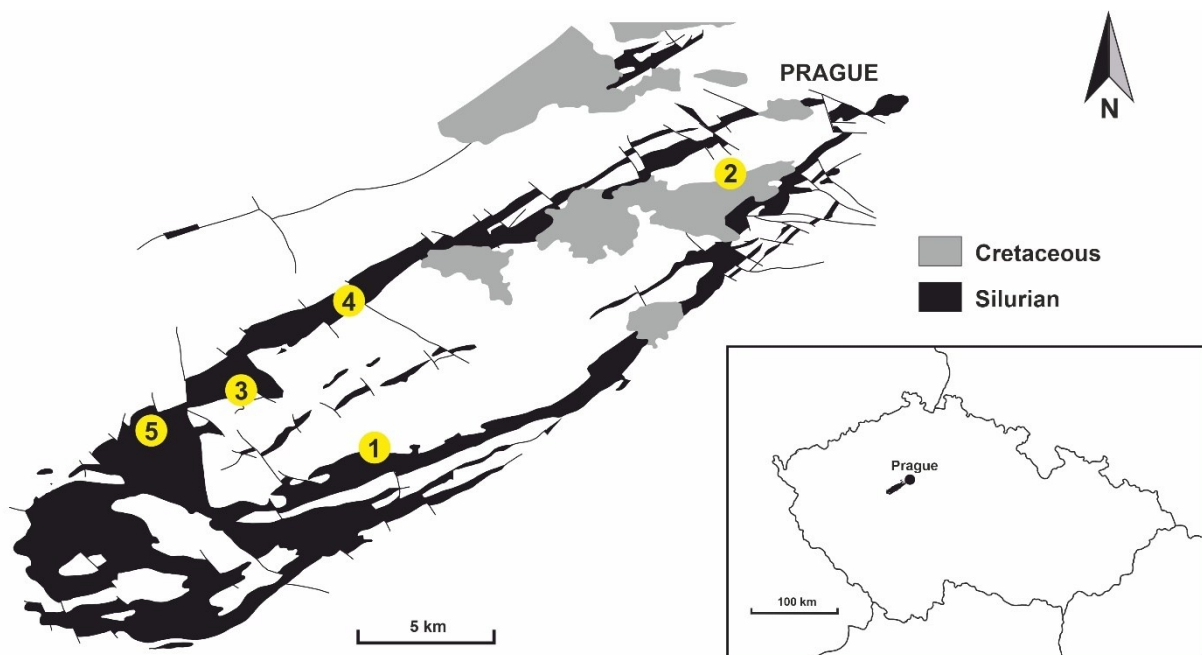


Fig. 1 Schematic map of the Prague Basin (modified after Štorch, 1994 and Kraft et al., 2019) showing locations (highlighted in yellow) of reported plant fossil findings from Silurian deposits (black). Locations marked with numbers: 1 – Karlštejn, 2 – Prague-Butovice, 3 – Lištice, 4 – Loděnice, 5 – Kosov quarry.

4.1 Brief geology and palaeogeography of the Prague Basin in the Silurian

The Silurian is regarded as the most widely explored geological period within the Prague Basin. Its diverse facies have influenced the formation of rich faunal communities, which allows to precisely correlate and determine the boundaries of the Silurian stages. This makes the Czech Silurian deposits an important area for the study of Silurian system on a global scale, together with the continuity of sediments unaffected by the Caledonian orogenic cycle (Chlupáč et al., 1998). This is also demonstrated by the established international stratotype of the lower boundary of the Přídolí stage in the Požáry quarry near Řeporyje (see Kříž et al., 1986).

At the end of the Ordovician period, a substantial decrease in global temperature occurred, resulting in notable shifts in the composition of the extant fauna and subsequently influencing the sedimentation patterns observed in the lower Silurian. The onset of the Silurian is characterised by the prevalence of black graptolite shales, which contain a substantial amount of organic matter, suggesting the presence of anoxic conditions at the seabed (Havlíček et al., 1958; Kříž, 1992, 1998). Contemporary with the gradual warming that characterised this period, a shift towards carbonate sediments became evident (Havlíček et al., 1958; Kumpera and Vašíček, 1988; Kříž, 1992, 1998). This phenomenon is indicative not only of climatic changes, but also of the movement of microcontinental blocks, including the Prague Basin (for two perspectives on the paleogeographic position of the Prague Basin, see von Raumer et al., 2003; Žák a Sláma, 2018, where it is considered as part of Armorican terrane assemblage, or, see Havlíček and Fatka, 1992; Fatka and Mergl, 2009, where it is situated within Perunica), towards the northern periphery of the Gondwana supercontinent (Chlupáč et al., 1998). The warm conditions of the Silurian become more intense as the equator is approached. This is indicative for the tropical climate of the upcoming Devonian (Kříž, 1992). This was also associated with the rise of warm-water faunal communities (Chlupáč et al., 1998).

During the Silurian period, the process of sedimentation was influenced by various factors, including the dynamics of water flow, along with oscillating changes in sea level, the movement of synsedimentary faults, as well as associated volcanic activity (Chlupáč et al., 1998; Kříž, 1992). Significant fluctuations in sea level, attributed to eustatic movements, can be identified across the sedimentary record, based on the nature and thickness of the deposited sediments. In the lower Silurian, the first of these events occurred in the form of a transgression that led to the flooding of the land around the basin. Thereafter, significant regression was evident in the

upper Wenlock, as well as in other world locations resulting in the formation of biodetritical limestones. Further regression events are documented in Ludlow and at the Ludlow/Přídolí boundary, as well as by the end of the Přídolí (Chlupáč et al., 1998).

Furthermore, significant movements along syndimentary faults in the basin occurred throughout the Silurian period, encompassing the Prague, Tachlovice, Koda, Tobolka and Barrandov faults. Formation of these faults was primarily induced by the extensional regime that prevailed during the initial stages of the Ordovician period, marking the rifting phase of the basin. Significant mobility occurred primarily in the Llandovery, exhibited by the Prague and Tobolsk faults, and in the upper Ludlow, as seen in the Tobolsk and Barrandov faults. In addition, the Koda fault was also traced by channels of extrusive volcanics extending between Karlštejn, Mořinka and Velká Chuchle (Chlupáč et al., 1998).

The activity of volcanic centres was predominately manifested during the Llandovery, upper Wenlock and upper Ludlow epochs, encompassing the Hýskov (exhibiting activity in Aeronian), Kosov (upper Homerian – lower Gorstian), Svatý Jan (upper Sheinwoodian – lower Gorstian) and Nová Ves volcanic centre (upper Homerian – lower Gorstian). An extensive accumulation of volcanic ash and effusive lava flows from eruptions was deposited in the surrounding sedimentary environment. These pyroclastic materials subsequently solidified, forming elevated platforms in close proximity to the volcanic centres (Chlupáč et al., 1998). These submarine structures offered favourable conditions that enabled highly diverse ecosystems to thrive, with a rich benthic community exploiting the nutrient-rich, shallow waters (Kříž, 1992). The distribution of biodetrital limestones helps to establish the relative position of the volcanoes and the stages of volcanic activity at that time (Chlupáč et al., 1998). There is also a lithological differentiation to be observed in the Prague Basin (Havlíček et al., 1958, Kříž, 1992) with the presence of coarse-grained benthic limestones of shallow-water origin and that of fine-grained sediments found in the deeper parts of the basin (Kříž, 1992).

The Silurian strata within The Prague Basin are divided into five distinct formations: the Želkovice, Litohlav, Motol, Kopanina and Požáry Formation (Kříž, 1992).

The oldest Želkovice Formation was initially documented by Perner and Kodým (1919) as the Želkovice strata, and subsequently defined by Kříž (1975) as a geological formation. It corresponds to the Rhuddanian to Aeronian stages, and consists mainly of black shales, derived from a substantial organic material content. According to Kříž (1992), the deposition of dark shales is associated with cold anoxic waters, resulting from eustatic sea level rise following the

Upper Ordovician glaciation (Kříž, 1992). The fossil record on the Želkovice formation contains abundant planktonic organisms, predominated by graptolites (Chlupáč et al., 1998). In this formation, basin deepening has been documented (Kříž, 1992), which has likely resulted in a decrease in facies diversity (Chlupáč et al., 1998). As in the preceding unit, the graptolite fauna is prevalent as well (Chlupáč et al., 1998).

The Litohlavy Formation, as defined by Kříž (1975), comprises the incomplete Telychian stage and is marked by a gradual increase in amounts of carbonates, which led to the deposition of predominantly clayey-calcareous shales (Horný; 1955, Kříž, 1992). During its formation, the basin deepened (Kříž, 1992), which probably led to a decrease in facies diversity (Chlupáč et al., 1998). Similar to the previous formation, the graptolite fauna prevails here (Chlupáč et al., 1998).

The Motol Formation is defined by sequences from the upper Telychian to Homerian stages and was first described by Perner and Kodým (1919) as the Motol beds. Subsequently, Bouček (1953) provided a revised definition, followed by Kříž (1975) who formally designated it as the Motol Formation. It is characterised by thick sequences of calcareous clay shales (Havlíček, 1958, Kříž, 1992), which exhibit marked differences in their development across different segments of the basin (Chlupáč et al., 1998). As a consequence of the coarsening of the basin due to the accumulation of volcanic material, there is an increase in benthic faunal development (Chlupáč, 1987). Despite this, graptolites remain prevalent in regard to paleontological content.

