

**Univerzita Karlova**  
**Přírodovědecká fakulta**

Studijní program: Geologie

Studijní obor: Geologie



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Cenomanská vegetace české křídové pánve

Cenomanian vegetation of the Bohemian Cretaceous Basin

Disertační práce

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Praha, 2024

**Charles University**

**Faculty of Science**

Study programme: Geology

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Doctoral thesis

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“Everything is leaf”

wrote Johann Wolfgang Goethe in 1787 in a letter to Charlotte von Stein.

## Abstrakt

Disertační práce popisuje, analyzuje a interpretuje rostlinné fosílie z paleoprostředí Perucko-korycanského souvrství.

Bylo popsáno olistění cykasu druhu *Nilssonia mirovanae* Čepičková et J.Kvaček včetně mikromorfologie jeho kutikuly. Druh vykazuje hluboce zanořené průduchy obklopené papilami, které přecházejí přes stomatální dvůrek. Průduchy jsou haplocheilní a jsou uspořádány do pásů. *Todziaphyllum saportanum* (Velen.) Čepičková et J.Kvaček je zubatý list se semikraspedodromní žilnatinou. Z důvodu chybějící zachované kutikuly bylo možné pouze makroskopické pozorování. *Ascarinophyllum pecinovense* Čepičková et J.Kvaček je list se zubatým okrajem, jehož abaxiální kutikula je pokryta vráskováním. Toto vráskování je náhodně orientované, pouze kolem průduchů je uspořádané radiálně. *A. pecinovense* je charakteristické kombinací několika druhů průduchů: laterocytními/laterocyklocytními, stephanocytními-bicyklickými, amphibrachyparacytními, méně často brachyparacytními a holoparacytními. Průduchy v některých případech mají z vnitřní strany na pólech ztlustěliny ve tvaru „T“. *Papillaephyllum labutae* Čepičková et J.Kvaček je list se zubatým okrajem. Vnější strana abaxiální kutikuly je velmi hustě pokryta velkými papilami. Průduchy se vyskytují dvojího typu: latero-cyklocytní a stephanocytní-bicyklické.

Pro zjišťování míry stresu z nedostatku sladké vody byla použita mikromorfologie kutikuly a izotopový signál rostlinných fosílií ( $\delta^{13}C$  v n-C29). Z lomu Pecínov byly k analýze použity listové fragmenty z jednotek U1-U5. Na základě paleobotanických, palynologických, paleoekologických, sedimentologických a geochemických dat byla rekonstruována následující paleoprostředí a rostlinná společenstva perucké flóry:

- 1) Vegetace slaných marší, společenstvo *Frenelopsis-Classopollis*
- 2) Vegetace příbřežních mokřadů, společenstvo *Cunninghamites-Taxodiaceapollenites*
- 3) Lužní vegetace meandrující řeky, společenstvo *Myrtophyllum-Perucipollis*
- 4) Lužní vegetace divočící řeky, společenstvo *Eucalyptolaurus-Mauldinia*
- 5) Vegetace svahů a sušších vyvýšených míst (kapradinovitá prairie s krytosemennými rostlinami a benetity) společenstvo *Zamites-Ephedripites*

Na příkladu lužních paleoprostředí byl zdokumentován proces ustupování nahosemenných rostlin ve prospěch rostlin krytosemenných. Diverzita a rozšíření krytosemenných rostlin albu a cenomanu jsou diskutovány v evropském kontextu.

## Abstract

Cenomanian plant fossils from the Peruc-Korycany Formation of the Bohemian Cretaceous Basin, Czech Republic are described, analysed and their palaeoenvironment is interpreted.

Cycad foliage *Nilssonia mirovanae* Čepičková et J.Kvaček including micromorphology of its cuticle was described. It shows deeply sunken stomatal apparatus surrounded by papillae overhanging the stomatal pit. The haplocheilic stomata are arranged in rows. *Todziaphyllum saportanum* (Velen.) Čepičková et J.Kvaček is a serrate-margined leaf with semicraspedodromous venation. Since the cuticle of this plant fossil has not been preserved, macro-observation is the only method available. *Ascarinophyllum pecinovense* Čepičková et J.Kvaček is a serrate-margined leaf, having an abaxial cuticle covered by striations, randomly oriented, and radially oriented striations around the stomata. This species shows a combination of laterocytic/laterocyclocytic, stephanocytic-bicyclic, amphibrachyparacytic, less frequently brachyparacytic and holoparacytic stomata, sometimes with T-shaped thickenings of the internal cuticle at the poles. *Papillaephyllum labutae* Čepičková et J.Kvaček is characterised by leaves with serrate margins. It shows an abaxial cuticle covered by large papillae. Its stomatal apparatus shows a combination of latero-cyclocytic and stephanocytic-bicyclic type of stomata.

Micromorphology of cuticle and its isotopic signal ( $\delta^{13}\text{C}$  in n-C<sub>29</sub>) was used for estimating water stress of the studied plant fossils. In the Pecínov quarry, selected plant fragments from units U1–U5 have been analysed. Palaeoenvironments and plant assemblages of the Peruc flora based on palaeobotany, palynology, palaeoecology, sedimentology and geochemistry analyses are reconstructed:

- 1) Saltmarsh vegetation, *Frenelopsis-Classopollis* assemblage
- 2) Coastal wetland vegetation, *Cunninghamites-Taxodiaceapollenites* assemblage
- 3) Meandering river floodplain vegetation, *Myrtophyllum-Perucipollis* assemblage
- 4) Braided river floodplain vegetation, *Eucalyptolaurus-Mauldinia* assemblage
- 5) Vegetation of slopes and drier upland areas (fern prairies with angiosperms and Bennettiales) *Zamites-Ephedripites* assemblages

Evidence of angiosperm dominance and gymnosperm decline in alluvial palaeoenvironments of the Peruc flora is documented. Distribution and dispersal of angiosperms in the Albian and Cenomanian are discussed in a European context.

## Poděkování

Mé největší díky patří mým rodičům, Petře Čepičkové a Vladimíru Čepičkovi, kteří mi nikdy neřekli, že něco nedokážu. Především jim je věnováno toto poděkování, v mluvě české, ve které mě vychovali. Dokončení práce by nebylo možné bez podpory a důvěry jejich, prarodičů a širší rodiny. Vytvářeli zázemí, které poskytovalo klid a velkou dávku motivace, s níž bylo snazší si udržet cíl ve chvílích zoufalství.

Mou velkou vděčnost a poděkování si zaslouží kamarádi, kolegové, spolužáci a známí, kteří poskytovali vše, co student potřebuje: společnost, kritický pohled, druhý názor, odreagování a velkou dávku srandy.

Velké poděkování patří mému školiteli, doc. RNDr. Jiřímu Kvačkovi, Csc. (Národní muzeum), který mě vedl jako konzultant od bakalářské práce a jako školitel od práce diplomové. Děkuji za jeho odborné vedení, pomoc a vstřícnost, konstruktivní diskusi, trpělivost a ledový klid ve vypjatých situacích. Taktéž děkuji svému konzultantovi doc. RNDr. Jakobovi Sakalovi, PhD. (Přírodovědecká fakulta Univerzity Karlovy) za jeho profesionalitu, vstřícnost a podporu. Své Alma mater děkuji za vědomosti, čas a příležitosti, kterých jsem se snažila maximálně využít.

V neposlední řadě děkuji Národnímu muzeu, které mi v čele s mým školitelem poskytlo práci, plně vybavené pracoviště vč. přístupu do depozitářů, prostor a stimulační prostředí pro psaní článků i disertační práce, děkuji zejména RNDr. Zuzaně Heřmanové, PhD., RNDr. Janě Bruthansové, PhD. a Ing. Lence Váchové. Za anglické korektury a hnidopišské dotazy děkuji Petru Danešovi.

Taktéž bych ráda poděkovala prof. dr. Jürgovi Schönenbergerovi a dr. Clémentovi Coiffardovi, kteří mi věnovali svůj čas a byli ochotni mě prostřednictvím několika stáží vzdělávat v oboru e-FLOWER a venation visualisation. Výzkum, kterého jsem byla součástí a díky němuž vznikly články přiložené k této práci, byl umožněn díky projektům GAČR GA-06134 a START/SCI/138.

Poslední a speciální poděkování patří mému příteli, Mgr. Jaroslavu Totuškoví, jenž mi po celou dobu věřil, podporoval mě a když mi bylo nejhůř, ke slovům podpory přidal tabulku čokolády.

## **Acknowledgements**

My deepest thanks go to my parents, Petra Čepičková and Vladimír Čepička, who always believed in me and continuously assured me that I could achieve my goals. The completion of this work would not have been possible without the unwavering support and trust from them, my grandparents and extended family. They provided a peaceful and motivating safe environment, making it easier to pursue my goals during challenging times.

I am profoundly grateful to my friends, colleagues, classmates, and acquaintances who provided everything a student needs: companionship, critical perspectives, second opinions, relief, and ample fun.

A special thank you to my supervisor, doc. RNDr. Jiří Kvaček, CSc. (National Museum Prague), who has been my consultant since my bachelor's thesis and supervisor throughout my master's thesis. I am grateful for his professional guidance, assistance, constructive discussions, patience, and composure under pressure. I also extend my gratitude to my consultant, doc. RNDr. Jakub Sakala, PhD (Faculty of Science, Charles University), for his professionalism, support, and helpfulness. I am grateful to my Alma mater that has given me invaluable knowledge, time, and opportunities, which I have endeavored to maximize.

Last but not least, I thank the National Museum for providing a fully equipped workplace under the leadership of my supervisor. This includes access to the depositories, space, and a stimulating environment for writing articles and my dissertation. Special thanks to RNDr. Zuzana Heřmanová, PhD., RNDr. Jana Bruthansová, PhD., and Ing. Lenka Váchová for their support. For English proofreading and detailed inquiries, I am grateful to Petr Daneš.

I would also like to express my gratitude to Prof. Dr. Jürg Schönenberger and Dr. Clément Coiffard, who generously offered their time and expertise in training me in e-FLOWER and venation visualisation through several internships. The research that contributed to the articles accompanying this thesis was supported by GACR projects GA-06134 and “Grant Schemes of the Charles University in Prague” (reg. no. CZ.02.2.69/0.0/0.0/19\_073/0016935) START/SCI/138.

A very special thanks to my boyfriend, Mgr. Jaroslav Totušek, who believed in me unconditionally, supported me through everything, and knew exactly how to lift my spirits with a bar of chocolate alongside his encouraging words, especially when I was at my lowest.



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## 1. Introduction

Plants are evolutionarily successful, highly diversified mostly photosynthetic eukaryotic organisms, which are widely distributed across all continents and even in oceans, particularly photic zones. Plants, *sensu strictissimo*, consist of algae, liverworts, hornworts, mosses, and vascular plants (Whittaker, 1969; Margulis, 1971). One of the best ways to study their evolution is the fossil record. In that record we find representatives of all these categories. But their appearance in the fossil record is largely dependent on the preservation potential of their bodies or body parts and on environmental conditions suitable for fossilisation. In general, the soft tissues of plants have less probability of being fossilised than tissues that are cutinised or lignified. Charcoalified and silicified plant remains usually pass through the taphonomic window. Plant fossils usually do not preserve entire, but only in fragments. Therefore, plant fossils are frequently described as separated fragments of: roots, stems, leaves, reproductive structures and pollen. All of these parts could get separate names being considered as fossil taxa, earlier known as morpho-taxa (Cleal and Thomas, 2010a,b).

The scientific discipline devoted to the study of such remains of plants in geological history is termed palaeobotany and is concerned with the identification and recovery of plant remains from geological settings, as well as their application to the biological reconstruction of historical ecosystems and the study of plant evolution as it relates to the evolution of life on Earth. Palaeobotany is essential to the study of plant evolution, and plays a significant role in reconstructing palaeoecological systems and past climates. The development of vegetation during Earth's geological evolution has responded to all changes of climate and fauna, and plate tectonics. On the other hand, vegetation has also been considered as a driver of events that have influenced and continue to influence the evolution of the biosphere. Plant evolution is divided into three stages, each of which has its own importance and order.

