

# HABILITAČNÍ PRÁCE

## Late Cretaceous Floras in Central Europe and their palaeoenvironment

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## **Abstrakt**

Svrchnokřídové flóry představují unikátní soubor dat, který je nezstupitelný pro pochopení svrchnokřídových terestrických ekosystémů střední Evropy. Na základě čtyř klíčových flór – perucké flóry z cenomanu, klikovské flóry ze santonu až koňaku, idzikowské flóry z koňaku a grünbašské flóry z kampánu lze rekonstruovat základní terestrické ekosystémy – lužní lesy divočících i meandrujících řek, příbřežních močálů, uhlotvorných močálů a slaných marší. Na základě detailních výzkumů lze stanovit vůdčí zkameněliny těchto prostředí. Cenomanské tafocenózy divočící chřek jsou charakteristické druhově chudým společenstvem s úzkými listy angiosperm *Grevilleophyllum* a *Pandemophyllum* s jejich reproduktivními orgány *Mauldinia* a *Pragocladus*. Tafocenóza meandrující řeky vyniká druhovou rozmanitostí s vůdčími typy platanoidních angiosperm *Ettingshausenia* a kopinatými listy *Myrtoidea* s reproduktivními orgány *Anthocephale*. Od santonu výše v říčních tafocenozách převládají listy juglandoidních typů *Juglandiphyllites* a *Dryophyllum*. Příbřežní močály jsou typické přítomností cupresoidních konifer (např. *Cunninghamites*) a velkým množstvím kapradin. Uhlotvorné močály kampánu jsou charakteristické přítomností jednoděložných rostlin (*Pandanites*, *Sabalites*). Typickým prostředím středoevropské pozdní křídy jsou slané marše, vůdčí koniferou je zde *Frenelopsis*. Na základě akcesorických výskytů lze částečně rekonstruovat mesofytní až xerofytní vegetaci tzv. uplandu. Tam se vyskytují xerofytní kapradiny a konifery. V cenomanu jsou pro toto prostředí charakteristické bennettity (*Zamites*, *Cycadeoidea*).

S použitím analýzy CLAMP lze na základě výše zmíněnných flór rekonstruovat paleoklimatické podmínky. Bylo zjištěno, že průměrná roční teplota (MAT) byla v období růstu perucké flóry v cenomanu  $16,5^{\circ}\text{C}$ . MAT v období růstu idzikowské flóry z koňaku byla  $17^{\circ}\text{C}$ . Klikovská flóra ze santonu až koňaku rostla v průměrné teplotě MAT  $15^{\circ}\text{C}$ . Nejchladnější průměrné teploty byly vypočteny pro období růstu flóry z lokality Grünbach z kampánu –  $13,5^{\circ}\text{C}$ . Délka vegetačního období byla nejdelší v cenomanu 9,7 měsíce, nejkratší v kampánu - 7,5 měsíce. Průměrné srážky ve vegetačním období vyšly u všech flór dosti podobně v intervalu 120-145 mm. Na základě výše zmíněnných dat lze konstatovat, že během svrchní křídy se klimatické podmínky ve střední Evropě nijak dramaticky neměnily. Nicméně doložená migrace flór na sever v turonu a na jih během kampánu dokládají teplotní oscilaci s vrcholem v turonu a postupným ochlazováním směrem ke konci křídy.

## Abstract

Late Cretaceous floras in Central Europe provide unique data for understanding Late Cretaceous terrestrial ecosystems. Based on four key floras – the Peruc Flora from Cenomanian, Klikov Flora from Santonian-Coniacian, the Coniacian Idzików Flora and the Campanian of Grünbach, basic terrestrial ecosystems were reconstructed – vegetation of braided and meandering river flood plains, vegetation of back swamps, coal swamps and saltmarshes. Using detailed investigations of fossil plants, we can determine index fossils for each of these environments. Cenomanian taphocoenoses from sediments of braided rivers are characterised by low diversity associations, dominated by entire-margined lanceolate leaves of angiosperms *Grevilleophyllum* and *Pandemophyllum*, with their reproductive structures *Mauldinia* and *Pragocladus*. Taphocoenoses from sediments of meandering rivers are typical in their high diversity, with dominating platanoid leaves (*Ettingshausenia*), and lanceolate leaves *Myrtoidea*, bearing reproductive structures *Anthocephale*. Back swamps are dominated by cupressoid conifers (e.g. *Cunninghamites*) and ferns. Campanian coal-forming swamps are characterised by the presence of monocotyledons (*Pandanites*, *Sabalites*). Saltmarshes dominated by conifer *Frenelopsis* are the most characteristic environment of the Late Cretaceous of central Europe. Based on rare occurrences of allochthonous elements of the flora, it was possible to reconstruct mesophytic/xerophytic vegetation of the uplands. This environment is characterised by the presence of xerophytic pteridophytes and conifers. In the Cenomanian, the most characteristic plant group of this environment are bennettits, with genera *Zamites*, *Cycadeoidea* etc.