The Kopanina Formation, as established by Prantl and Přibyl (1948), corresponds to the Gorstian to Ludfordian stage. It is distinguished by predominant calcareous shales with tuffite admixture interspersed with limestone lenses (Havlíček et al., 1958; Kříž, 1992). This phase of sedimentation is characterised by significant volcanic activity, leading to the accumulation of tuffite material (Kříž, 1992). There is also an increase in the carbonate content of the sediments into the overlaying beds. Variations in the development of different segments of the basin can be observed, particularly during the period of regression, when bioclastic limestones were formed in the vicinity of volcanoes (Chlupáč et al., 1998).

The Požáry Formation represents the youngest of the Silurian formations, corresponding to the Přídolí series and being described by Prantl and Přibyl (1948) as the Přídolian beds (Prantl and Přibyl, 1948). These beds were the subject of further investigation by Kříž et al. (1986) as the Přídolí Formation. In order to avoid any potential confusion between the name of the formation itself and that of the series, Kříž (1986) subsequently renamed it as the Požáry Formation. This

formation varies in its development in different segments of the basin. The alternation of limestones with comparatively thinner layers of calcareous shales is characteristic for the Požáry Formation (Havlíček et al., 1958; Kříž, 1992). As the transgression was compensated by the uplift of the basin floor, a constant sedimentation pattern maintained. For the purpose of defining the international basal stratotype, the Požáry quarry section has been chosen (Kříž, 1992). Furthermore, the upper boundary of the Požáry Formation is formed by the international stratotype for the Silurian/Devonian boundary in Klonk near Suchomasty.

4.2 Land plant fossil record in the Silurian of the Prague Basin

The following spore and macrofossil occurrences are marked on the map of the Prague Basin in Fig. 1 together with the corresponding stratigraphic level in Fig. 2.

The research of sporomorphs from the Silurian sediments of the Prague Basin was primarily undertaken by palynologists Blanka Pacltová and Pavel Dufka (summarised in Fatka, 1999; Morávek, 2004). Among the earliest records, the occurrence of poorly preserved isolated tetrads was documented by Dufka (1990a) in the Llandoveryian sediments (Rhuddanian and Aeronian stages) of the Karlštejn and Nové Butovice localities. Additionally, Dufka (1990b) noted the presence of spores in the locality in Karlštejn of the Aeronian stage as well. The occurrence of morphologically simple bodies of the Motol Formation (Telychian) was further mentioned by Dufka (1990b) and Dufka and Pacltová (1988).

A rich spore assemblage of the Sheinwoodian age from Lištice near Beroun was documented by Dufka (1990b). This was followed by the description of an exceptional spore accumulation in the same locality by Dufka (1995) in the *Monograptus dubius parvus* to *M. vulgaris* biozone, corresponding to the Homerian stage. The study described twenty-nine sporomorphs, including the establishment of a new genus, *Rugosisporites* Dufka, and species *Rugosisporites kozlicus* Dufka, *Synorisporites maculosus* Dufka, and *Artemopyra rugaticosa* Dufka.

Although the aforementioned spore assemblage from the Wenlock represents the richest one from the Silurian sediments of the Prague Basin, it could also be caused by the fact that there were not many palynologists who specialised in isolating spores from younger Silurian sediments. Based on the ongoing diversification of plants, which is most pronounced at the end of the Silurian, it could be assumed that the abundance and diversity of dispersed spores will

increase towards the younger strata. However, the record of dispersed spores from the upper Silurian of the Prague Basin is lacking to date in order to support this hypothesis.

The oldest macrofossil clearly attributable to terrestrial plants was found in the Wenlock of the Prague Basin. The specimen comes from the collection of Joachim Barrande from Loděnice (Barrandovy jámy site), of the Middle Sheinwoodian (from the *Monograptus belophorus* biozone) and was described in detail by Libertín et al. (2018a). This specimen is represented by the species *Cooksonia barrandei* Libertín et al., which was newly established based on characteristic features. The plant shows a dichotomously branched sporophyte terminated by lenticular sporangia, and *in situ* trilete spores confirming the terrestrial plant affinity (Libertín et al., 2018a). Other reported plant fossils determined as *Cooksonia* sp. also come from the same strata of the Špičatý vrch site in Loděnice (Libertín et al., 2018b), as well as the palynomorph assemblage (Bek et al., 2022), which comprises cryptospores and spores including the trilete-type *Ambitisporites* Hoffmeister and *Aneurospora* Streeel. The Stydlé vody site in Loděnice, which is analogous in stratigraphic range, has also been revealed to contain numerous fossiliferous layers comprising abundant fragments of *Cooksonia* sp. (Libertín et al., 2024b). Another record of *Cooksonia* sp. comes from the upper layers in the *Cryptograptus rigidus* biozone (Libertín et al., 2003).

Further findings of plant macrofossils are of Přídolian age. These are represented by a diversified plant assemblage as documented in a number of publications (Obrhel, 1962; Schweitzer, 1980; Kraft et al., 2019; Uhlířová et al., 2022; Bek et al., 2024; Uhlířová et al., 2024a, b; in prep. b) coming from the Kosov Quarry near Beroun, a locality rich in palaeontological material. The plant assemblage consists of at least 6 species belonging to four genera including *Aberlemnia*, *Capesporangites* Uhlířová et al., *Cooksonia* and *Tichavekia* Pšenička et al. All of the reported specimens come from the base of the Požáry Formation (*Neocolonograptus parultimus*–*Neocolonograptus ultimus* biozone) corresponding to the base of the Přídolí. Firstly, Obrhel (1962) described specimens from the base of the Požáry Formation including *Cooksonia* sp., *Cooksonia* cf. *hemisphaerica* and a specimen of *Tichavekia grandis* Pšenička et al., which was originally identified by Obrhel (1962) as *Cooksonia* sp. and reassigned by Kraft et al. (2019). Additionally, the genus *Cooksonia* is, in my opinion, represented here by the occurrence of the species *Cooksonia pertoni*, as originally figured by Kraft et al. (2019, p. 150, fig. 4D) as *Cooksonia* sp.

Other plant fossils described by Kraft et al. (2019) also come from the basal part of the Kosov quarry. Among them, the genus and species *Tichavekia grandis* is exceptional, established in

the publication by Kraft et al. (2019) and subsequently described in detail by Uhlířová et al. (2022). The plant is exceptional especially for its stature measuring more than 13 centimetres in height, while exhibiting axial and sporangial features related to the lineage of basal lycophytes (Kraft et al., 2019; Uhlířová et al., 2022). Its affinity to terrestrial plants was confirmed by the *in situ* trilete spores by Bek et al. (2024), while the dark lines of the coaly matter observed inside the axes may indicate the presence of potential conducting tissues, which could also indicate a probable vascularity of the plant (Uhlířová et al., 2022).

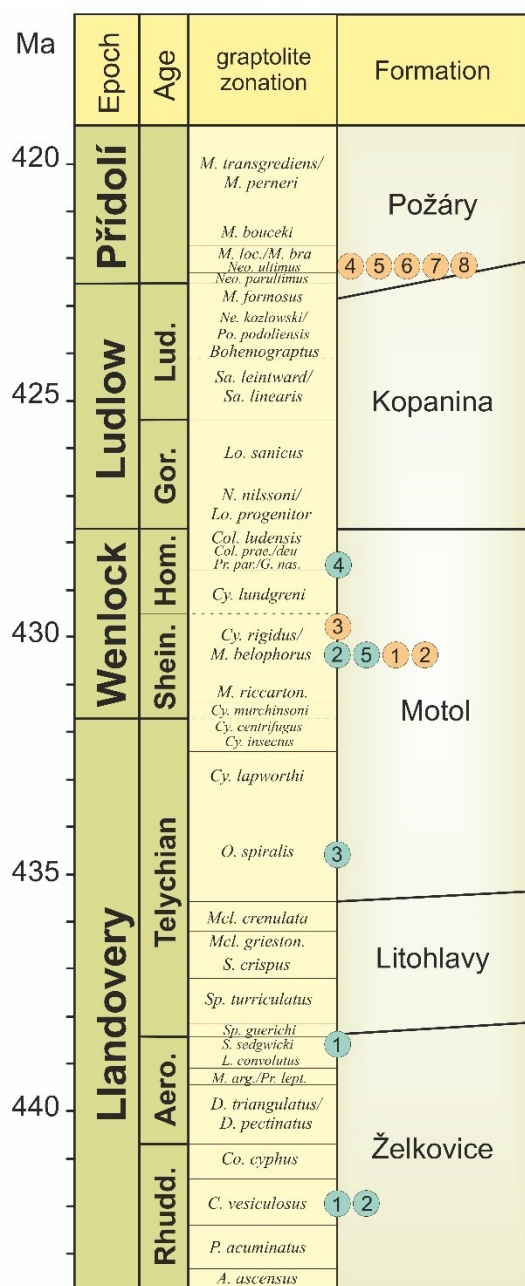
Recently, Uhlířová et al. (2024b, in prep. b) described a curiously preserved plant fossil of the same stratigraphic level of the Kosov quarry that shows atypical axis terminations in the form of trilobed structures (Fig. 3). Upon observation and consideration of possible scenarios, Uhlířová et al. (2024b, in prep. b) are inclined towards the possibility that the structures represent coiled fertile parts of the axes. Based on their interpretation, as sporangia are concealed coiled within the terminal structures, their morphological characteristics cannot be well compared with other taxa and therefore the plant is left undetermined (Uhlířová et al., 2024b, in prep. b). However, the relation with the genus *Tichavekia* is considered to be most probable, especially because some of the plant characteristics and the pattern of sporangia grouping observed in *Tichavekia* could correspond to those of the studied plant. Thus, Uhlířová et al. (2024b, in prep. b) speculate that it could even represent the same taxon, being preserved in different developmental stages. The authors give this fossil primarily as an example of a specific type of axial and sporangial development, which resembles the circinately coiled axial apices observed, for example, in many zosterophylloids, and could also occur in other similar taxa tending towards this plant lineage in their features.