The Palaeophytic (mid-Ordovician – mid-Permian) (Gray, 1993) is characterised by evolution of Lycophytes and Euphyllophytes. Euphyllophytes are characterised by the production of "true leaves" with branching veins, a significant evolutionary advancement has made it possible to create more intricate and effective leaf structures. Two primary subgroups of the Euphyllophytes are the Monilophytes and the Lignophytes plants. Monilophytes are further divided into Polypodiopsida and Equisetopsida (Pryer et al., 2004; Rothwell and Nixon, 2006). The oldest known Lignophytes have been recovered from Devonian strata. The Carboniferous is a period of dominance of arborescent Lycophytes, Monilophytes and early Lignophytes (*Cordaites*).

The Mesophytic (mid-Permian – Lower Cretaceous) is a time period of dominance of gymnosperms. At the beginning of the Triassic there is a period of development of cycads, ginkgophytes, bennettites, conifers and gnetophytes. In the Lower Cretaceous, the first angiosperms appeared. In the end of Mesophytic, angiosperms soon after their appearance began to spread. The dominance of gymnosperms gradually receded (Kvaček et al., in press). An important period in the development of angiosperms was the Albian-Cenomanian (Friis et al., 2024). Because of their multiple genetic, morphological and physiological changes, angiosperms started to rapidly expand into numerous ecological niches (Friis et al., 2011; Feild et al., 2011; Coiffard et al., 2006; Kvaček et al., 2020; Kvaček et al., in press). In the 1970s, research on basal angiosperms was originally concentrated on the Early Cretaceous Potomac flora of the United States. They were termed "magnoliids" at the time, and were recognized by their pollen and leaves (Doyle, 1969; Muller, 1970; Doyle et al., 1975; Walker, 1976; Walker and Walker, 1984). Additional (and ongoing) research focused on the extant Chloranthaceae family, and has revealed several traits that may be ancestral, such as ascidiate carpels, simple flowers, huge anthers, and monosulcate and derived pollen. The reproductive structures of early angiosperms have also been researched in the form of mesofossils from the USA and Europe. The ANA group made up the basis of our present understanding of angiosperm phylogeny, which later evolved into the five angiosperm clades (Chloranthoids, Magnoliids, Monocots, Eudicots, and *Ceratophyllum*) (Friis et al., 1986, 1997, 1999, 2000, 2011, 2018; Hickey and Doyle, 1977; Soltis et al., 2018; Upchurch, 1984).

The Cretaceous in relation to plant evolution contains two periods (Mesophytic and Cenophytic), roughly corresponding to the stratigraphic Lower and Upper Cretaceous, and is a significant historical period in the evolution of the vascular land plants, lasting about 80 million years. The Upper Cretaceous saw a change of flora globally, in favour of the angiosperms, at the expense of gymnosperms. The Cenophytic period is considered to have begun during this gymnosperm-angiosperm transition. As a result of the Cenomanian transgression and the gradual shift in flora from Mesophytic to Cenophytic, various distinct palaeoenvironments were created. This thesis intends to reconstruct plant assemblages, based on fossil plant content coming from various palaeoenvironments of Cenomanian age to cover a typical example of plant diversification, from the Bohemian Cretaceous Basin. Material recovered from the Pecínov quarry that exposes fossil-bearing strata of the Peruc-Korycany Formation contains a number of very well-preserved plant organs and has enabled the revision of several previously described taxa.

Vegetative organs – particularly leaves – preserved as macrofossils, provide a considerable amount of information about the original plant, including its systematics and palaeoecology. Obtained data are integrated with datasets from other geoenvironmental disciplines such as geochemistry to create and interpret wider context of inter-relations of a chain of successive steps beginning with individual plants, through plant assemblages, local environment with the final aim to provide information on the plant diversification and related development of Earth's geo- and biosphere evolution in the crucial time of the Late Cretaceous.

Plant cuticle is a thin waxy layer consisting of hydrophobic biopolymers that are soluble in organic solvents. Its main functions are to limit uncontrolled transpiration (water evaporation) and provide protection against various abiotic stresses such as desiccation, UV radiation, high temperature and mechanical damage.

Changes in cuticle structure are a key adaptive mechanism by which plants respond to drought conditions (Bhanot et al., 2021). Under conditions of water stress, several changes of cuticle morphology usually develop. Increasing thickness of the cuticle is one of the most significant adaptations. By restricting the amount of water that can evaporate through the epidermis, a thicker cuticle effectively lowers water loss. This is especially helpful in situations where plants are exposed to high temperatures, particularly sunlight and high salinity. Cuticle thickness is highly variable among plant taxa, ranging from a few hundred nanometers to more than 10 micrometres (Kerstiens, 2016).

Although thicker cuticles effectively reduce water loss, they can also have an impact on gas exchange, particularly uptake of CO<sub>2</sub>, which is crucial for photosynthesis. Plants must therefore strike a balance between reducing transpiration loss and maintaining sufficient CO<sub>2</sub> uptake for photosynthetic processes. Plants have the ability to alter the cuticle's chemical composition, which includes increasing the wax concentration.

The cuticle is closely associated with the epidermal cells of the leaf, and any changes in the cuticle may be associated with physiological and morphological changes in these cells, including changes in their size, shape and function. There are ordinary and specialised (guard and subsidiary) cells of the epidermis, including stomata, papillae and trichome bases. The development of folds, wrinkles/striations, or ridges on the cuticle's surface is known as cuticle wrinkling. Striation can help the plant respond better to mechanical stress or changes in tissue volume. They can also improve the resistance of leaves to abrasion or pests, and increase their ability to capture and retain water and dew (Riglet et al., 2021).

Another ornamentation, papillae, are tiny projections that emerge from the cuticle's surface and frequently resemble bumps. They are often found on leaves, flowers, and other plant components, and their shapes range from rounded to angular. These structures may aid in increasing light interception by raising the leaf's surface resistance (Upchurch, 1984). In certain situations, they are connected to plant reproduction and can also help with defence against diseases and pests. In dry environments where rainwater is scarce, papillae on leaves can help plants trap dew and mist. Papillae can increase the surface roughness of the leaf, allowing dew to condense and remain on the leaf instead of evaporating or running off immediately (Stace, 1965; Yeats and Rose, 2013).

In terms of water management, cuticles play a crucial role. In arid environments, a thicker cuticle can significantly reduce water loss through transpiration. In extreme environments with limited water resources, this adaptation is essential for plant survival. In more humid conditions, since there is less chance of dehydration, a thinner cuticle might be adequate. An adaptive response to environmental demands is the balance between cuticle thickness and those demands.

The aim of this thesis is to expand knowledge about Cenomanian plants from the studied area using cuticle analysis supplemented by venation visualisation. The research is directly related to the master thesis "Paleoecological study of the Cretaceous extremophilic flora with emphasis on xerophytes", in which three new species were described: *Nilssonia mirovanae*, *Ascarinophyllum pecinovense* and *Papillaephyllum labutae*. These described species show characteristics of plants adapted to more extreme environments, which are discussed further in this thesis. Based on micromorphology of cuticles and isotopic signal ( $\delta^{13}\text{C}$  in  $n\text{-C}_{29}$ ) this thesis attempts to distinguish the studied plant fossils into possible groups of hygrophytes, mesophytes and xerophytes.

## **2. History of the research**

The most complete Cretaceous flora in our country and one of the best-preserved floras in Europe is the Cenomanian flora from the Peruc-Korycany Formation of the Bohemian Cretaceous Basin (Čech et al., 1980; Čech, 2011; Uličný and Špičáková, 1996; Uličný et al., 1997a; Uličný et al., 2009). This flora in the territory of the Czech Republic (in the Lands of the Bohemian Crown of the Empire of Austria) has been known for over 200 years.

The first Cenomanian plants that were studied in our territory were gymnosperms and ferns, because of their higher abundance in the fossil record. They were studied, along

with mostly Palaeozoic plants, by Kašpar Maria Sternberg (\*1761 – †1838). He described the conifer *Lycopodiolites lignitum* (Sternb.) J.Kvaček, later assigned to the genus *Cunninghamites* C.Presl in Sternb. (Sternberg, 1825; Kvaček J., 2000; Bosma et al., 2012), and the fern *Protopteris punctata* Sternb. (Sternberg, 1820; Greguš et al., 2013). Later the description of Cretaceous plants was continued by Karel B. Presl (\*1794 - †1852). Among others, he described *Cunninghamites oxycedrus* C.Presl in Sternb. and *Dammarites albens* C.Presl in Sternb. (Presl in Sternberg, 1838; Hlušík, 1977). The study of Czech Cretaceous plants was continued by Josef A. Corda (\*1809 – †1849), who dealt mainly with ferns and gymnosperms. Corda mentions angiosperms plants as an important part of the Peruc Member, and noted them in his work (Corda, 1845; Corda in Reuss, 1846), although most of the material he had access to was in the form of fragments.

The Bohemian Cretaceous was further explored by Oswald Heer (\*1809 – †1883), who concentrated his interest mainly on study of the Maletín sandstone in Moravia. There he described 14 new species (Heer, 1869). Heer's findings were subsequently followed up by Josef Velenovský. A revision of this flora was published by Greguš (Greguš and Kvaček J., 2015).

At the same time, Karl Feistmantel (\*1819 – †1885) and his son Ottokar (\*1848 – †1891) were active in the field of palaeobotany (Feistmantel K., 1881, 1885). O. Feistmantel made himself famous by studying flora from Gondwana of India (Feistmantel O., 1880, 1881, 1882). K. Feistmantel focused his interests on the Bohemian Late Paleozoic in the Slaný-Rakovník Basin. Although his main interest was in Carboniferous plants, he described the Cretaceous plant *Sclerophyllum alatum* K.Feistm., which he erroneously considered to be Carboniferous. This plant was later properly identified by Velenovský as Cretaceous, and described and given the name *Frenelopsis bohemica* (Velenovský, 1888). According to the priority rule, it is now referred to as *Frenelopsis alata* (K.Feistm.) Erw.Knobloch (Knobloch, 1971).

The Peruc Member began to be studied in detail in the second half of the 19<sup>th</sup> century by Josef Velenovský (\*1858 – †1949), professor of botany at Charles University in Prague. Velenovský (Velenovský, 1882, 1885, 1888) published the first comprehensive descriptions of Cretaceous flora, including their taxonomic classification (Velenovský, 1889). Although Velenovský did not have available material from Pecínov near Nové Strašecí, from where comes the major part of the material studied in the present thesis, he had mentioned the finding of the species *Tempskya varians* Corda from Rynholec, which is located nearby.

It was Antonín Frič who attracted O. Feistmantel and J. Velenovský to Cretaceous flora. Frič obtained fossil plants from the Peruc Member as early as 1865 mainly by buying them from quarrymen. He began his activities in documentation of the Bohemian Cretaceous, being focused mainly on Cretaceous fauna. For the next few decades, he collected plant fossils with Josef Velenovský and later with Edvín Bayer (\*1862 – †1927). Later, when J. Velenovský left investigations in palaeobotany for some time to focus on botany and mycology, it was E. Bayer who began working on the Peruc flora and described new Cenomanian plants (Bayer, 1899). Bayer compiled all the knowledge on the Peruc flora, firstly in a German edition: *Studien im Gebiete der Böhmisches Kreideformation – Perucer Schichten* (Frič and Bayer, 1901), recently translated to the Czech language: *Studie křídového útvaru českého – Perucké vrstvy* (Frič and Bayer, 1903). This publication also describes the landscape around Rynholec, specifically the steep hillside near an abandoned mine and tunnel, where a large number of remains of *Tempskya varians* Corda tree fern remains were found (Velenovský, 1888). Extensive mining began there in the second half of the 20<sup>th</sup> century (Holý, 1962) and continues to this day. J. Velenovský resumed his studies of Cretaceous plants, newly aided by his younger colleague Ladislav Viniklár (\*1898 – †1933). Their collaboration gave rise to a large four-part work on Cenomanian plants, which represent two decades of active collecting and study (Velenovský and Viniklár, 1926, 1927a, 1929, 1931).