Using CLAMP analysis for the above-mentioned floras, palaeoclimatic data were calculated for periods of time when they grew. Mean annual temperature (MAT) for Peruc Flora in the Cenomanian was 16.5 °C; MAT for Idzików Flora from Coniacian was 17 °C; the Klikov Flora of the Santonian flourished in MAT 15 °C; the lowest MAT was calculated for the Grünbach Flora as 13.5 °C. The length of the growing season was longest in the Cenomanian (9.7 months) and shortest in the Campanian (7.5 months). Mean annual precipitation during the growing season was calculated to be quite similar for all floras (120-145 mm). Based on this data, it is possible to state that climatic conditions in Central Europe did not change dramatically during the Late Cretaceous. However, migration of floras northbound in the Turonian and southbound in the Campanian confirms a temperature increase culminating in the Turonian, and a gradual decrease towards the end of the Cretaceous.



## 1 Introduction

Late Cretaceous floras of Central Europe represent one of the most important Cretaceous floras in global scale. Together with the North American Cretaceous floras, they are found in classical areas under investigation since the nineteenth century (e.g. Lesquereux 1892, Berry 1916). Although from a relatively small area, the floras are highly diversified. Their diversification was driven strongly by palaeoecological conditions reflecting their palaeogeographical and geological pathways.

Central Europe was part of the European continental plate, where numerous basins developed as a result of global processes, particularly plate tectonics and eustatic sea level change. Long term eustatic sea-level rise resulted in the highest sea level during the entire Phanerozoic (Hardenbol et al. 1998). In the Late Cretaceous, Central Europe formed an archipelago of several islands in an epicontinental sea, with the largest island formed by the Bohemian and Rhenish Massifs (Voigt et al. 2008, Wilmsen et 2014). Consolidated bedrock of Variscan and Prevariscan age formed most of the basins. Excellent example of such a basin is the Bohemian Cretaceous Basin. In the southern and eastern parts of the studied area, basins associated with Alpine-Carpathian orogeny were formed. Their sediments containing terrestrial palaeobiota are integrated in the Alpine – Carpathian System. They are represented e.g. by the Austro-Alpine Gosau basins.

Generally, the Cretaceous experienced the climax of Mesozoic-Cenozoic greenhouse warming. Climate belts expanded towards the high latitudes and polar ice caps were mostly absent. The Cretaceous thermal maximum, frequently termed the Cretaceous hothouse (Norris et al. 2002), was reached in the early Turonian, with high sea-surface temperatures. Equatorial Atlantic Ocean (~33°C) waters were substantially warmer than today (~27-29°C) (Forster et al. 2006). Beginning in the Coniacian, gradual long-term cooling took place (Jenkyns et al. 1994). Due to its geographical position, Central Europe saw climate fluctuations with alternating Boreal and Tethyan influence.

The Late Cretaceous floras of Central Europe belong to the Southern Laurasian Province, according to Batten (1984) and Crane (1987), and into the European subprovince designated by Vakhrameev (1991). Typical central European Late Cretaceous flora consists of a number of pteridophytes and gymnosperms, but

angiosperms are most common, usually forming prevailing plant groups of palaeoecosystems. Coexistence of ancient Mesozoic gymnosperm taxa e.g. *Sagenopteris*, *Nilssonia*, *Nilssoniopteris*, *Zamites*, *Eretmophyllum* and modern elements, particularly angiosperms, but also the conifer families Pinaceae and Cupressaceae, makes the flora interestingly multiform. This coexistence of new and ancient taxa in one area is a result of long-term evolution and stability of the Tethys coast and its palaeoenvironments in Europe during the Mesozoic.