The last of the taxa described so far from the Přídolian strata (belonging to the *Neocolonograptus parultimus*–*N.ultimus* biozone as well) of the Kosov quarry is *Capesporangites petrkraftii* Uhlířová et al. The plant fossil was originally described by Kraft et al. (2019) as *Fusiformitheca* sp. and later, based on further comparisons and a detailed description by Uhlířová et al. (2024a), established as a new genus and species of *Capesporangites petrkraftii* Uhlířová et al. It represents a fossil with dichotomously branched axes and a single preserved vertically elongated sporangium. The structures observed in the sporangium, however, suggest a clue to its internal organization. Some sporangial structures are resembled to those of the capsule of bryophytes (e.g., cap-like structure at the apex and a basal columella-like structure). Although the evolutionary relationship between bryophytes and polysporangiophytes is still unresolved (see e.g., Morris et al., 2018; Tomescu, 2022), new

insights have been provided by the discovery of eophytes sensu Edwards et al. (2022a, b, c), which represent a group of plants combining characters of both lineages. Thus, the question remains regarding the classification of *Capesporangites* and as to whether the structures exhibited by it might represent a kind of homoplasy.

Another significant specimen of the same stratigraphic level from the locality nearby the Kosov quarry, from Dlouhá hora (situated south and southwest from the Kosov quarry) is represented by *Aberlemnia bohémica* (Schweitzer) Sakala et al. This specimen was reported by Schweitzer (1980), who initially assigned by him as a new species of *Cooksonia bohémica* Schweitzer. Based especially on features referring to basal lycophytes, Sakala et al. in Kraft et al. (2019) proposed a new combination and reassignment to the genus *Aberlemnia*. However, in response, there was also a contrary opinion from Libertín et al. (2023), who argued for placing the specimen within the genus *Cooksonia*. The latter publication by Libertín et al. (2023) also continued by referring to another new specimen of *C. bohémica* from the Kosov quarry, on which he tried to prove his statement. This is also related to the specimen described by Obrhel (1962, pl. 1, figs 4–5) as *Cooksonia* sp and recently assigned by Libertín et al. (2023) to *Cooksonia bohémica*.

A representative of the basal lycophyte lineage, *Baragwanathia brevifolioides* Kraft et Kvaček, originally described in detail by Kraft and Kvaček (2017) as *Baragwanathia brevifolia* Kraft et Kvaček, come from the Karlštejn locality. In contrast to the aforementioned fossils from the Kosov quarry, the stratigraphic occurrence also corresponds to the Požáry Formation, but from a slightly younger stratigraphic level (*N. ultimus* biozone). The whole plant measures 9.5 centimetres in height and is characterised by dichotomously to trichotomously branched axes with densely growing 2–4.7 mm long microphylls with midribs grow along the entire axes (Kraft and Kvaček, 2017). There is a view that disputes the plant affinity of *Baragwanathia brevifolioides*, suggesting that it rather represent a graptolite (P. Kenrick, oral communication in Libertín et al., 2024a). Fragments of *Cooksonia* sp. were also found at the same locality (Štěpán Manda, oral communication in Kraft et al., 2019). In a recent study, Libertín et al. (2024a) also described plant fossils from the Karlštejn locality, the Požáry Formation (*Skalograptus parultimus*–*S. ultimus* Biozone), for which they established a new species, *Aberlemnia krizzi* Libertín et al.



Macrofossils

- | | | |
|----|-------------------------|--|
| 1. | Libertín et al. (2018a) | <i>Cooksonia barrandei</i> |
| 2. | Libertín et al. (2018b) | <i>Cooksonia</i> sp. |
| 3. | Libertín et al. (2024b) | fragments of <i>Cooksonia</i> sp. |
| 4. | Libertín et al. (2003) | <i>Cooksonia</i> sp. |
| 5. | Obrhel (1962) | <i>Cooksonia</i> cf. <i>hemisphaerica</i>
<i>Cooksonia</i> sp. |
| 6. | Schweitzer (1980) | <i>Aberlemnia bohémica</i> |
| 7. | Kraft et al. (2019) | <i>Capesporangites petrkraftii</i>
<i>Cooksonia</i> cf. <i>pertoni</i>
<i>Tichavekia grandis</i> |
| 8. | Kraft and Kvaček (2017) | <i>Baragwanathia brevifolioides</i>
<i>?Cooksonia</i> sp. |
| 9. | Libertín et al. (2024a) | <i>Aberlemnia krizzi</i> |

Spores

- | | |
|----|---------------------------|
| 1. | Dufka (1990a) |
| 2. | Dufka (1990b) |
| 3. | Dufka and Pacltová (1988) |
| 4. | Dufka (1995) |
| 5. | Bek et al. (2022) |

Fig. 2 Stratigraphic occurrence of early land plant spores and macrofossils (only reported findings) in the Prague Basin. Silurian time scale with graptolite zonation modified after Pšenička et al. (2021), lithostratigraphy according to Kříž (1992).

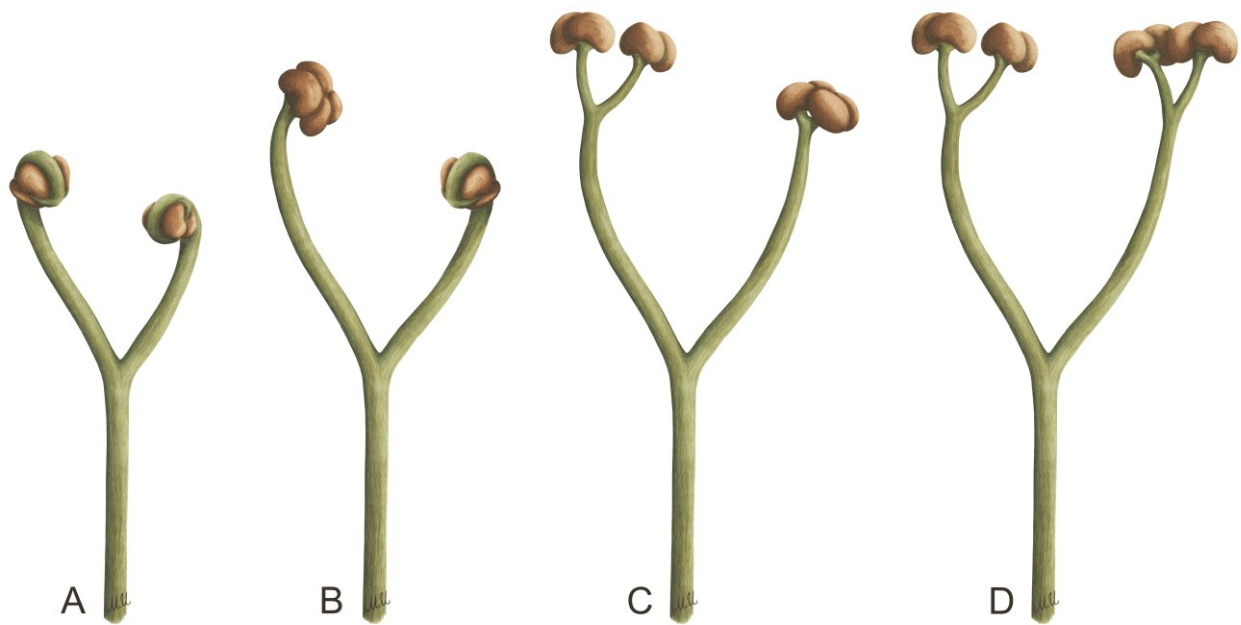
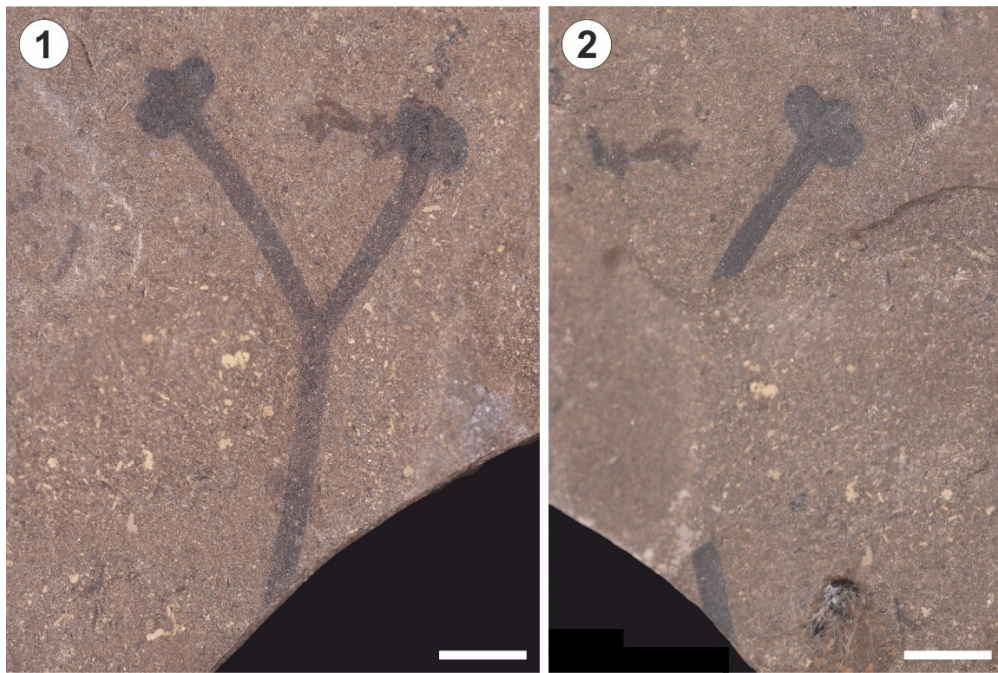


Fig. 3 Photos (1, 2) of the plant macrofossil (specimen No. F23638A – part, and F23638B - counterpart, housed in WBM) possessing trilobed terminal structures, interpreted by Uhlířová et al. (2024b) as probable coiled fertile tips (scale bars 5 mm). A presumed reconstruction of the plant (A–D) in various stages of development – A, reconstruction of the plant fossil with unevenly coiled terminal parts. B, gradually unfolding tips where the one terminal part is already unfolded, and C, with fully developed terminal parts with sporangia.