## **2.1. Studies on Cretaceous plant macro-remains in Europe**

The study of fossil leaves was initially limited to macroscopic observation, and can be traced back to the 19<sup>th</sup> century. The first scientific descriptions of Cretaceous fossil plants were written by Oswald Heer, Gaston de Saporta, Constantin von Ettingshausen and Josef Velenovský. Oswald Heer (\*1809 – †1883) was a Swiss geologist and naturalist, one of the first pioneers of palaeobotany, who focused mostly on Miocene flora, but worked also on Cretaceous plants in Moravia (1869), Germany (Heer, 1871) and Portugal (Heer, 1881). Gaston de Saporta (\*1823 – †1895) was a French palaeobotanist and a supporter of Charles Darwin's theory of evolution. He worked on French Jurassic and Cretaceous floras (de Saporta, 1872, 1875, 1884), and on Portuguese Cretaceous flora (de Saporta, 1894). Constantin von Ettingshausen (\*1826 – †1897) was an Austrian botanist and palaeobotanist. His work mainly dealt with the Tertiary flora of Europe and the fossil floras of Australia and New Zealand. He also published on Cretaceous flora of Austria (Ettingshausen, 1852). Together with Maria Debey (\*1817 – †1884), they published a two-volume monograph on Maastrichtian flora (Debey and Ettingshausen, 1859a,b). Cretaceous plants were also studied by the influential Austrian palaeobotanist Franz Unger (\*1800 – †1870), an author of several palaeobotanical

synopses (Unger, 1842, 1850, 1867). Naming of Cretaceous plants was initially based on the pattern of recent species (Unger, 1852), but this was later judged to be inappropriate (Nathorst, 1888; Velenovský, 1889). However, the original method has not completely disappeared, and was still often applied in the 20<sup>th</sup> century (Hollick, 1936).

The study of Cretaceous plants has progressed through macromorphological descriptions and leaf architecture in general by Ettingshausen (1861), but Hickey's classification (1973) was the one that was accepted by most of the scientific community. This concept was subsequently built upon by Hickey and Wolfe (1975) and Wolfe et al. (1975), whose work also uncovered additional phylogenetic possibilities. Currently, the "Manual of Leaf Architecture" by Ellis et al. (2009) is the most widely used terminology for describing leaf architecture. Combining this manual with the MORPHYLL database developed by Traiser et al. (2018) gives us the most comprehensive method currently available for complete description of leaves. With the involvement of chemical processes, it became possible to extend the knowledge of leaves to include a micromorphological component.

## **2.2. History of cuticle analysis on a global scale**

The history of research on plant cuticles dates back to the first half of the 19<sup>th</sup> century, when Adolphe-Théodore Brongniart (\*1801 - †1876) prepared the first cuticle of recent angiosperm plants in 1834 (Brongniart, 1834). In the 1850s, the methodology of cuticle analysis was further developed. Micromorphology of fossil leaves, e.g. epidermal structures and cuticle perforations were observed by Philipp Wessel and Carl O. Weber (1855) from Tertiary lignite. Johann G. Bornemann (1856) subsequently made additional observations of similar material. Wessel, Weber and Bornemann realised that they could use micromorphology to enhance taxonomic classification. Alfred G. Nathorst (\*1850 - †1921) and Albert C. Seward (\*1863 - †1941) further developed their work (Nathorst, 1908; Seward, 1926).

In 1855, cuticle analysis was improved by the use of the Schulze's reagent, named after its discoverer (Schulze, 1855). However, it was not until the 20<sup>th</sup> century that cuticle analysis began to be used on a larger scale, not only for angiosperms, but especially for gymnosperms.

Cuticle analysis was greatly further developed by Carl R. Florin (\*1894 - †1965), a Swedish botanist who studied mainly gymnosperms. Florin significantly advanced the use of fossil cuticle studies, especially stomatal morphology, to identify fossil gymnosperms (Florin, 1931, 1944).



Worldwide, many scientists are currently working in the field of cuticle analysis. In the 1990s, Hans Kerp, along with his students and colleagues were working on further development of cuticle analysis (Kerp, 1990; Kerp and Krings, 1999). Howell and Gossmann (2022) recently published a paper detailing the methodology of cuticle analysis on delicate cuticles of fossil conifers; in particular, the authors modified the section on bleaching.

### 2.3. History of cuticle analysis in Czechia

Cuticle analysis was historically first performed in Czechia by Edvín Bayer, who started his first preparations in 1893 on material from collections of the National Museum. Through cuticle analysis he attempted to determine some Cenomanian gymnosperms (*Frenelopsis*) (Bayer, 1914a). Bayer used cold maceration of the cuticles from his specimens in concentrated nitric acid with a concentrated solution of calcium hypochlorite  $\text{Ca}(\text{ClO})_2$ , which he had discovered rendered the cuticle fossils translucent. He then stained them with fuchsin and cyanine, to emphasise contrast in the structures he was studying. This staining was also carried out on recent material (Bayer, 1921).

Macromorphological observation was unable to determine this, but Němejc's micromorphological observations of cuticles were detailed enough to confirm that the two species were truly the same. Instead of copying Bayer's method of nitric acid and calcium hypochlorite, Němejc processed his cuticle by means of Schulze's reagent, after which he soaked the specimen in water diluted with ammonia. His subsequent examination of cuticles and stomata from samples of the two species, he was able to show that *Sclerophyllum alatum* and *Frenelopsis bohémica* are identical species (Němejc, 1926). However, a new combination (i.e., *Frenelopsis alata* (K. Feistm.) Erw. Knobloch) was published many years later by Knobloch (1971).

Study of *Eucalyptus geinitzii* cuticle was carried out by Blanka Pacltová (\*1928 – †2019) (Pacltová 1961). Cretaceous gymnosperm cuticle was further studied by Antonín Hlušík (\*1946 – †2016). Hlušík devoted his attention to the cuticle analysis of the species *Frenelopsis alata*, *Dammarites albens* and the order Ginkgoales (Hlušík 1972, 1974a, 1976, 1977a,b).

Study of Peruc Member fossil plants was also undertaken by Ervín (Erwin) Knobloch (\*1934 – †2004), who additionally studied lesser-known species of ferns, gymnosperms and angiosperms, especially species of the genus *Dicotylophyllum* (Knobloch 1999).

From the 1970s, Zlatko Kvaček (\*1937 – †2020), who specialised in Tertiary plants, was involved in cuticle analysis at the world level. Kvaček (1983) classified the Cenomanian plants of the Bohemian Cretaceous Basin into several groups based on the characteristics of their leaf pattern and cuticles. These were leaf shape, venation, and especially the type of stomata and trichome bases (Kvaček Z., 1983, 1992). His work on Cretaceous flora was further developed by his son Jiří Kvaček. He worked with genera: *Konijnenburgia*, *Schizaeopsis*, *Sagenopteris*, *Jirusia*, *Pseudoctenis*, *Mesenea*, *Microzamia*, *Bayeriteca*, *Nilssoniopteris*, *Zamites*, *Anomozamites*, *Frenelopsis*, *Alvinia*, *Sphenolepis*, *Cunninghamites*, *Quasisequoia*, *Brachyphyllum*, *Pseudoasterophyllites* and *Ettingshausenia* (Kvaček J., 1995, 1997a,b, 1999, 2000, 2007, 2008, 2022; Knobloch and Kvaček, 1997; Kvaček and Váchová, 2006; Kvaček et al., 2016).

### 3. Geological settings

The Bohemian Cretaceous Basin (BCB) was defined by Čech et al. (1980) and Čech (2011); it is located in the Bohemian Massif, Central Europe. The BCB was formed from the Cenomanian to the Campanian and was infilled by Upper Cretaceous freshwater, brackish and marine sediments. The BCB was formed by reactivation of the main fault zones of the Variscan basement underlying the Bohemian Massif in combination with elements of global Cenomanian transgression, probably during the mid-Cretaceous. River systems and the Cenomanian landscape were inundated by transgressions from the south-east Tethyan realm and the north Boreal realm (Niebuhr and Wilmsen, 2023; Špičáková and Uličný, 2014). The Cenomanian transgression into the Bohemian Cretaceous Basin is divided into five units, designated CEN 1 to CEN 5 (6), starting from early Early Cenomanian and terminating at Cenomanian-Turonian Boundary. These units represent successive phases of geological and sedimentary evolution during the Cenomanian (Uličný et al., 2009; Voigt et al., 2021; Niebuhr and Wilmsen, 2023). Additionally, Uličný et al (2009) described three main palaeo-drainage systems; two systems drained to the N – NW and one to the SE.

The Peruc-Korycany Formation (Čech et al., 1980) is the basal-most layer over most of the BCB. Its stratigraphic position (Upper Cenomanian) is determined by the presence of the ammonite *Calycoceras naviculare* (Mantell) of the *Metoicoceras geslinianum* Zone. These index fossils are found in marine levels directly overlying the formation's freshwater deposits (Košťák et al., 2018).

Peruc-Korycany Formation consists of the Peruc Member, comprising fluvial and brackish sediments, as well as the Korycany and Pecínov members, which are of marine origin. The Peruc Member was first described by Krejčí in 1870. He named it after the village of Peruc, north of Slaný, where he had found an outcrop showing Cretaceous sandstone containing impressions of ferns (*Pecopteris*) and twigs of coniferous plants (*Widdringtonites* and *Cunninghamites*), as well as shells of river bivalves. Based on these findings, Krejčí (1870) identified these layers as freshwater. The name Peruc Member has been in use since then (Čech et al. 1980). The Peruc-Korycany Formation is diachronous throughout the Bohemian Cretaceous Basin (Uličný et al., 1997, 2009). As a result of long-term erosion during the Triassic to Lower Cretaceous, the Palaeozoic bedrock was subsequently denuded. In Cenomanian marine transgression gradually flooded the river valleys and formed estuaries (Kvaček et al., 2006; Uličný et al., 2009).

The best-preserved site of the Peruc-Korycany Formation is the active quarry Pecínov in Central Bohemia. It is the open-pit mine owned by České lupkové závody a.s., located 60 km west of Prague, in continuous operation since 1952. The quarry has exposed an exceptionally illustrative profile of the Peruc-Korycany Formation (Fig. 2).

Based on samples from boreholes, Holý (1962) released a preliminary study on fossil plants from the Pecínov region. E. Knobloch later gathered a vast quantity of information in the 1960s and 1970s (Knobloch, 1969a, c). These holdings are kept in the Český geologický ústav, National Museum, Dresden, Staatliches Museum der Geologie, and Museum Berlin. S. Opluštil collected there later, in 1986, and since 1991, J. Kvaček has been collecting there continuously.

Uličný and Špičáková (1996) described five para-sequences based on sequence stratigraphy and additional sedimentological studies at the Pecínov quarry in the Peruc-Korycany Formation. In their later study, which also included plant fossils and palynology units were used instead of parasequences (Uličný et al., 1997). The units are interpreted to have a periodicity of about 100-120 thousand years; during that time a gradual rise of sea level can be observed. It is concluded that the territory of Central Europe was gradually flooded during the Cenomanian by the Tethys Sea from the southeast and the Boreal Sea from the northwest. In the course of this transgression, several types of environments evolved in the peripheral parts of the Bohemian Massif landmass. Remains of all these environments have been found in most of the currently known localities of the Peruc-Korycany Formation. These environments were influenced by depth of groundwater, fluctuation of sea level, relief of the landscape, and other

physical and chemical conditions. Several types of environments were distinguished: anastomosing river (Unit 1), tidally influenced river (Unit 2), supratidal marsh (Unit 3), tidal channel environment (Unit 4) and estuarine environment (Unit 5) (Uličný et al., 1997).