4.3 Palaeoecology and evidence of the first fires

The occurrence of macrofossils of terrestrial plants in Silurian sediments of the Prague Basin is associated with their transport from nearby land. Given that plant fossils are found exclusively within interbeds of tuffaceous calcareous shales, volcanic islands are considered their likely source (Kraft et al., 2019). These islands emerged temporarily during distinct periods (Fiala, 1970) in response to eustatic sea-level fluctuations, which coincided with peaks in volcanic activity (Kříž et al., 1992). From the upper Wenlock to the lower Ludlow, the elevations of the Svatý Jan and Kosov volcanic centres were reported (Kříž, 1992; Kraft et al., 2019). Evidence for this at the Svatý Jan volcanic centre includes sedimentary beds containing distinctly abraded fragments of coral and stromatoporoid skeletons from the upper Wenlock (Horný, 1955), indicating a dynamic intertidal environment. A significant marine regression likely contributed to the exposure of the volcano (Chlupáč et al., 1998). Around the Svatý Jan volcanic centre, repeated lava flows until the Lower Ludlow resulted in the formation of the massive lava sheet. The top of the volcano was also covered by lava, remaining above sea level from the lower Gorstian to the upper Přídolí. A stratigraphic hiatus at Herinky near Svatý Jan pod Skalou testifies to the prolonged exposure of the volcanic top above sea level. The Kosov volcanic centre became active in the upper Homerian and lasted until the lower Gorstian, similar to the Svatý Jan volcano (Kříž, 1992). The Kosov volcanic centre was also emerged during maximum of its volcanic activity.

Volcanic islands may have provided transfer points for spores from the marine environment, allowing them to colonize and establish populations (Kraft and Kvaček, 2017). Interestingly, despite the well-documented deposits of the Kopanina Formation, no macrofossil evidence of terrestrial plants from the Ludlow period have been recorded in the Prague Basin. As suggested by Kraft et al. (2019), this may be attributed to either the complete absence of plant fossils or, more likely, their extreme rarity. The rarity is likely due to the nature of the volcano islands at the time, with steep, rocky slopes and a dynamic environment, as well as a lack of suitable substrate due to slow erosion processes, making colonization difficult following the last volcanic activity in the middle Ludlow (Kraft et al., 2019).

When volcanic activity ceased in the middle Ludlow, ongoing erosion gradually flattened the coastal landscape, creating a more favourable environment for plant colonization (Kraft et al., 2019). The presence of plant communities in the early Přídolí documented at Kosov near Beroun (summarised in Kraft et al., 2019; Uhlířová et al., 2022, 2024a) and Karlštejn (Kraft

and Kvaček, 2017) confirms that conditions had significantly improved. Kraft et al. (2019) suggest that these plants had likely colonised the coastline in a patchy distribution, forming either monotypic plant communities or assemblages of species with similar ecological requirements. Based on the localities of Přídolian plant macrofossils, Kraft et al. (2019) distinguished three segments: the southern Kosov area (*Aberlemnia bohémica*), the northern Kosov area (genera *Cooksonia*, *Capesporangites*, *Tichavekia*), and the Karlštejn segment (?*Cooksonia*, *Baragwanathia brevifolioides*).

These sites were probably not far from the original sources of the plants, as the preserved macrofossils show minimal fragmentation, indicating short-distance transport. It is thought that these plants originated from nearby volcanic centres and were washed into the marine environment, and subsequently buried. Given the proximity of these sites to former volcanic islands, the plants from the Kosov area are considered to have originated from the Kosov volcanic centre, while the ones from Karlštejn were derived from the Svatý Jan volcanic centre (Kraft et al., 2019). The probable source of *Cooksonia barrandei* described from the Wenlock deposits at Loděnice is also considered to be the Svatý Jan volcanic centre, which was active from the Upper Sheinwoodian onwards (Libertín et al., 2018a). However, the successful growth of these early terrestrial plants on volcanic islands probably required specific environmental conditions. A key factor was a low-energy coastal environment, such as the leeward side of the island or the sea influenced only by local winds and currents, according to Kraft et al. (2019). In addition, these plants required a reliable source of freshwater, which they likely obtained from streams and seeps of groundwater rather than direct rainfall (Kraft et al., 2019).

It is likely that the environment of volcanic islands, and thus plants, could have been influenced by some of the earliest fires at that time. Their presence is evidenced by fossils of *Pachytheca* and *Prototaxites*, preserved as charcoals from the Homerian of Lištice near Beroun and from other localities described in Uhlířová et al. (in prep. c) (Fig. 4). These findings were briefly mentioned by Pšenička et al. (2021), where isolated fragments of *Pachytheca*, *Prototaxites*, and *Nematasketum* Burgess et Edwards, obtained through bulk maceration are figured (the same herein as Fig. 5). Confirmation of wildfires occurrence during the colonization of volcanic elevations by plants in the Silurian would represent another factor that plants had to cope with. The influence of early wildfires on past ecosystems is discussed by Glasspool and Gastaldo (2023), and also in relation to higher atmospheric oxygen levels during the Early Paleozoic by Glasspool et al. (2015). Although vegetation at that time consisted of small plants and was not abundantly represented, fires may have had a beneficial effect on it (comparison with modern

post-wildfires ecosystems in Boerner, 1982). For example, fire could have enabled plants to thrive better by providing ash as a more accessible source of nutrients (Blank et al., 2017) and accelerating erosion (Depountis et al. 2020) for the formation of a suitable substrate.

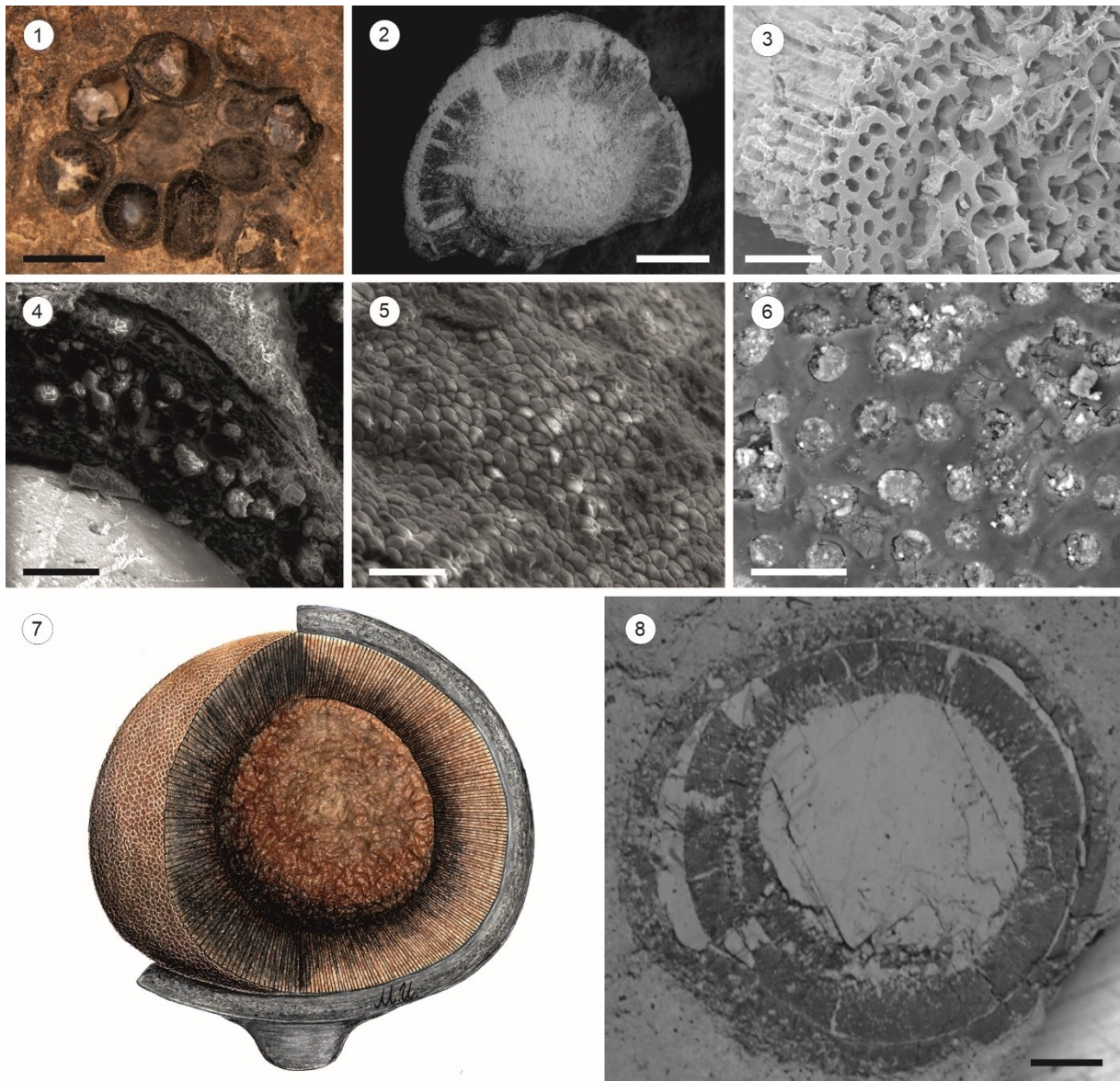


Fig. 4 *Pachytheca* from the publication in progress by Uhlřřova et al. (in prep. c). 1 - cluster of *Pachytheca* bodies (scale bar 2 mm), 2 – specimen in SEM, low vacuum (scale bar 1 mm), 3 – isolated cortex (100 μm), 4 – outer layer in SEM, low vacuum (100 μm), 5 – vesicular tissue covering the cortex (50 μm), 6 – detail of the cortex with secondary mineral fill inside channels (25 μm), 7 – presumed reconstruction of *Pachytheca*, 8 – specimen in cross section (SEM, low vacuum) showing cortex covered by outer layer (500 μm).

4.4 Comparison with floras of other global areas

Macrofossils of the earliest land plants have been found in Silurian sediments of the Prague Basin at several sites, namely Loděnice (Libertín et al., 2002, 2018a, b, 2024b), Karlštejn (Kraft and Kvaček, 2017; Libertín et al., 2024a), and the Kosov quarry near Beroun (Obrhel, 1962; Schweitzer, 1980; Kříž, 1992; Kraft et al., 2019; Uhlířová et al., 2022; Bek et al., 2024; Uhlířová et al., 2024a, b, in prep. b). A total of eight plant species of five genera have been documented from these sites, including *Aberlemnia bohemica*, *A. krizzi*, *Cooksonia barrandei*, *C. hemisphaerica*, *C. pertoni*, *Baragwanathia brevifolioides*, *Capesporangites petrkraftii* and *Tichavekia grandis*.

Concerning the comparable Silurian floras worldwide, the plant assemblage from the Czech Republic is relatively diverse. More than twenty Silurian localities with reported plant macrofossils have been reported, including those from the Prague Basin (summarized in Wellman et al., 2014; Pšenička et al., 2021). In terms of regional composition, the Anglo-Welsh Basin records the greatest generic diversity of Silurian land plants, comprising fossils of eight genera, including *Caia* Fanning et al., *Cooksonia*, *Hollandophyton* Rogerson et al., *Pertonella* Fanning et al., *Psilophytites* Hoeg, *Salopella* Edwards et Richardson, *Steganotheca* Edwards and *Tortillicaulis* (summarised in Wellman et al., 2014). Besides, the Junggar Basin in China yielded a community of five genera consisting of *Lycopodolica* Ishchenko, *Cooksonella* Nagy, *Junggaria* Dou, *Salopella* Edwards et Richardson, and *Zosterophyllum* Penhallow (Cai et al., 1993). Another notable locality is Bathurst Island in Arctic Canada, where four genera – *Bathurstia* Hueber, *Distichophytum* Magdefrau, *Macivera* Kotyk et al., *Zosterophyllum* and unidentified rhyniophytoids have been discovered (Kotyk et al. 2002). Similarly, a four-generic assemblage from Ukraine includes *Cooksonia*, *Eorhynia* Ishchenko, *Lycopodolica* together with fossils resembling zosterophylls (Ishchenko, 1975).

Raymond (2006) made an extensive comparison of morphological characteristics of the upper Silurian and Lower Devonian plants using a cluster and correspondence analysis. This study identified four distinct phytogeographic units (North Laurussian, South Laurussian-Northwest Gondwanan, Kazakhstanian, and Northeast Gondwanan) based on multivariate analysis of macrofossil genera and morphological characteristics. The results suggest that differences in the composition of the macroflora reflect the climatic conditions of these units, while the presence of different endemic taxa indicates geographic isolation of some regions (Raymond et al., 2006). The closest similarities were observed between the South Laurussian and Northeast

Gondwanan units, with some shared plant genera, but they differ in morphological traits recorded. The North Laurussian (Bathurst Island) and Kazakhstan units also display similarities, particularly in the dominance of basal lycophytes, consistent with their equatorial position during the Late Silurian. However, their floras were distinct enough to be separated, mainly due to endemic genera unique to each region - such as *Bathurstia* and *Distichophytum* on Bathurst Island, and *Jugumella* and *Cooksonella* in the Kazakhstan unit. In contrast, the South Laurussian-Northwest Gondwanan Unit encompassed a wide latitudinal range during the Late Silurian supporting a diverse flora dominated by rhyniophytes such as *Cooksonia*, *Caia*, *Steganotheca* and *Tortillicaulis* (Raymond et al., 2006). Although the Prague Basin was part of the Northwest Gondwanan Unit, it was not involved in the analysis by Raymond et al. (2006).

The conclusions of Raymond et al. (2006) were further supported by Pšenička et al. (2021), who analysed the distribution of plant macrofossils to determine the predominance of either rhyniophyte-like or zosterophyll-like plants in each region. This study also correlated the stratigraphic distribution of plants with trends in spore abundance and temperature fluctuations. The results indicate an increase in plant diversity starting in the Ludlow, probably as a response to the end of the Homeric glaciation, reaching its highest point in the Přídolí. The study also included data of Silurian plant macrofossil assemblages from the Prague Basin. During the Wenlock, the Prague Basin flora developed in a temperate zone, forming a monogeneric assemblage represented by *Cooksonia* (see Libertín et al., 2002, 2018a). By the Late Silurian (Přídolí), this assemblage had diversified considerably with the genera *Aberlemnia*, *Cooksonia*, *Baragwanathia* Lang et Cookson, *Capesporangites* and *Tichavekia* (summarised in Kraft et al., 2019; Uhlířová et al., 2024a). This assemblage represents a rhyniophyte-dominated flora, with *Baragwanathia* as the only basal lycophyte. The ratio of rhyniophyte-like plants to basal lycophytes was similar to that of the Anglo-Welsh Basin, however, there are significant differences concerning the species composition.

Results

4.5 Pšenička et al. (2021)

Pšenička, J., Bek, J., Frýda, J., Žárský, V., Uhlířová, M. & Štorch, P. 2021. Dynamics of Silurian plants as response to climate changes. *Life* 11(9), 906.

This study utilised a multidisciplinary approach to analyse the impact of climate changes during the Silurian period on the evolution and diversification of early land plants. The research integrated geochemical data and the fossil record to provide a comprehensive dataset. In particular, the dispersal spore record was incorporated to ascertain the diversity of the flora during this time. Further support is provided by the record of Silurian plant macrofossils. A more comprehensive analysis was obtained by utilising data originating from multiple sources, including own records as well as data collected from other sources. These additional records referred to Silurian plant macro- and microfossils, as well as data relating to carbon and oxygen isotope stratigraphy.

The results yielded quantitative data on the occurrence of different spore types in relation to global fluctuations in temperature as well as oxygen concentrations in the atmosphere. In this context, the results obtained from curve plots revealed that cryptospores exhibited resilience during the glacial event in the Homerian, with no observed decline in diversity. In contrast, the diversity of trilete spores was significantly affected. Consequently, following the glaciation, a rapid increase in plant diversity was documented, suggesting warmer conditions enabled accelerated evolution. During the Silurian, a significant increase in atmospheric oxygen was also observed. By the end of the period, concentrations far exceeded contemporary levels, that was likely associated with an expansion of terrestrial flora. These data therefore demonstrate a correlation between variability in embryophytes and global ecosystem changes. In addition, the differing responses of trilete spore producers and cryptospores to stress factors indicate their divergent ecological strategies.

The geographical distribution of plant assemblages during the Silurian period is also examined. For this purpose, data on plant macrofossil records (summarised in Wellman et al., 2014) were utilised, encompassing rhyniophyte-dominated and zosterophyll-like dominated communities. Notably, the provincialism of the four continents was evident, supporting the conclusions of Edwards (1990). Furthermore, photographs of fossil representatives of the flora from the Bathurst Island locality in Canada were published, with kind permission from Patricia Gensel

on behalf of the collectively authorship of Kotyk et al. (2002). New records of nematophytes, including the genera *Nematasketum*, *Prototaxites* and *Pachytheca*, from the Prague Basin were also presented (Fig. 5).