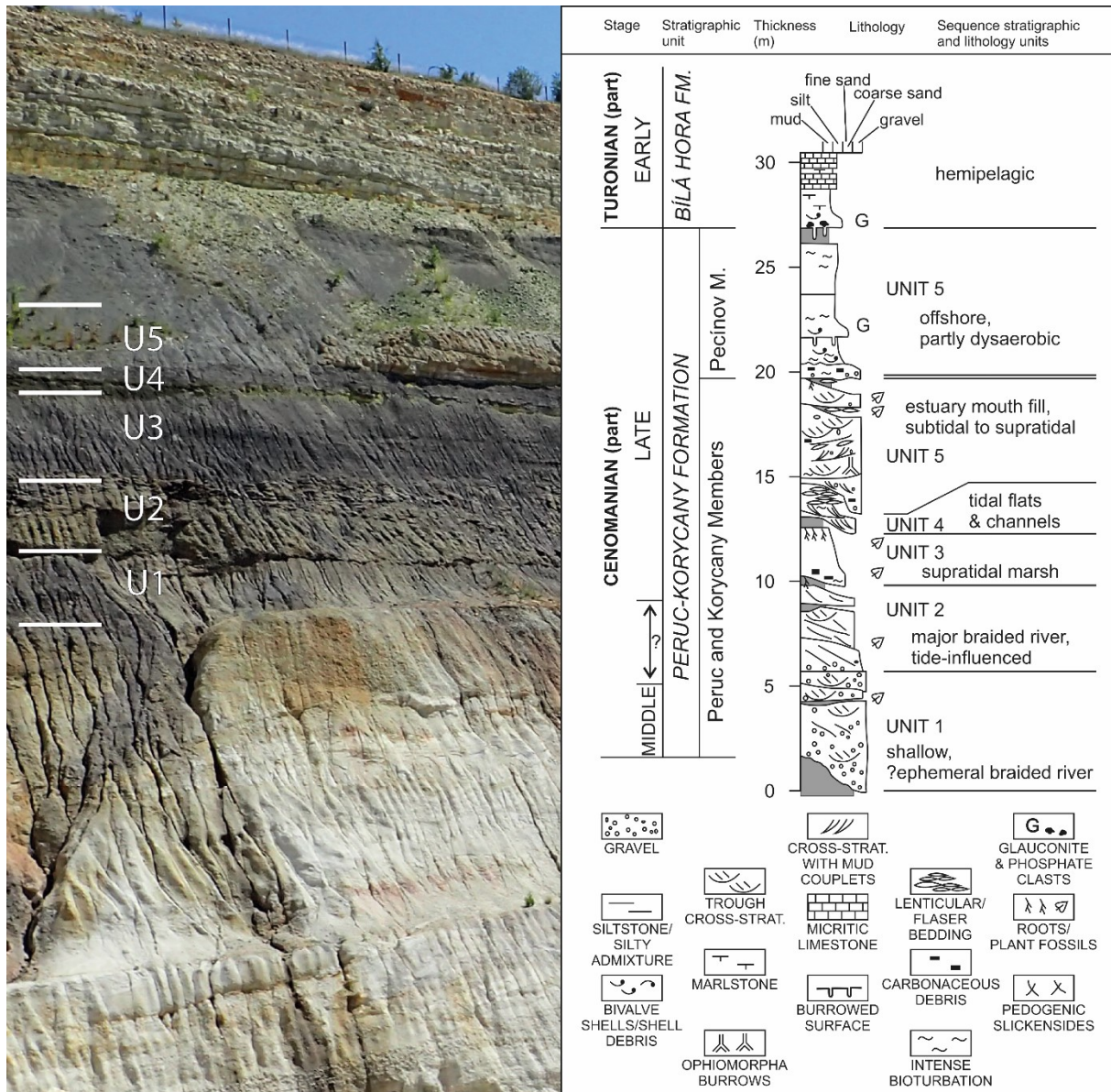


Fig.1 - Stratigraphy of the Peruc-Korycany Formation. Adapted from Uličný et al. 1997.

There are many localities in the Czech Republic where outcrops of the Peruc-Korycany Formation are found, e.g. Lipenec, Touchovice, Kounov, Slaný, Otruby u Slaného, Kladno. In or close to Prague, there are also such localities, e.g. Malá Chuchle, Slivenec, Hloubětín, Hutě, Nehvizdy, Vyšehořovice. Most of the sites known to us were discovered and described by A. Frič, J. Velenovský and E. Bayer. However, most of them have been repurposed and are no longer in a fit state for easy and accessible collecting.

Although research is still underway on finds from the original sites, the most active collecting is currently taking place at the Pecínov quarry, followed by collections from Kamenná Panna, Brník, Praha - Hloubětín.

The Horoušany quarry, often referred to as the "Kamenná Panna" quarry, is located along the eastern erosional boundary of the central part of the BCB, approximately 12 km east of Prague. In the 1960s, Knobloch (1969c) collected in the clay pit. Since 1993, J. Kvaček has been collecting there. The Lower to Middle, and maybe the lower part of the Upper Cenomanian, are represented in the sequence of strata revealed in the quarry, which goes from bottom to top as fluvial, estuary, and open-marine deposits. Freshwater, marine, and sea-influenced sediments are visible in a 25 m high section at the Kamenná Panna pit. Špičáková and Uličný (1996) separated the facies succession of the Horoušany quarries distinguishing nine genetic sequences out of them seven are products of terrestrial sedimentation (CEN1, CEN2a,b, CEN 3a,b, CEN4a,b). The primary fossiliferous horizons are located in units CEN 2-3. Unit CEN 2 is characterised as predominantly fluvial, valley-filling strata and CEN 3 is defined as estuaries often flooded by tide.

CEN 2a interpreted as laterally migrating fluvial channel by Špičáková and Uličný (2009) contains rich mudstone lenses with ferns (*Schizaeopsis ekrtii* J.Kvaček, Dašková et Pátová, *Anemia* sp.) and angiosperms (*Myrtophyllum geinitzii* Heer in Saporta, *Araliphyllum kowalewskianum* (Velen.) Velen., whereas conglomerates and sandstones make up the majority of the lithologies. Kvaček et al. (in press.) define this unit as PE 3 - alluvial plain of meandering river.

CEN2b and CEN2c are products of coastal plain sedimentation with coastal wetland flora (*Cunninghamites lignitum* (Sternb.) J.Kvaček, *Elatocladus velenovskyi* J.Kvaček). CEN2b consists of mudstones, sandy siltstones, and isolated sandstone bodies. Špičáková and Uličný (2014) interpret this unit as a wet coast-proximal floodplain. Kvaček et al. (in press) define unit CEN 2b as PE 2 - coastal wetland. CEN2c consists mostly of grey sandstones and was interpreted by Špičáková and Uličný (2014) as a tide-influenced river. Kvaček et al. (in press.) do not correlate to specific PE unit due to lack of plant fossils. CEN 3a,b consists of sandstones, mudstones, and siltstones containing phytodebris. There are numerous fragments of allochthonous elements (angiosperms) in channel deposits. The taphocoenosis mainly shows palaeoenvironment of supratidal salt marsh with dominant elements *Frenelopsis alata*, *Eretmophyllum obtusum* (Velen.) J.Kvaček, *Cunninghamites lignitum* (Špičáková and Uličný, 2014). According to Kvaček et al. (in press.), units CEN3a,b are defined as PE 1 - saltmarshes.

Located east of the village of Brník there is the Keramost a.s. mining company's Brník open pit, which was opened in the 1970s. Since then, it has been continuously worked. In the 1970s. Numerous plant fossils were collected by E. Knobloch in 1970-1985, later J. Kvaček collected there (1990-2020) gathering leaf compressions and impressions there. Angiosperms and ferns are present in the fossil plant assemblages in high abundance, whereas conifers are largely absent. Kvaček et al. (in press.) assign the environment from this site to two environments, namely PE 3 - alluvial plain of meandering river and PE 4 - alluvial plain of braided river (correlated to CEN2b in the Horoušany quarry).

The locality Praha, Hloubětín-Hutě was firstly studied by Velenovský in the 1880s. The geological profile of Hloubětín-Hutě location documents the development of terrestrial palaeoenvironments within the Peruc-Korycany Formation. Claystones that are brown and black contain fossils. In addition, there are sandstones that are white, grey and black that include some coal particles. Velenovský collected here, e.g. *Cunninghamites oxycedrus*, *Aralia daphnophyllum* Velen., *Proteophyllum araliopsis* and *Eucalyptolaurus* sp. (Hlušík, 1974, 1985; Kvaček J., 1992; Kvaček Z., 1992)

In 2013, the site was visited again and two drill cores PV1 and PV2 were drilled successively in 2013/2014 and 2015 and are housed in the National Museum Prague. Dispersion samples have been recovered from the drill cores, and the cores continue to be studied, both macro and palynological (pers.comm. J. Kvaček).

The locality Praha, Hloubětín- Cihelna V Bažantnici, a more commonly known locality than Hloubětín-Hutě, was declared a natural monument in 1988, due to its importance for geology and palaeontology. In the bedrock, there is shale from the Bohdalec Formation (Upper Ordovician), followed by layers of sandstone to siltstone. This is followed by a refinement of the material to laminated claystones and dusty claystones with charcoal residues. Above the claystones are kaolinic sandstones.

In total, four terrestrial environments can be reconstructed on the Praha - Hloubětín site (including Hutě and Cihelna V Bažantnici), beginning with brackish and progressing inland: saltmarshes, wetlands, alluvial plains of braided rivers, and drier upland with slopes. Saltmarshes are defined by the presence of brackish and seawater that significantly affected the environment, evidenced here by the halophytic *Frenelopsis alata* and its pollen, *Classopollis classoides*. Next inland are wetlands along the coast, estuarine habitats influenced by freshwater streams and coastal swamps, wetlands are typified by pollen genera and *Cunninghamites*, *Elatocladus*, and *Quasisequoia* species. Wetland is followed by alluvial plains of braided rivers,

an environment with streams and rivers of varying sizes, and subject to frequent floods. Angiosperm species *Mauldinia bohémica* Eklund et J. Kvaček, *Eucalyptolaurus* sp. were common. Among autochthonous plant fossils from fluvial sediment, there are fragments of plant fossils coming from slopes and drier upland. It is composed of fragmentary preserved leaves *Dicotylophyllum araliopsis* (Velen. et Vin.) Knobl., reproductive structures *Zlatkocarpus pragensis* (J.Kvaček et H.Eklund) J.Kvaček et E.M.Friis and other dicot leaves.

The Praha - Malá Chuchle mine was utilised to extract fireclay for making stoneware. The locality fell into disuse after mining there stopped. Situated in the Bohemian Massif's freshwater Cenomanian, Praha - Malá Chuchle is one of the oldest locations. The plant fossils from this site come from fluvial sediments of a smaller river originally bounded by Devonian limestone rock walls (Herman et al., 2002). It has produced a characteristic fossil plant assemblage, with *Zamites bayeri* Kvaček (Knobloch and Kvaček, 1997), *Nilssonia bohémica* Velen., and *Sagenopteris variabilis* (Velen.) Velen. (Kvaček, 1999) being prominent (Frič and Bayer, 1901, 1903; Velenovský and Viniklár, 1931).

The Vyšehořovice (earlier Vyšerovice) locality was described by Velenovský (1882, 83, 84, 85a, 85b). Frič hired collectors who collected a substantial number of fossilised plants in the 1870s. In addition to leaves, there are fossils of twigs, fruits, flowers, and ovuliferous cones. The fossil plant assemblage found in the classical outcrops is primarily composed of angiosperms, such as *Ettingshausenia bohémica* (Velen.) J.Kvaček et Váchová and *Araliphyllum kowalewskianum* (Sap. et Mar.) Velen., *Aralia daphnophyllum*, *Myrtophyllum geinitzii* and *Ettingshausenia* sp. In addition to the angiosperms, a lesser number of gymnosperms are also present, such as *Widdringtonia reichii* (Ettingsh.) Velen., and the cycad *Microzamia gibba* (Reuss) Corda. Fern-like plants are extremely uncommon in this area. Over these strata is a layer of charcoal plant remains, including wood, branches, and fruits. Knobloch and Hlušík collected from a clay pit on the eastern edge of the village of Vyšehořovice throughout the 1960s and 1970s. The site is currently listed as a natural monument.

Though the most significant locations have been highlighted, this is not a complete list; other, lesser-known, or now-abandoned locations include Lipenec, Touchovice, Kounov, Slaný, Podlešín, Otruby, Kladno, Motyčín, Slivenec, Zadní Kopanina, Břežany II, Černíky, Kounice, Perálec, Bohdánkov, Brtev, Lanšperk, Mělník nad Sázavou.

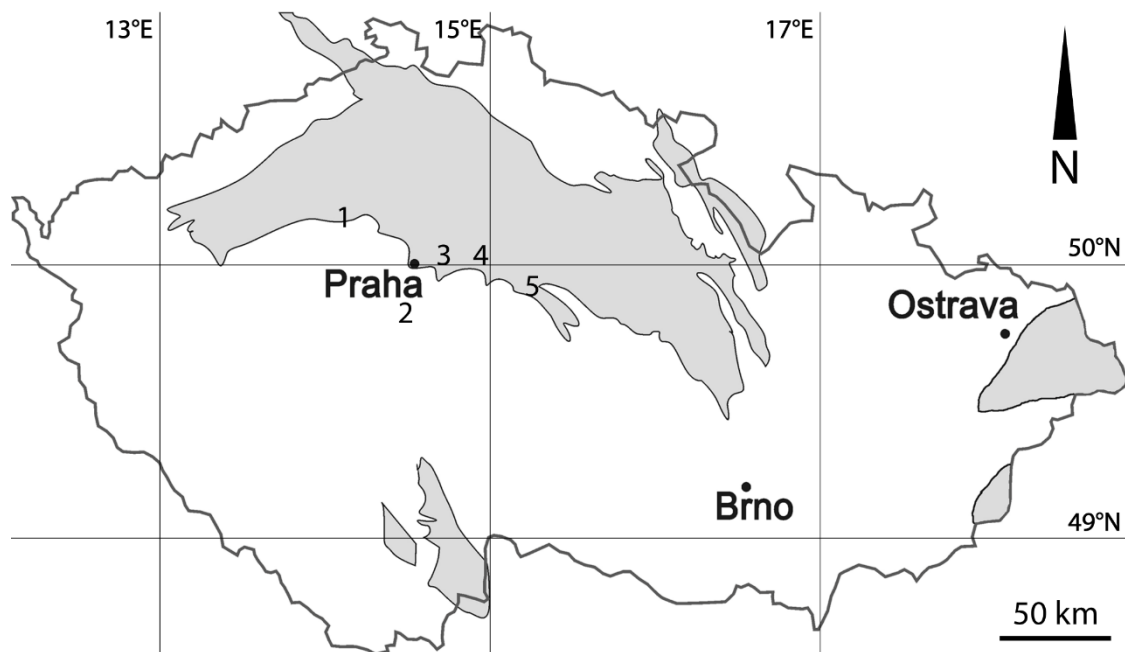


Fig.2 - Map of localities. 1 – Pecínov; 2 – Praha - Malá Chuchle; 3 – Praha - Hloubětín; 4 – Vyšehořovice, Horoušany; 5 – Brník.

#### 4. Comparison

##### 4.1. Comparison of Czech Cenomanian flora with other Cenomanian floras

Regarding palaeoclimate and diversity, Cenomanian of the USA are similar to Cenomanian flora in Bohemian Cretaceous Basin. The best-preserved floras come from the Dakota Formation, the Cedar Mountain Formation, the Tuscaloosa Formation, the Potomac Group (Mauldin Flora) and Woodbine Formation.

One of the longest-studied Cretaceous floras is that flora of the Dakota Formation (Lesquereux, 1891; Upchurch and Dilcher, 1991; Kvaček and Dilcher, 2000; Wang et al., 2011; Wang and Dilcher, 2018; Manchester et al., 2018). The Dakota Formation is of Albian-Cenomanian age and comprises rich fossil flora. The Dakota and Bohemian floras have some species in common, but there are also differences. Common elements are *Gleichenia delicatula* Heer, *Brachyphyllum squamosum* (Velen.) Palibin - *Brachyphyllum crassum* (Lesq.) Lesq., and angiosperms *Mauldinia bohémica* and *Platanus velenovskiana* Krasser.

From both the Peruc-Korycany and the Dakota floras, there is a number of major plant assemblages that are recognized and utilised for additional comparisons, and provide



information about entire habitats. While upland vegetational features are also present in the Peruc-Korycany Formation, the two primary environmental types that occur in both places are the freshwater wetland (fluviolacustrinal) and coastal environments.

Out of the all compared sites, the Dakota Formation yielded fossil plant material most comparable to the species mentioned in this thesis (Čepičková and Kvaček, 2022, 2023). For the leaf fossils from some localities, comparisons are still only possible at the macroscopic level, but some could be analysed in greater detail. For instance, some species were analysed using cuticle analysis, which greatly increased the accuracy of comparison, e.g. *Longstrethia varidentata* Upchurch et Dilcher from the Dakota Formation was found to have similar cuticle pattern to *Ascarinophyllum pecinovense* from the Peruc-Korycany Formation, allowing to conclude that they are likely related.

The macroscopic record of the Cedar Mountain Formation (Arens and Harris, 2015) in the Western Interior Basin consists of 18 morphotypes of dicotyledonous angiosperms. The record contains 4 serrate leaves with various differences that are comparable to the species in this thesis.

The Tuscaloosa Formation of the U.S. Gulf Coast (Berry, 1919; Ufnar, 2007; Zhang et al., 2020) is well-described from an isotopic and reproductive organ point of view. From this locality more than 150 described species are known, but mostly not revised.

The Mauldin Flora from the Cenomanian Elk Neck beds of the Potomac Group (Drinnan et al., 1990) consists mostly of flowers and inflorescences (e.g. *Mauldinia mirabilis* Drinnan, Crane, Friis et Pedersen), which are quite similar to flowers and inflorescences of *Mauldinia bohemica* Eklund et J.Kvaček from the Peruc-Korycany Formation, while leaves are not so similar (Drinnan et al., 1990). The Woodbine Formation of the East Texas Basin (Berry, 1922; MacNeal, 1958) was compared by Berry with the European Upper Cretaceous flora. Berry (1922) briefly compared Woodbine and Tuscaloosa floras and found that these two localities have 22 species in common, and that both deposits could be interpreted as continental, deltaic and coastal.

The above-mentioned floras contain lauroid leaves of the *Myrtophyllum-Pandemophyllum* complex and platanoids that are shared with the Peruc flora. While angiosperm leaves with serrate margins are less common in the North American floras. This fact is interpreted here as a feature characterising North American floras as more modern,

lacking neither early angiosperm foliage neither older Mesozoic taxa as bennettites (*Zamites*, *Cycadeoidea*), cycads (*Pseudoclenis*) and ginkgophytes (*Eretmophyllum*).

#### **4.2. Comparison of Peruc flora with Early Cretaceous flora of Lusitanian Basin, west Portugal**

Although the flora from the Lusitanian Basin (Barremian-Albian) does not correspond to the age of the material studied in this paper, their comparison shows several interesting facts (Teixeira, 1948, 1950). The present findings from the localities mostly contain mesofossils of reproductive organs (Friis et al., 1999, 2011). A few similarities can be found in sharing lauroids and the magnoliid *Serialis* E.M.Friis, P.R.Crane et K.R.Pedersen (Friis et al., 2019). The reconstructed environments in Portugal correspond to some extent with those of Pecínov. Based on the findings of Friis et al. (2020, 2024), it is likely that the first angiosperms there were tiny shrubby plants that grew in open, disturbed environments or in the understory.

#### **4.3. Comparison of Peruc flora with Cenomanian flora of western France**

There are also similarities between the Peruc flora and the Cenomanian flora of western France. There are two areas where Cenomanian fossil plants are found: Anjou and Charente-Maritime (Coiffard et al., 2009). The similarities between the French and Peruc Cenomanian flora can be seen in the example of the *Frenelopsis-Classopollis* assemblage consisting of *Frenelopsis*, *Eretmophyllum* (Pons, 1979, 1981; Pons et al., 1976) and *Pseudoasterophyllites* (Kvaček et al. 2012). There are other shared genera such as *Dammarophyllum* and *Eucalyptolaurus*. The fossil flora of the French Cenomanian, especially those of Anjou, were extensively studied and described by Berthelin and Pons (1999), Néraudeau et al. (2013) and Fleury et al. (2017).

#### **4.4. Comparison of Peruc flora with North Sudetic Basin flora, Lower Silesia**

Positioned on the northern foreland of the Sudetes, which form the northeastern boundary of the Bohemian Massif, lies the North Sudetic Basin, also known as the North Sudetic Synclinorium (Niecka Północnosudecka). While younger deposits are of marine origin in the western portion of the Basin and of brackish to alluvial origin in its central and eastern regions, the rocks of the Cenomanian to middle Coniacian are of marine origin (Śliwiński et al., 2003; Żelaźniewicz, 2005). Unfortunately, the majority of the time, small quarries disappeared and were not replaced by an increase in the number of large quarries. Because of this, the description of the megaflores is primarily dependent on specimens from the past.

The vegetation appears to be dominated by angiosperms in the mega- and mesofossil record, and this is most likely the case for the forest-forming species. Ferns predominate in the microfossil record, which is consistent with understorey vegetation, and potentially other non-forest palaeocommunities. In terms of taxa and specimens, angiosperms dominate the flora. However, the conifer *Geinitzia reichenbachii* is the most abundant species alone, followed in abundance by the dicotyledonous *Dewalquea haldemiana*. Most of the finds come from the Rakowice Małe, Wartowice, Assemblages 2-5. Among the similar or identical findings from the Bohemian Cenomanian it is worth mentioning that the ovuliferous cone of *Pinus longissima* Velen. (Velenovský, 1885; Kvaček, 2013b; Halamski et al., 2020), *Protodammara* sp. is similar to *Dammara borealis* Heer from the Bohemian Cenomanian (Heer, 1882; Halamski et al. 2020), and reproductive structures of *Platananthus* sp. from Žerkowice locality resemble *Platananthus* sp. (Kvaček, 2003; Halamski et al., 2020). In contrast to the rich and diverse Cenomanian palaeofloras in Bohemia and southernmost Lower Silesia, no plant fossils have been discovered in the Cenomanian layers within the mentioned area (Niebuhr, 2019).

#### **4.5. Comparison of Peruc flora with South Bohemian Basin flora**

Sedimentologically and paleontologically, the Bohemian Cretaceous Basin and the South Bohemian Basins differ in sediment composition and diversity of fossil finds. The Bohemian Cretaceous Basin, a more extensive and geologically complex area, contains a richer palaeontological record, especially of marine organisms, and exhibits more diverse sedimentary structures. In contrast, the South Bohemian Basins are a smaller and less studied area.

Divided by the Lišov Horst, the basins are made up of two lengthy depressions, the Třeboň Basin and the Budějovice Basin. The two subbasins together occupy an area of about 2300 km<sup>2</sup>, developed on the Moldanubian crystalline bedrock of the Bohemian Massif.

Sedimentation in the basins began in the Late Cretaceous and continued sporadically through the Pliocene (Slánská, 1974). Stratigraphic units are: the Klikov Formation (Upper Turonian – Santonian), the Lipnice Formation (Oligocene), the Zliv and Mydlovary formations (Miocene) and the Ledenice Formation (Pliocene) (Slánská, 1974). The most widely distributed unit in the South Bohemian Basins, with primarily river sediment infill, is the upper Turonian - Santonian Klikov Formation with an average thickness of 100–150 m. Three distinct lithological types are found in asymmetrical cyclic sequences within the Klikov Formation. These are: 1) Conglomeratic light grey and yellow sandstones; 2) Red beds of poorly sorted

sandstones; 3) Grey sandstones and claystones with inclusions of coalified, unevenly dispersed plant fragments (Slánská, 1976, 1974)

The South Bohemia Basins and the Bohemian Cretaceous Basin are two distinct geological formations in the Czech Republic. The South Bohemia Basins are two small basins located in the southern part of the country, while the Bohemian Cretaceous Basin is a larger basin located in the northern part of the country. While the Bohemian Cretaceous Basin is affected by marine influences and contains marine sediments, the South Bohemian Basins contain only continental deposits. The Late Cretaceous sediments of South Bohemian Basins (the Klikov Formation) represent cyclic sedimentation, as opposed to Late Cretaceous sediments of the Bohemian Cretaceous Basin.