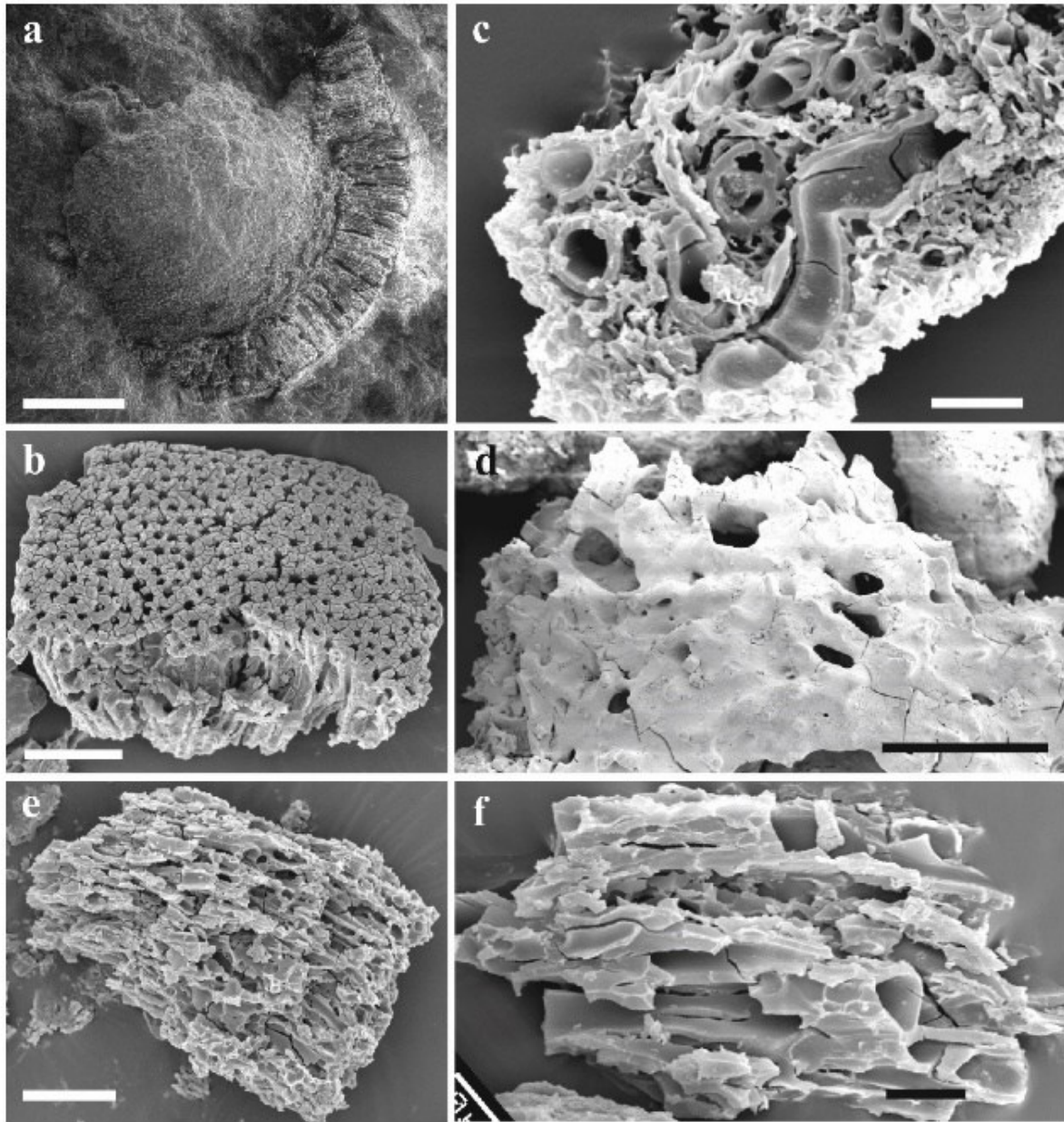


Fig. 5 Enigmatic fossils from the Lištice locality, observed in SEM, adapted from Pšenička et al. (2021). (a) *Pachytheca* showing medulla (inner) and cortex (outer part), scale bar = 500 μm ; (b) Cortical fragment of *Pachytheca* in detail, scale bar = 20 μm ; (c) cf. *Nematasketum*, scale bar = 200 μm ; (d) Cf. *Cosmochlaina*, scale bar = 200 μm ; (e) tubes of *Prototaxites*, scale bar = 100 μm ; (f) Detail of tubes of *Prototaxites*, scale bar = 20 μm .

4.6 Uhlířová et al. (2022)

Uhlířová, M., Pšenička, J., Sakala, J. & Bek, J. 2022. A study of the large Silurian land plant *Tichavekia grandis* Pšenička et al. from the Požáry Formation (Czech Republic). *Review of Palaeobotany and Palynology* 298, 104587.

The subject of this study is a specimen of *Tichavekia grandis* plant fossil (Fig. 6), which was firstly documented by Kraft et al. (2019) and examined in greater detail herein. The plant is remarkable given its size, reaching 13 centimetres. The specimen comes from the Kosov quarry near Beroun, from the basal part of the Požáry Formation (base of the Přídolí), where other significant plant macrofossils have been reported (summarised in Kraft et al., 2019; Uhlířová et al., 2024a).

The material constitutes the holotype (specimen WBM F21761b - part, coll. WBM) and isotype (specimen WBM F21761a - counterpart, coll. WBM), based on which the genus and species of *Tichavekia grandis* were established by Kraft et al. (2019). A recent study (Uhlířová et al., 2022) has focused on a detailed description of the plant fossil, yielding notable conclusions. The plant is six times dichotomously branched, with five distinct dichotomies and one less conspicuous terminal dichotomy. The axes of the plant are leafless and slightly concave, reaching widths of 0.8–1 mm. The length of the axes shortens towards the apical part. Additionally, there is a gradual decrease in the diameter of the axes towards the distal end, accompanied by a tendency for slight widening within the axes from the narrow base to the wider distal end. The apical part of the plant consists of very short terminal dichotomies, with each axis bearing a single sporangium. However, some axes at the same branching level exhibit a marked difference in length, resulting in asymmetric development of the plant. Sporangia are spherical to kidney-shaped and exhibit a wide base and gradual narrowing towards the apex.

A discussion on the palaeoecology of the plant is also included. Growth in terrestrial environments could be suggested by axes exhibiting slight bending, resulting from loads imposed by branches. The preserved axes show no signs of bends or twists, indicating their integrity and apparent robustness. The distinctly narrow bases of *Tichavekia* axes are not commonly observed in land plants. It is challenging indeed to imagine that a plant growing in this manner would be stable in a terrestrial environment. Therefore, it is plausible to assume that the plant grew in clusters and may also have been supported within an aquatic environment, potentially growing partially submerged. The reconstruction of the plant shown growing in clusters was also proposed. In conclusion, *Tichavekia* exhibits a complex of simple traits, such

as dichotomously branched leafless axes and terminal sporangia, which are common among rhyniophytoid genera of Silurian plants. However, it also exhibits unique axial (especially the very short dichotomies and growth pattern) and sporangial features and the unusually large stature, which might suggest that the plant could belong to more derived plant representatives with a more complex structure.