The cyclical alternation of three lithological types was observed only in the Klikov Formation. In terms of palaeobotanical findings there are both macro-, meso- and micro-finds.

Systematic affinities have been suggested for only two types of fossil leaves from the Klikov Formation, while a number of other taxa remain without systematic assignment to present-day groups (Knobloch, 1964; Němejc, 1961). The two identified genera are *Cocculophyllum*, assigned to the Laurales (Němejc and Kvaček, 1975), and *Ettingshausenia* of platanoid affinity (Kvaček and Váchová, 2006).

The Klikov Formation mesofossil flora is comparable to other Late Cretaceous mesofossil floras (including the Bohemian Cretaceous Basin) in the organisation of the angiosperm floral structures and in the small size of all reproductive structures. The flora documents the presence of a diverse, angiosperm-dominated vegetation in the late Turonian-Santonian of Central Europe (Heřmanová et al., 2021). The Klikov Formation is renowned for its abundance of Late Cretaceous mesofossils, and high proportion of taxa related to the wind-pollinated fagalean Normapolles complex. The Normapolles complex is a likely polyphyletic group of eudicot angiosperms known from various Late Cretaceous and Paleogene localities in the Northern Hemisphere (Friis et al., 2011). Fossils assignable to the Normapolles complex (Fagales) and of possible ericalean affinity dominate the mesofossil flora of Klikov Formation.

Charcoalified mesofossils, microfossils, silicified wood, and fossil leaves were abundant in the claystones and sandstones that crop out in the areas of Zliv-Blana, Dobrá Voda, and Pohůrka.

## 5. Palaeoecological settings

The collection of material used in this thesis has been assembled over a period of almost a quarter-century from the Pecínov quarry, units 1-3. The specimens are stored in the collections of the National Museum. For the analysis, the material was pre-selected on the basis of morphological features that might indicate an extremophilic character of the plant.

The origin of the plant fossils should be viewed in two ways. The material was pre-selected for the analysis on the basis of macro- and micro-morphological features that might indicate an extremophile character of the plant. The river deposits contain remains of both autochthonous and allochthonous flora. The division is possible on the basis of cuticle micromorphology and then by Carbon isotopes.

The first approach offers, quite logically: the units of discovery (U1-U3). The second approach requires more interpretation and the data obtained from cuticle and carbon isotope analyses, and that is the place where the plants grew. These two approaches may not always be consistent.

### 5.1. Distribution of plants according to the distance from springs downstream to the river estuary on the example of the Pecínov quarry

Sediments of unit 1 lay on the Carboniferous bedrock. It is described as a small, shallow, frequently migrating, anastomosing river whose channels overlapped laterally and vertically. It contains poorly sorted conglomerates, as well as medium-grained sandstones, claystones and clayey lenses (Uličný and Špičáková, 1996). Vegetation of this unit is interpreted as alluvial plain forest with a high portion of upland taxa. The alluvial plain is narrow, and slopes were close to the river bed. Among the plant fossils, it is possible to find mainly angiosperms, especially the plane tree *Ettingshausenia laevis* (Velen.) J.Kvaček et Váchová with reproductive structures *Platananthus* sp., the lauroid *Myrtophyllum* sp. and *Eucalyptolaurus* sp., with inflorescences *Mauldinia bohemica* and *Pragocladus lauroides* J.Kvaček et Eklund. Further, there are: probably chloranthoid *Papillaephyllum labutae* and *Araliphyllum kowalewskianum* (Sap. et Mar.) Velen. of unknown affinity. There are some gymnosperms, especially cycads *Nilssonia mirovanae* and *Pseudocatenis babinensis* J.Kvaček (Čepičková and Kvaček, 2020; Kvaček, 2008), and bennettites (*Zamites pateri* J.Kvaček). The palynological record is dominated by pollen of angiosperms (Uličný et al., 1997; Kvaček et al., in press). The local environment of floodplain and floodplain forests around rivers was dominated by gallery forests; moving gravel bars were overgrown by shrubby vegetation.

The slopes were covered with vegetation composed of ferns, shrubby angiosperms and conifers (Kvaček et al., 2006).

Unit 2 is characterised by a predominance of fine-grained sediments and frequent occurrence of pyrite concretions, which demonstrate the tidal influence of the sea (Uličný and Špičáková, 1996). Uličný et al. (1997) reconstruct the environment as a tidally influenced river. Lithologically, this unit is composed of fine-grained conglomerates, ranging from pebbly sandstones to fine-grained sandstones and claystones. It is again dominated by lauroid angiosperms, mainly leaves of *Myrtophyllum* sp. and *Eucalyptolaurus* sp. and inflorescences of *Mauldinia bohémica* and *Pragocladus lauroides*. In contrast to the previous unit, the environment here is more humid. The vegetation of the broad river floodplain is reconstructed by Uličný et al. (1997) as shrubby sandy river bars. Local marsh vegetation generally includes cupressoid conifers. In the more stable parts of the floodplain, larger trees, relatives of today's plane trees, *Ettingshausenia laevis* grew. Shrubs of the Chloranthaceae family also occur here with one representative *Ascarinophyllum pecinovense*, which also occurs in unit 3. There were also cycads and ferns (Kvaček et al., 2006).

Unit 3 consists of grey to black claystones and pyrites often occur here in form of concretions. The base of the unit is composed of dark grey sandstones. It is divided into two subunits, coastal wetlands, which are characterised by cupressoid conifers, and saltmarshes or mangroves. This environment is interpreted as a shallow, inter- to supratidal marsh. Vegetation of the saltmarshes is dominated by the conifer *Frenelopsis alata* with the ovuliferous cones *Alvinia bohémica* (Velen.) J.Kvaček (Kvaček, 2000a). In addition, the ginkgophyte *Nehvizdyella bipartita* with leaves *Eretmophyllum obtusum* (Kvaček et al., 2005) and the halophytic herbaceous angiosperm *Pseudoasterophyllites cretaceus* Feistm. ex Velen. occur there (Kvaček et al., 2016). Wetlands are dominated by *Cunninghamites lignitum*.

## 5.2. Vertical layout

The usual approach to subdivision into units 1-5 is based on the sedimentary environment, which in this case is provided by the river. However, the environment in which the vegetation actually grew can be subdivided in a different way, namely vertically and on the basis of how the plants obtained water. In this way, the environment can be divided into places with zonal and azonal vegetation.

The uppermost environment is slope and drier upland area, in which fresh water comes only from seasonal precipitation. Plants from this environment were most susceptible to drying out due to the only seasonal supply of water, so many of them developed protective tissues.

Next down is the environment of the alluvial plain. This environment can be further divided into meandering river and braided river. Fresh water comes from an alluvial underground and precipitation. Plants from this environment did not suffer from a lack of fresh water and did not have to adapt to drought caused by seasonality of the climate. For this reason, representatives from this level are not equipped with water retention features.

Below that are coastal wetlands, which have similar water availability to alluvial plains. The water table even reaches the surface causing low oxygenation of soil therefore, mudstones and siltstones as products of this environment are rich in pyrite. This rather extreme environment is populated mostly by cupressoid conifers.

The last, lowest zone is the environment influenced by sea water, the saltmarsh. The fresh water comes from the river, and the sea delivers salt water. The resulting brackish water profoundly influences the saltmarsh vegetation. Although water resources at this level are sufficient, it is the brackish water causing water stress.

## 6. Methods

The main methodology of this study was cuticle analysis and study of venation patterns using the 'venation visualisation' method.

A detailed description of the method of cuticle analysis was given in publications by Čepičková and Kvaček (2020, 2023).

The following samples were used in the process of macro-observation, cuticle analysis, venation visualisation method and observation under microscopes: *Nilssonia mirovanae*: NMP-F 4593, F 4698a, F 4699c (coll. National Museum, Prague), *Todziaphyllum saportanum*: NMP-F 307, F 308, F 729 (coll. National Museum, Prague), *Ascarinophyllum pecinovense*: NMP-F 4585, F 4586, F 4591, F 4715, F 4776, F 4777, F 4778, F 4779ab (coll. National Museum, Prague), *Papillaephyllum labutae*: NMP-F 2317, F 5279, F 5280, F 2317, F 4979, F 5279, F 4740, F 4741, F 5278, F 5280, F 5281, F 5282, F 5283, F 5358, F 5359 (coll. National Museum, Prague).

In all cases for this thesis, the leaf material had to be freed from the rock matrix, following the removal of silicate material with 38–40% hydrofluoric acid (HF), in which

the samples are macerated for 15-20 min. After using HF, isolated leaf fragments were rinsed with water, then macerated in Schulze's reagent. Schulze's reagent is a very reactive mixture that can destroy the sample if the maceration is too long, so it is necessary to monitor the reaction. When it is used, there is significant oxidation and decomposition of organic matter, which allows better visualisation of the inorganic components of the sample under a microscope. Maceration time depends on the degree of cutinisation; while weakly cutinised samples can be macerated for a few seconds, strongly cutinised leaves can be macerated for hours. After using Schulze's reagent the sample was rinsed with water again, followed by maceration in potassium hydroxide (KOH). KOH acts as a strong base that dissolves and removes intercellular substances and other tissue components, leaving only the cuticle. It allows the cuticle to be examined with no interference from organic materials that could distort the observation. After maceration in KOH, the sample is rinsed with water one final time.

The leaf fragments were then carefully prepared with fine needles under a binocular microscope in order to divide the abaxial and adaxial cuticles. One fragment was mounted in glycerine as a permanent slide for light microscopy (LM), the other was fixed on a small sheet of negative photo film mounted on an aluminium stub for scanning electron microscopy (SEM). When placing the cuticles on the aluminium stub, it was important to be able to observe the external and internal surface of both (abaxial and adaxial) cuticles at the same time, so ideally, 4 cuticles were placed on the stub. Cuticles on permanent slides were documented using an Olympus BX-50 light microscope equipped with a DP-72 digital camera. Cuticles on aluminium stubs were coated with gold or palladium for 60 seconds in a sputter coater and examined using a Hitachi S-3700N SEM and JEOL JSM-6380 SEM. Adobe Photoshop, Adobe Illustrator, GIMP and Inkscape programs were used for graphic processing.

By bulk-macerating material in a 20% sodium bicarbonate solution in lukewarm water, dispersed fragments were produced. Screens having hole diameters of 1.6 mm, 0.5 mm and 0.125 mm are then used to sieve the material that has dissolved in the solution. Subsequently, the leaf fragments were extracted mechanically from the remaining wet substance. Following this procedure, the standard maceration method with Schulze's reagent was applied.

In botany and paleobotany, the "venation visualisation" approach is a technique used to analyse and visualise the pattern of venation on plant leaves in detail. This approach is essential to comprehending the physiological characteristics, evolutionary background,



and ecological adaptations of leaves. In the case of charcoalfied material, the usual observation of leaf venation is difficult, mostly dependent on state of conservation. For the purpose of visualising the vein pattern of leaf fossils mentioned in this thesis, it is important that the leaf fossil is at least partially translucent; the ideal condition is when the fossil comes from sieves where it is partially macerated. In some cases the leaves need to be chemically treated with KOH to make them translucent. This is followed by observation, documentation and processing in graphic editors.

With distinct PFN numbers, the new names and nomenclatural activities are recorded in the Plant Fossil Names Registry, which is administered by the National Museum, Prague on behalf of the International Organization of Palaeobotany (IOP). Todzia and Keating (1991), and Ellis et al. (2009) provide the terminology for venation and teeth, while Carpenter (2005) provides the terminology for stomata.

## **7. Results**

In this part of the thesis results gathered from all the published papers are briefly summarised. The detailed descriptions of these results are part of the publications attached at the end of this thesis. Based on the material described in the papers using cuticle analysis, taphonomy and other palaeoecology methods, the following environments were interpreted.

### **7.1. Reconstructed palaeoenvironments**

#### **7.1.1 Vegetation of slope and drier upland areas**

This environment is reconstructed based on fragmentary preserved plant fossils that are found as allochthonous elements in alluvial sediments of small rivers. This zonal vegetation is reconstructed as consisting of ferns, bennettites and early angiosperms, while the plants growing on slopes are generally characterised as prairie and shrubby vegetation. Slopes and upland areas were probably covered by open fern steppe and sparse woodland. On sunny slopes, there dominated ferns, bennettites and cycads (e.g. *Konijnenburgia*, Schizaeaceae, *Nilssonia mirovanae*, *Pseudecten pecinovens*, *Pseudecten babinensis*, *Zamites pateri*, *Brachyphyllum squamosum*, *Papillaephyllum labutae*). North-facing slopes are more shady, and these hosted mostly early angiosperms (e.g. *Ascarinophyllum pecinovense*, *Dicotylophyllum* sp.). The leaf fragments found are fewer in number and more fragmented. The presence of fragmented preserved plants from slopes and dry upland is a significant marker in the sediments of braided rivers, especially in their higher sections. More charcoalfied pieces

suggest that wildfires occur more often (Falcon-Lang et al., 2001). The paleovegetation characteristic of slopes and upland can be inferred through the analysis of allochthonous vegetative detritus found within fluvial sediments at higher riverine locales. From a taphonomic perspective, the botanical detritus from such vegetation is typically encountered in the form of rare megafossil fragments or as charcoalfied mesofossils (Scott, 2009).

### 7.1.2 Vegetation of alluvial plains

Rivers and river floodplains are environments of azonal palaeovegetation. The environments of alluvial plains differ according to the nature of the river flow and substrates that comprise those plains. Braided rivers as high energy environments have a very unstable central part of the riverbed. Sand bars travelling down the river frequently change the alluvial plain in this part of the river. The river produces oligotrophic sandy and gravelly substrates that were a suitable growing environment only for a few taxa. Shrubs lauroid angiosperms *Mauldinia bohémica* with leaves *Eucalyptolaurus* sp. and *Pragocladus lauroides* with leaves *Myrtophyllum* sp. grew there. More stable parts of the braided river alluvial plain were formed by more nutrient-rich substrates, hosting vegetation dominated by arborescent *Ettingshausenia* cf. *laevis* with reproductive structures *Platananthus* sp. Understorey of this forest was formed by ferns (*Gleichenia* sp.), cycads (*Nilssonia holyi* J.Kvaček et Erw. Knobloch) and shrubby angiosperms (*Araliphyllum kowalewskianaum*).

Meandering rivers are typically low energy environments. Their alluvial plains are rich in nutrients, providing ideal environments for plant growth. Dominant plants of the meandering rivers were angiosperms, particularly lauroid angiosperm *Myrtophyllum geinitzii* with reproductive structures *Antocephale* sp. and platanoid angiosperm *Ettingshausenia bohémica* with reproductive structures *Platananthus* sp. Communities of trees, shrubs, understorey ferns and cycads made up the majority of this assemblage.

### 7.1.3 Vegetation of saltmarshes

Saltmarshes are an environment, which has been best documented at the Pecínov locality in recent years, using sedimentological and palaeobotanical data. Saltmarshes surrounded tidal and river channels. High tide floodings in estuaries may account for occasional inundation of this environment by sea water. This unit is clearly dominated by *Frenelopsis alata* and a ginkgophyta with leaves *Eretmophyllum obtusum*. *Frenelopsis alata* and *Eretmophyllum obtusum* - *Nehvizdyella* J.Kvaček are the most common species because of their high salt tolerance. Their resistance to extreme salinity can be observed in the cuticles, which are heavily

cutinised, with costal and intercostal bands. Stomata are in both taxa deeply sunken and surrounded by strongly cutinised subsidiary cells. Other plants in this group are the conifer *Dammarites albens* (Hlušík, 1976, 1977a), and the angiosperms "*Diospyros*" *cretacea*, and *Pseudoasterophyllites cretaceus* (Kvaček et al., 2012, 2016). Záhajská et al. (2024) concluded that all studied members of the saltmarsh vegetation (*Eretmophyllum*, *Pseudoasterophyllites*) are either water stressed or exhibit adaptation to salinity (*Frenelopsis*) through the use of carbon isotopes from fossil leaf cuticles (n-alkanes,  $\delta^{13}\text{C}_{\text{n-alkanes}}$ ) for water stress determination.

## 7.2. Adaptation based on morphology

The morphology of an extremophile plant is typically adapted to the risk of severe water stress. These morphologies are very often fleshy coriaceous leaves or stems that store water, waxy light-reflecting leaf surfaces, specially modified roots for water storage, etc. However, leaf fossils preserve mainly micromorphological features. These include thick cuticle, the presence of indumentum (presence of trichomes and papillae), and stomata sunken in pits.

### 7.2.1 Micromorphology of plants in mesophytic conditions

Mesophytic plants have moderate stomatal density for efficient gas exchange, and a cuticle that provides some protection against water loss without being overly thick. The periclinal wall is not wrinkled in any way, which can be observed very often in plants stressed by lack of fresh water. Mesophytic plants are typically found in habitats where soil moisture is adequate but not excessive, and where evapotranspiration rates are balanced by rainfall. In this case, there is no need to protect the plant from excessive evaporation, nor is there a need to deal with a salty environment by osmosis. A typical example of a mesophytic plant that is common in the fossil record of the Pecínov locality is *Araliphyllum*.

Alluvial plains also hosted hygrophytic plants, which are plants adapted to environments with high moisture availability. These plants are typical in environments with lots of water and usually humid atmospheres, such as marshes, swamps, and rainforests. Hygrophytic plants have developed specific adaptations, such reduced water-conducting systems, because water scarcity is rarely a constraint. In a humid environment, their big, often-thin leaves with a high stomatal density allow for greater transpiration and gas exchange. A typical example of a hygrophytic plant that is common in the fossil record of the Pecínov locality is *Eucalyptolaurus* sp. with reproductive structures *Mauldinia bohémica*, *Myrtophyllum geinitzii*, a species with unembedded stomata and smooth periclinal walls. In addition

to the micromorphological features of the unstressed plant, macromorphological features can also be observed. *Eucalyptolaurus* has an entire-margin leaf shape with drip-tip, which is common in plants that occur in areas of high water supply. Drip-tips are used to get rid of excess water on the leaf.

### 7.2.2 Cuticle micromorphology of plants in extreme conditions

Extreme conditions are those that force plants to prevent water loss in some way. At the micro level, plants have several such possibilities; for instance, they can modify the immediate surroundings of the stomata or the periclinal wall. Stomata are used for gas exchange, but in extreme conditions it is necessary to ensure that no more water escapes than is strictly necessary when opening and closing the stoma. This is the purpose of embedding stomata in stomatal pits. Placing papillae around the stomata prevents evaporation. Usually, these papillae are arranged around the stoma, sometimes forming a wreath. In addition to stomatal adaptation, the plant can use its periclinal wall, which can be wrinkled. These striations can be arranged radially around the stomata, or randomly oriented and distributed on the whole periclinal wall. Not only striations, but papillae can cover periclinal walls. Thick cuticles are a defining property of xeromorphic plants among gymnosperms (Veromann-Jürgenson et al., 2019). Recent xeromorphic (but not succulent) plant traits were compiled and characterised by Fahn and Cutler (1992).

The analysed taxa's cuticles exhibit sunken stomata and significant cuticle shedding; in the instance of *Nilssonia mirovanae*, the stomata are furthermore protected by papillae, all of which are indicative of xeromorphic plants (Fahn and Cutler, 1992). According to the uniformitarian principle (Scott, 1963), we think it plausible that the fossil plants were likewise xeromorphic, because they exhibit very similar, if not identical, cuticle characteristics to those that are known to be present in extant xeromorphic plants.

Axes of cheirolepidiaceous conifer *Frenelopsis alata* are separated into internodes and nodes. There is a significant reduction of foliage. The abaxial cuticle's ordinary cells are heavily cutinised with deeply sunken stomata and occasionally placed in bands. Around the stomata are four to five subsidiary cells. The stomata are protected from the outside by an inner and outer wreath made up of four to five papillae.

The ginkgophyte leaf *Eretmophyllum obtusum* has strongly cutinised abaxial cuticle. The stomata are evenly distributed over the abaxial cuticle and surrounded by a wreath of four

to five subsidiary cells. On the outer surface of the abaxial cuticle, the stomata are surrounded by a rim. The periclinal wall of some ordinary cells is slightly wrinkled.

Since both species (*Frenelopsis alata* and *Eretmophyllum obtusum*) are typical elements of saltmarshes, their micromorphological structures are very protective (thick cuticle, structures around the stomata). Isotope analysis of *Eretmophyllum* leaves showed high values of stable carbon isotope in n-C29 alkanes. It is stated that *Eretmophyllum* is a strong halophyte, while *Frenelopsis* seemed to be less water stressed according to the lower values of n-C29 alkanes.

Leaf of *Ascarinophyllum pecinovense* is serrate and leathery with rounded chloranthoid teeth bearing a papilla. Cuticle pattern of *Ascarinophyllum pecinovense* shows combination of stomata (typical for Chloranthaceae) and specific periclinal wall of abaxial cuticle. Periclinal walls of ordinary and subsidiary cells are covered by well-pronounced striations. These striations are randomly oriented on ordinary cells, however, around stomata they show radial orientation. In addition to striations, stomata are protected by stomatal rims. These features are indicators of possible water stress. Nevertheless, more was shown by isotope analysis, which proved that *Ascarinophyllum pecinovense* grew under water stress.

Leaf of *Papillaephyllum labutae* is characterised by having serrate, occasionally double-serrate margins with rounded chloranthoid teeth, each bearing a papilla. As in the case of *Ascarinophyllum pecinovense*, this is a character that would place the plant in the Chloranthaceae. *P. labutae* shows periclinal walls bearing thick cuticle, very densely covered by papillae. These papillae are randomly placed on periclinal walls of ordinary and subsidiary cells. Papillae of subsidiary cells form a wreath which surrounds and protects stomata. This character proves that the plant grew under water-stress. The comparatively higher  $\delta^{13}\text{C}$  in n-C29 values confirm that this plant grew in a dry upland with limited water availability.

## 8. Conclusions

Paleobotanical studies of the Peruc-Korycan Formation have been conducted for a number of decades, and their findings have been supported by an extensive amount of evidence. This knowledge was expanded by the master thesis, which was followed by the present dissertation. However, for the purpose of the research, it was necessary to broaden the scope of interest to include a larger number of samples, as well as expand the scope of data acquisition by extending the methodology to include new analysis of venation

visualisation, modifications of cuticle analysis, and isotopic analysis. The thesis also contains data that have been modified or superseded based on new findings.

The data published in the papers included in this thesis focus on taxonomy, palaeoecology and geochemistry in the context of paleoclimate. Their findings add more information to the overall picture of the Cenomanian environment. Through the methods mentioned above and previously published data it was possible to define major environments, with their plant content. Contemporaneously as the environments were expanded to include new species that are very specific in their micromorphological structures. Observations of microstructures, macro-observations, the sedimentological record and isotope signals all allowed us to determine the ecological requirements of the newly described species, which were typically species that were water-stressed. With the new species and their isotopic signals, it was possible to further expand our knowledge about the above described palaeoenvironments.

In Čepičková et Kvaček 2020 (Appendix 1) the cycad species *Nilssonia mirovanae* from unit 1, Peruc-Korycany Formation of the Bohemian Cretaceous Basin was described. *Nilssonia mirovanae* is so far found in the depositories of the National Museum in only two specimens, as strap-shaped fragments of an entire-margined hypostomatic pinnae. The stomata are haplocheilic. Cuticles of the studied taxa are strongly cutinized and show sunken stomata surrounded by papillae, characters of xeromorphic plants indicating that the plant suffered from water stress. Unit 1 in Pecínov where the species was found, contains fossil plants from slopes and uplands. Given that there was a seasonal climate there, the plants were exposed to periods of drought, to which they responded by forming protective structures. *N.mirovanae* is often found in the sediment together with plant remains of the cycad species *Pseudoctenis babinensis*. Both of these cycads have developed similar adaptations to withstand water stress: sunken stomata and thick cuticles, which are traits common to gymnosperms that show drought tolerance.