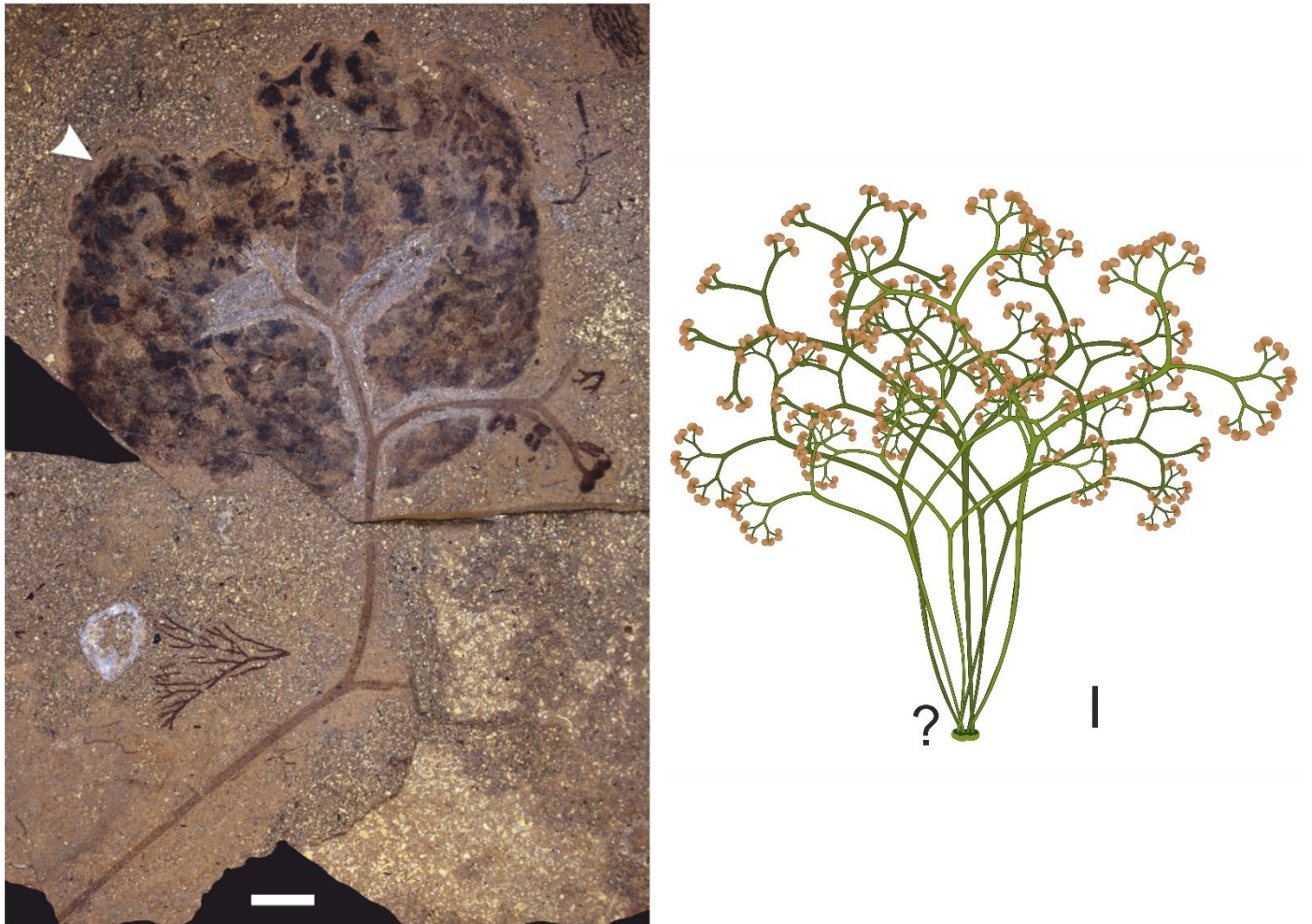


Fig. 6 *Tichavekia grandis* (specimen No. WBM F21761a). White arrow points to an enigmatic algal-like fossil. Scale bar 20 mm. Right in picture shows the suggested reconstruction of whole plant showing possible tufted character. Scale bar 10 mm. Adapted from Uhlířová et al. (2022).

4.7 Bek et al. (2024)

Bek, J., Uhlířová, M., Pšenička, J. & Sakala, J. 2024. Preliminary results on reproductive organs and *in situ* spores of an early land plant *Tichavekia grandis* Pšenička et al. from Přídolí (upper Silurian) of the Prague Basin, Czech Republic. *Palaeoworld*, 33(2), 299–306.

Following a previous study (Uhlířová et al., 2022) of the type material of the Upper Silurian *Tichavekia grandis* (specimens WBM F21761b, b, coll. WBM), a recent publication by Bek et al. (2024) presents additional key findings. *In situ* trilete spores were isolated from the sporangium of the fossil plant, indicating its clear affinity to embryophytes. The terrestrial origin of the plant was already suggested by Uhlířová et al. (2022), who discussed the morphological characteristics of the plant, pointing to its probable growth in a terrestrial environment.

Isolated spores were obtained by the maceration technique, consisting of application of 35% hydrochloric acid for 48 h and 38% hydrofluoric acid for 28 h, followed by neutralisation of the samples with distilled water. The residues obtained were coated in gold and observed in SEM. Given the rarity of this material, only a small amount of coaly matter was removed from the sporangium, yielding only a few spores to allow determination.

The spores preserved *in situ* are subcircular with an average diameter of 28 x 17 µm, having an equatorial crassitude up to 2 µm wide. The spore sculpture is microgranulate to microverrucate to vermiculate to rugulate. The trilete scar rays reach up to a half of the radius. The characteristics of the studied spores do not match those of spores of other Silurian and Devonian plant taxa. However, since we consider such a small number of spores obtained to be insufficient, we could not propose a modification of the original diagnosis of *Tichavekia* in order to maintain scientific objectivity. Nevertheless, this discovery is, in our opinion, of great importance as it provides insight into the reproductive strategy of one of the earliest representatives of land plants.

4.8 Uhlířová et al. (2024)

Uhlířová, M., Pšenička, J. & Sakala, J. 2024a. New early land plant *Capesporangites petrkraftii* gen. et sp. nov. from the Silurian, Prague Basin, Czech Republic. *Review of Palaeobotany and Palynology* 322, 105048.

The focus of this study was the examination of the plant fossil taxon *Capesporangites petrkraftii* (Fig. 7) from the same stratigraphic level as the previous plant fossil (biozones *N. parultimus*–*N. ultimus*, corresponding to the base of the Přídolí). The specimen (F21762, coll. WBM) was originally briefly described by Kraft et al. (2019) and assigned to cf. *Fusiformithec*a sp. Based on detailed comparisons of characteristics with other taxa, including *Fusiformithec*a, it was found that its characteristics do not correspond to any of them, and therefore a new genus and species *Capesporangites petrkraftii* has been established. The fossil was described morphologically within this study and its systematic placement was discussed given its unique combination of characters typical of different plant lineages.

According to the observations, the plant reaches a height of 1.8 cm and represents a dichotomously branched sporophyte terminated by a single preserved sporangium. The axes are leafless and slightly curved. Their diameter is 0.35–1 mm and decreases towards the distal part. A single sporangium is preserved at the end of one of the axes; the remaining sporangia are apparently not preserved due to splitting during transport to the depositional site. The sporangium is vertically elongated, reaching a length of 3.5 mm and a width of 1.2 mm. There is a protruding structure in the basal part of the sporangium, formed by an accumulation of coaly matter, and a cap-like structure in the apical part of the sporangium.

On the basis of the branched axes with terminal sporangium, the plant is classified within the polysporangiophytes. Nevertheless, we also consider the observed sporangial structures (structure at the base of the sporangium and cap-like structure at the apex), which may in some respects be resembling features of bryophytes, especially the internal organisation of the capsule. The question arises as to whether these characters may represent a form of analogy (homoplasy), since polysporangiophytes and bryophytes represent two distinct evolutionary lineages of plants.

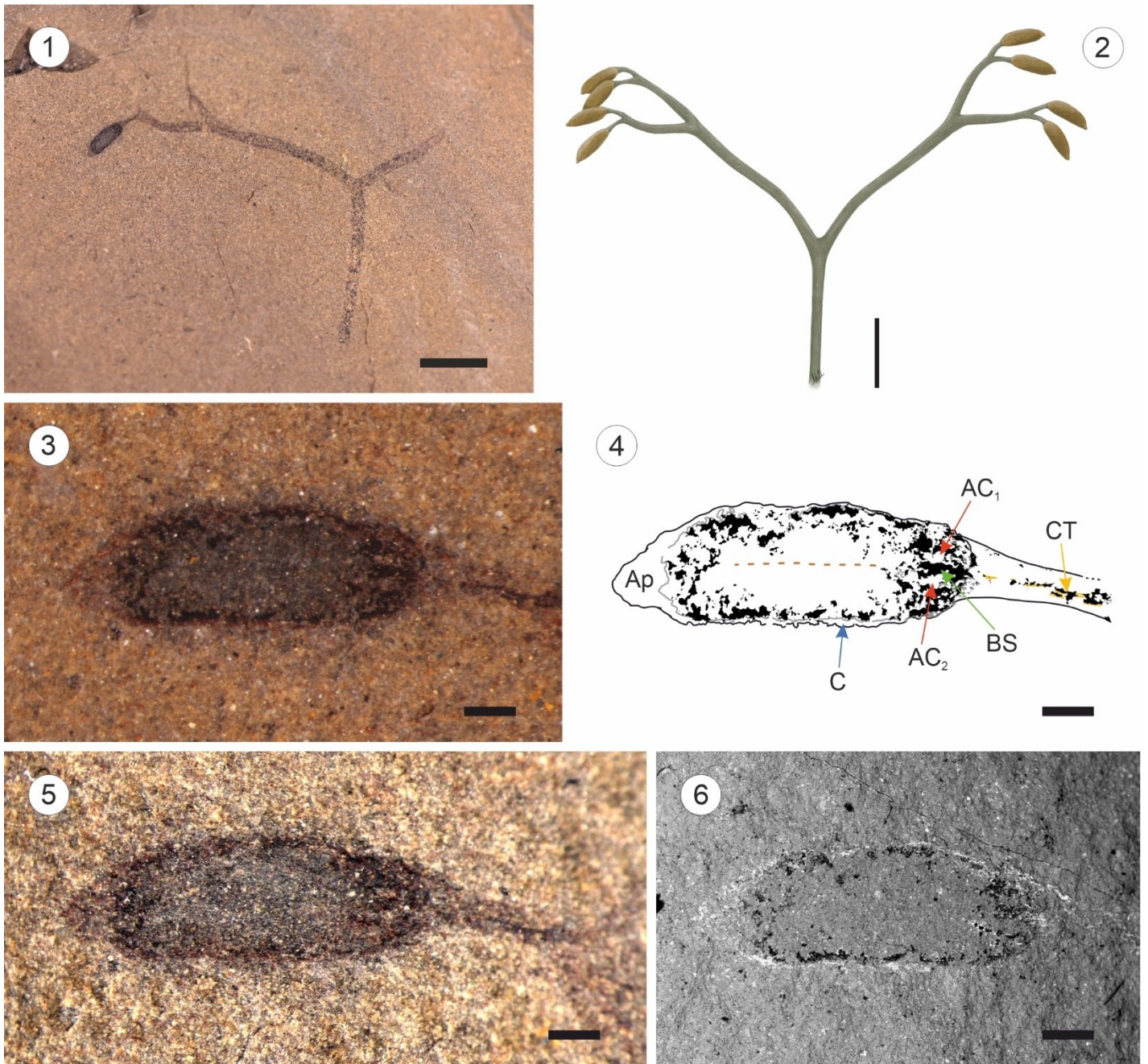


Fig. 7 *Capesporangites petrkraftii* (modified from Uhlířová et al, 2024a). 1 – the plant fossil in overall view (scale bar 5 mm), 2 – suggested reconstruction of the plant, 3–6 – detail of the sporangium (scale bars 0.5 mm), 3 – fossil immersed in ethanol, 4 – line drawing of the sporangium, structures within the sporangium distinguished in Uhlířová et al. (2024a), 5 – in stereomicroscope, 6 – in SEM, low vacuum.

5 Conclusions

The thesis is focused on the evolution and diversification of early land plants during the Silurian. It involved a practical part, processing detailed morphological descriptions of plants, as well as processing summary data for analyses of terrestrial plant evolution and subsequent interpretation.

The first output was a study using a multidisciplinary approach to link geochemical data, the fossil record and plant spore distribution analysis. The objective was to examine the impact of climatic changes on the development of embryophytes and contribute to a deeper understanding of the relationship between global ecosystem changes and the variability of early land plants. The findings indicate that global temperature fluctuations and changes in atmospheric oxygen concentrations had a significant impact on species diversity and the ecological strategies of different plant groups.

One of the key findings is the distinct response of cryptospores and trilete spores to climatic stressors. Cryptospores demonstrated considerable resilience to the glacial events in the Homerian, whereas the diversity of trilete spores was negatively affected. Following glaciation, a rapid expansion of plant diversity was documented, suggesting that warmer conditions facilitated accelerated evolution of terrestrial flora. A crucial factor in this process was the increasing atmospheric oxygen concentration, which by the end of the Silurian exceeded contemporary levels. These results confirm the close relationship between global ecosystem changes and embryophyte variability.

A detailed study of the fossil specimen *Tichavekia grandis* provided new insights into its morphology and probable ecological classification. Its six-branched dichotomous structure, leafless axes, and presence of terminal sporangia indicate similarities with rhyniophytoid Silurian plants. However, some unique features, such as short dichotomies and pronounced growth asymmetry, suggest that it might have been a more advanced taxon with a complex structure. The environmental context of this plant remains partially open—while some morphological characteristics support terrestrial growth, the narrow base of the axes and the possible need for structural support suggest that it may have grown in clusters or been at least partially submerged in an aquatic environment. A significant discovery was the isolation of trilete spores directly from the sporangium of the fossil plant *Tichavekia grandis*, confirming its classification as an embryophyte.

Another important contribution to the understanding of Silurian flora is the description of the newly established taxon *Capesporangites petrkraftii*, which is characterized by dichotomous branching and terminal sporangia. Although classified within the polysporangiophytes clade, certain structural features of its sporangium resemble characteristics of bryophytes, particularly in terms of capsule organization. This combination of features raises questions regarding the possible homoplastic development of these traits in different plant lineages.

Overall, this research highlights critical aspects of the early evolution of land vegetation, its diversity, and ecological strategies. The study of spores and fossil morphology not only allows for a more precise taxonomic classification of individual species but also enhances our understanding of the impact of climatic and ecological factors on their evolution. New discoveries, including the unique characteristics of *Tichavekia grandis* and *Capesporangites petrkraftii*, open further questions regarding phylogenetic relationships and adaptations of early land plants, which could be addressed through future research combining palaeobotanical, geochemical, and evolutionary data.

The significance of this work lies not only in the documentation of new species but also in the methodological approach that integrates multiple scientific disciplines. This approach provides a more comprehensive perspective on the dynamics of early plant communities and their responses to changing environments. Continued research in this field may further contribute to the understanding of early embryophyte ecological strategies and their adaptation to diverse climatic conditions. At the same time, it underscores the complex factors that influenced the transition of plants from aquatic to terrestrial environments, a key aspect of plant evolutionary biology. Future research should focus on a more detailed analysis of spores and other microstructural elements of fossil plants, which could yield further significant insights into their phylogenetic relationships and ecology.

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7 List of attachments

Appendix no. 1

Pšenička, J., Bek, J., Frýda, J., Žárský, V., Uhlířová, M. & Štorch, P. 2021. Dynamics of Silurian plants as response to climate changes. *Life* 11(9), 906. DOI: 10.3390/life11090906

Appendix no. 2

Uhlířová, M., Pšenička, J., Sakala, J. & Bek, J. 2022. A study of the large Silurian land plant *Tichavekia grandis* Pšenička et al. from the Požáry Formation (Czech Republic). *Review of Palaeobotany and Palynology* 298, 104587. DOI: 10.1016/j.revpalbo.2021.104587

Appendix no. 3

Bek, J., Uhlířová, M., Pšenička, J. & Sakala, J. 2024. Preliminary results on reproductive organs and *in situ* spores of an early land plant *Tichavekia grandis* Pšenička et al. from Přídolí (upper Silurian) of the Prague Basin, Czech Republic. *Palaeoworld*, 33(2), 299–306. DOI: 10.1016/j.palwor.2023.01.014

Appendix no. 4

Uhlířová, M., Pšenička, J. & Sakala, J. 2024a. New early land plant *Capesporangites petrkraftii* gen. et sp. nov. from the Silurian, Prague Basin, Czech Republic. *Review of Palaeobotany and Palynology* 322, 105048. DOI: 10.1016/j.revpalbo.2023.105048

Prohlášení školitele o podílu studenta na publikacích, které jsou součástí

doktorské práce

Jako školitel studentky Mgr. Moniky Uhlířové prohlašuji, že studentka se podílela na pracích, které byly předloženy jako součást její disertační práce, následujícím podílem:

I. Pšenička, J., Bek, J., Frýda, J., Žárský, V., **Uhlířová, M.** & Štorch, P. 2021. Dynamics of Silurian plants as response to climate changes. *Life 11(9)*, 906. DOI: 10.3390/life11090906

30% - sumarizace silurských rostlinných společenstevs, podíl na interpretaci výsledků a finalizaci a konečné úpravě rukopisu

II. **Uhlířová, M.**, Pšenička, J., Sakala, J. & Bek, J. 2022. A study of the large Silurian land plant *Tichavekia grandis* Pšenička et al. from the Požáry Formation (Czech Republic). *Review of Palaeobotany and Palynology* 298, 104587. DOI: 10.1016/j.revpalbo.2021.104587

80% - návrh hlavního textu, morfologický popis rostliny, úprava rodové a druhové diagnózy, tvorba obrázků a tabulek, paleoekologické interpretace, diskuse o systematickém zařazení, finalizace rukopisu

III. Bek, J., **Uhlířová, M.**, Pšenička, J. & Sakala, J. 2024. Preliminary results on reproductive organs and *in situ* spores of an early land plant *Tichavekia grandis* Pšenička et al. from Přídolí (upper Silurian) of the Prague Basin, Czech Republic. *Palaeoworld*, 33(2), 299–306. DOI: 10.1016/j.palwor.2023.01.014

50% - podíl na úvodu a závěru, popis sporangii rostliny, tvorba obrázků, podíl na konečné úpravě rukopisu.

IV. **Uhlířová, M.**, Pšenička, J. & Sakala, J. 2024a. New early land plant *Capesporangites petrkraftii* gen. et sp. nov. from the Silurian, Prague Basin, Czech Republic. *Review of Palaeobotany and Palynology* 322, 105048. DOI: 10.1016/j.revpalbo.2023.105048

80% - návrh hlavního textu, systematická část, morfologický popis rostliny, tvorba tabulek a obrázků, podíl na úvodu a závěru, interpretace, tvorba tabulek a kresba rekonstrukce rostliny, závěrečná úprava rukopisu

RNDr. Josef Pšenička, Ph.D.

vedoucí práce

The declaration of the supervisor

As the supervisor of Mgr. Monika Uhlířová I declare her participation in the studies that were submitted as a part of her Ph.D. thesis by the following contribution:

I. Pšenička, J., Bek, J., Frýda, J., Žárský, V., **Uhlířová, M.** & Štorch, P. 2021. Dynamics of Silurian plants as response to climate changes. *Life 11(9)*, 906. DOI: 10.3390/life11090906

30% - summary of Silurian plant assemblages, contribution to the interpretation of results and finalization and final editing of the manuscript

II. **Uhlířová, M.**, Pšenička, J., Sakala, J. & Bek, J. 2022. A study of the large Silurian land plant *Tichavekia grandis* Pšenička et al. from the Požáry Formation (Czech Republic). *Review of Palaeobotany and Palynology* 298, 104587. DOI: 10.1016/j.revpalbo.2021.104587

80% - main text draft, morphological description of the plant, emendation of genus and species diagnosis, creating figures and plates, paleoecological interpretations, discussion on systematic classification, finalization of the manuscript

III. Bek, J., **Uhlířová, M.**, Pšenička, J. & Sakala, J. 2024. Preliminary results on reproductive organs and *in situ* spores of an early land plant *Tichavekia grandis* Pšenička et al. from Přídolí (upper Silurian) of the Prague Basin, Czech Republic. *Palaeoworld*, 33(2), 299–306. DOI: 10.1016/j.palwor.2023.01.014

50% - contribution to the introduction and conclusion, description of reproductive organs, creation of figures, contribution to the final editing of the manuscript

IV. **Uhlířová, M.**, Pšenička, J. & Sakala, J. 2024a. New early land plant *Capesporangites petrkraftii* gen. et sp. nov. from the Silurian, Prague Basin, Czech Republic. *Review of Palaeobotany and Palynology* 322, 105048. DOI: 10.1016/j.revpalbo.2023.105048

80% - main text draft, systematic part, morphological description of the plant, creation of plates and figures, contribution to the introduction and conclusion, interpretation, creation of plates and plant reconstruction drawing, final editing of the manuscript

RNDr. Josef Pšenička, Ph.D.

The Ph.D. supervisor