Čepičková, J., Kvaček, J. 2023 (Appendix 2) focuses on the two taxa, probably belonging to the family Chloranthaceae. *Todziaphyllum saportanum* is a serrate leaf with semicraspedodromous venation. This taxon, originally described by Velenovský (1883) as *Banksites saportanus* Velen., was revised and its diagnosis was emended. Specimens of *Todziaphyllum saportanum* were included in the publication on the basis of its macromorphological similarity to a fossil leaf described as *Ascarinophyllum pecinovense* Čepičková et J.Kvaček, published in the same publication. *Ascarinophyllum pecinovense*, found in units 2 and 3, is characterised by serrate margins with rounded chloranthoid teeth

bearing papillae. Its affinity with the family Chloranthaceae is evidenced by macro and micromorphological characters. The already mentioned papillae are typical for the family Chloranthaceae, but also occur in some members of the basal ANA lineages and in basal eudicots. Semicraspedodromous venation of *Todziaphyllum saportanum* and festooned - semicraspedodromous venation of *Ascarinophyllum pecinovense* are also typical for Chloranthaceae.

The name of the taxon is derived from the considerable similarity with recent taxon *Ascarina rubricaulis* Solms. *Ascarina rubricaulis* has serrate margins with chloranthoid teeth terminated in papilla, which is similar to the tooth type in *Ascarinophyllum pecinovense*. Festooned semicraspedodromous venation is a unique characteristic of *A.pecinovense* and *Ascarina rubricaulis*, where the finer venation tends to align with the secondary veins. Striation on the external surface of the abaxial cuticle of *Ascarina rubricaulis* is similar to that in *Ascarinophyllum pecinovense*, but striation of *Ascarinophyllum pecinovense* is less pronounced. Stephanocytic-bicyclic stomata, which are also present in *Ascarinophyllum pecinovense*, are the predominant kind. Additionally, the adaxial cuticle pattern resembles that of *Ascarinophyllum pecinovense* (Kong, 2001; Carpenter, 2005).

The micromorphological aspect is more complicated, since the cuticle of *Ascarinophyllum pecinovense* contains several types of stomata, so it cannot be characterised on the basis of only one stomatal type. Cuticle of the *A. pecinovense* bears a combination of laterocytic/ laterocyclocytic, stephanocytic-bicyclic and amphibrachyparacytic stomata. Less frequently, there are also brachyparacytic and holoparacytic stomata. Similar combinations of stomata are found among plants from the ANA group and Chloranthaceae. The periclinal sides of the abaxial cuticle are always wrinkled, with striations arranged radially around the stomata and randomly arranged striations on ordinary cells. This feature is considered a micromorphological structure intended to prevent desiccation of the plant. Various types of above-mentioned stomata and cuticle wrinkling are typical characters of basal angiosperms from ANA group and the Chloranthaceae. Semicraspedodromous venation pattern, parallel tertiaries and its stomatal pattern support the interpretation of *Ascarinophyllum* as belonging to Chloranthaceae.

Čepičková et J.Kvaček, 2023 (Appendix 3) is devoted to the description and paleoecology of an angiosperm *Papillaephyllum labutae*. The material for description of this species in the thesis was initially limited to fossil leaves preserved as leaf compressions. However, during the preparation of the paper, it was discovered that there are more specimens

of isolated leaf fragments in the bulk macerated and sieved material. Those fragments showed well-preserved semicraspedodromous to festooned-semicraspedodromous venation of the leaves. Macromorphologically, this species resembles the family Chloranthaceae in the type of teeth, which are chloranthoid, and the type of venation. Stomata are stephanocytic-bicyclic and latero-cyclocytic, which are types often found in family Chloranthaceae. Completely unique is the periclinal wall of the abaxial cuticle, which is densely covered with papillae, both around the stomata and on each ordinary cell. No species with such a cuticle pattern has yet been formally described. As in the previous case of *Ascarinophyllum pecinovense*, its cuticle shows signs of xerophytism. It occurs in unit 1, where fragments of fossil plants growing on slopes and drier upland areas are present. The papillae on its cuticle probably served to prevent water loss.

Zahajská et al., 2024 (Appendix 4) combines a modern dataset of stable carbon isotopes of leaf cuticular waxes (*n*-alkanes,  $\delta^{13}\text{C}_{n\text{-alkanes}}$ ) along osmotic stress gradient with  $\delta^{13}\text{C}_{n\text{-alkanes}}$  extracted from fossil leaf cuticles and cuticular morphology, to reconstruct palaeohabitats of individual fossil species. Positive correlation between modern  $\delta^{13}\text{C}_{n\text{-alkanes}}$  and osmotic stress (salinity and/or drought) was found and used to build an interpretative framework further applied on the fossil data. Results of the isotope analysis confirm data obtained from cuticle analysis; *Ascarinophyllum pecinovense* grew under osmotic stress (by either drought or salinity). Its isotopic signal ( $\delta^{13}\text{C}$  in *n*-C<sub>29</sub>) ranges -30 - -22‰, where the less negative values are interpreted as stress conditions. Unfortunately, isotope analysis requires enough material to perform a valid extraction, which was problematic for species *Nilssonia mirovanae* and *Papillaephyllum labutae*, of which we had extremely few (see *N. mirovanae* at the time of extraction - 1 piece, *P. labutae* - 1 piece). However, values were obtained even from that small amount of material and the analysis suggested drought stress (*Papillaephyllum labutae*) and order-specific fractionation with additional drought stress (cycad *Nilssonia mirovanae*).

The co-author of the publication (Appendix 4) that is included in this thesis was studying the micromorphology of fossil leaf cuticles. The results of this research have been used in the paper as supporting data for the detection of water stress.

Kvaček et al. (in press) (Appendix 5) summarises the findings of several decades of research on Cenomanian strata in the Bohemian Cretaceous Basin. It focused on the rise of angiosperms and the decline of gymnosperms. In this article five terrestrial palaeoenvironments are reconstructed:



- 1) Saltmarsh with *Frenelopsis-Classopollis* assemblage
- 2) Coastal wetland with , *Cunninghamites-Taxodiaceapollenites* assemblage
- 3) Meandering river floodplain with , *Myrtophyllum-Perucipollis* assemblage
- 4) Braided river floodplain with, *Eucalyptolaurus-Mauldinia* assemblage
- 5) Slopes and drier upland areas covered by fern prairies with angiosperms and Bennettitales *Zamites-Ephedripites* assemblages

This study demonstrates the diversity of angiosperms throughout the Cenomanian, especially in alluvial plains, where lauroid and platanoid angiosperms were more common.

The reconstructions are based on data from palaeobotany, palynology, palaeoecology, sedimentology and geochemistry analyses, from long-term observations.

The author of this thesis examined the macro- and micromorphology of fossil leaves for the publication (Appendix 5).

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## 10. List of publications included in this thesis

This dissertation thesis is based on the following articles:

1. Čepičková, J. Kvaček, J., 2020. Two cycads *Nilssonia mirovanae* sp. nov. and *Pseudoctenis babinensis* J.Kvaček from the Cenomanian of the Bohemian Cretaceous

Basin (Czech Republic) as indicators of water stress in the palaeoenvironment. *Fossil Imprint*, 76(2), 315–324.

2. Čepičková, J., Kvaček, J., 2023. Fossil leaves of Cenomanian basal angiosperms from the Peruc-Korycany Formation, Czechia, central Europe. *Review of Palaeobotany and Palynology*, 104802.
3. Čepičková, J., Kvaček, J., 2023. *Papillaephyllum*, a new genus of angiosperm foliage from the Cenomanian of the Czech Republic. *Review of Palaeobotany and Palynology*, 104990.
4. Zahajská, P., Čepičková, J., Trubač, J., Pedentchouk, N., Kvaček, J., 2024. Modern calibration of plant leaf  $\delta^{13}\text{C}_{\text{n-alkanes}}$  in coastal ecosystem applied to palaeoenvironment: Case study from the Cenomanian of the Bohemian Cretaceous Basin, Czechia, *Palaeogeography, Palaeoclimatology, Palaeoecology*
5. Kvaček, J., Svobodová, M., Čepičková, J., Veselá, V., Špičáková, L., Uličný, D., Dašková, J., Mendes, M.M., Zahajská, P., in press. Terrestrial palaeoenvironments from the Cenomanian strata of the Bohemian Cretaceous Basin in Central Europe: evidence of the rise to ecological dominance of angiosperms and the decline of gymnosperms, *Palaeogeography, Palaeoclimatology, Palaeoecology*

#### **Other publications on related topic but not included in this thesis:**

6. Heřmanová, Z., Čepičková, J., Kvaček, J., von Balthazar, M., Schönenberger, J., 2022. A multicarpellate fruit from Late Cretaceous sediments of South Bohemia, Czech Republic. *Palaeontologia Electronica*, 25(1), 1-14.
7. Heřmanová, Z., Kvaček, J., Čepičková, J., von Balthazar, M., Luthardt, L., Schönenberger, J., 2023. *Slavicekia* gen. nov., a New Member of the Normapolles Complex from Late Cretaceous Sediments of the Czech Republic. *International Journal of Plant Sciences*, 184(3), 201-213.

#### **Conference contributions:**

Preliminary results and final outcomes of research related to this thesis were presented at the following conferences and congresses:

1. Čepičková, J., Kvaček, J., 11/2019. Palaeoecological study of the Cretaceous extremophilic flora with emphasis on xerophytes. 28<sup>th</sup> International Plant Taphonomy Meeting. Münster, Germany.
2. Čepičková, J., Kvaček, J., 6/2021. New taxon *Nilssonia mirovanae* sp. nov. as indicator of water stress in the palaeoenvironment. *Progressive Palaeontology*. Online.
3. Čepičková, J., Kvaček, J., 8/2021. Paleoekologická studie extremofilní flóry cenomanu české křídové pánve. 10. křídový seminář, Brno, Czech Republic.
4. Čepičková, J., Zahajská, P., Kvaček, J., 6/2022. Palaeoecological study of Cenomanian flora with emphasis on extremophilic angiosperms. 11<sup>th</sup> European Palaeobotany and Palynology Conference. Stockholm, Sweden.
5. Čepičková, J., 3/2023. Cuticle analysis as the most effective tool in describing Cenomanian leaf fossils. Zlatko Kvaček Memorial. Praha, Czech Republic.
6. Čepičková, J., 9/2023. Nové listové formy bazálních angiosperm v perucko-korycanském souvrství. 11. křídový seminář, Praha, Czech Republic.
7. Čepičková, J., Kvaček, J., 10/2023. Basal angiosperms - New leaf forms from the Peruc-Korycany Formation. 22<sup>nd</sup> Czech-Slovak-Polish Palaeontological Conference, Ostrava, Czech Republic.

**Conference contributions on related topics but not included in this thesis:**

1. Čepičková, J., Veselá, V., Chernomorets, O., Kvaček, J., Sakala, J., Svobodová, M., 11/2021. News from the palaeobotanical research of the Klikov Formation in the South Bohemian Basins. 29<sup>th</sup> International Workshop on Plant Taphonomy. Online.
2. Čepičková, J., Kvaček, J., 5/2022. Dispersed cuticles of the Klikov Formation and their diversity. 21<sup>st</sup> Slovak-Czech-Polish Paleontological Conference. Bratislava, Slovakia.
3. Veselá, V., Čepičková, J., Chernomorets, O., 6/2022. Palaeobotanical research of the Klikov Formation in the South Bohemian Basins (with emphasis on fossil leaves, wood, and palynomorphs). 11<sup>th</sup> European Palaeobotany and Palynology Conference. Stockholm, Sweden.