## 2 History of research

The first fossil plants from the Central European Late Cretaceous were described by Sternberg (1825) as *Lycopodiolites lignitum*, and by Presl in Sternberg (1838) as *Cunninghamites oxycedrus*, *Dammarites albens* and *Thuites gramineus*. Other early papers dealing with Cretaceous plants from central Europe were published by: Zenker (1833), Geinitz (1839-42, 1849, 1850a,b), Reuss (1844), Corda (in Reuss 1846), Ettingshausen (1852), Renger (1866), (Unger (1867), Stur (1873), O. Feistmantel (1870, 1875), K. Feistmantel (1881, 1885) and others. The most important publications of this first period (1820-1885) is probably the contribution by Corda (in Reuss 1846), dealing monographically with flora of the Bohemian Cretaceous. Another important work describing both Cretaceous flora and fauna from the German Late Cretaceous was published by Geinitz (1839-42, 1849-50). Smaller but important papers were published by Göppert (1841) and Heer (1869, 1871). The most important work on Aachen Cretaceous was published by Debey and Ettingshausen (1859a,b). The flora of the Westphalian Cretaceous was described by Hosius and Marck (1880, 1885). Austrian Cretaceous flora was studied by Unger (1852, 1867).

In the 1870s and 1880s, Professor Antonín Frič from the National Museum organized extensive collecting campaigns of fossils, including fossil plants, in the Bohemian Cretaceous Basin. Description of fossil plants was initially in the hands of Otakar Feistmantel (1875), but later the flora was comprehensively described by Josef Velenovský. The monograph on fossil Cretaceous gymnosperms was published by Velenovský (1885a) in his book "Die Gymnospermen aus dem böhmischen Kreideformation". Angiosperms he described several shorter contributions (Velenovský 1882 1883, 1884, 1885b) and a book written in Czech (1889). Ferns were also

monographically described in the book Die Färne der böhmischen Kreideformation descr(Velenovský 1888). Flora of the German Late Cretaceous from Niederschöna was described in shorter contributions by Engelhardt (1885, 1892a,b) and Ettingshausen 1867).

Their work was continued by Bayer (1900; 1901; 1914a,b; 1020, 1921; in Frič & Bayer 1901, 1903), Mařík (1901) and later by Němejc (1926). During the 1910s and 1920s, Velenovský & Viniklář collected and studied a large collection of Cenomanian fossil plants, including numerous reproductive structures. Their work was published monographically in four parts (Velenovský & Viniklář 1926, 1927a, 1929, 1931). Additionally, shorter papers were published by Velenovský & Viniklář (1927b), and Viniklář (1933).

Bayer (1914b, 1921) was the first to use cuticle analysis for description and identification of Cenomanian plants. Němejc (1926), using cuticle analysis correctly identified the fossil plant *Sclerophyllum* as being identical with *Frenelopsis*.

Intensive collecting of Cretaceous plants has been underway since the 1950s, initialized by E. Knobloch, who gathered numerous specimens from newly opened quarries and boreholes. Preliminary data was published by Holý (1962) and Knobloch (1964, 1966a,b, 1967, 1969 a, b, c, 1971, 1985, Knobloch et al. 1968). Later palaeobotanists focused on selected groups, using modern taxonomic and preparation approaches (Hluštík 1972, 1974, 1977a,b, 1976, 1980, 1986, Hluštík and Konzalová 1976a, b, Knobloch 1973, 1974, 1979, 1987a,b; Knobloch & Mai 1984, 1986, 1991, Knobloch & J. Kvaček 1997, J. Kvaček 1992a,b, 1994, 1995, 1997a,b, J., 1999, 2000a,b, Kvaček and Pacltová 2001, Kvaček and Herman 2004, Kvaček et al. 2005). During the 1990s, the Cenomanian palaeoenvironment in the Pecínov and in the Horoušany - Kamenná Panna quarries was studied (Uličný et al. 1997, Nguyen-Tu et al. 2002), in cooperation with sedimentologists, palynologists and geochemists. A monographical description of the Gosau Flora from Grünbach was published by Herman and Kvaček (2010). A number of floras were recently described by the present author in co-authorship with other colleagues. These papers are mentioned in the present text and a selection of them included in the appendix of the present study.

### 3 Geology

In the following chapter all the studied localities including their typical palaeofloristic content are described. Their position is shown in the Fig. 1.

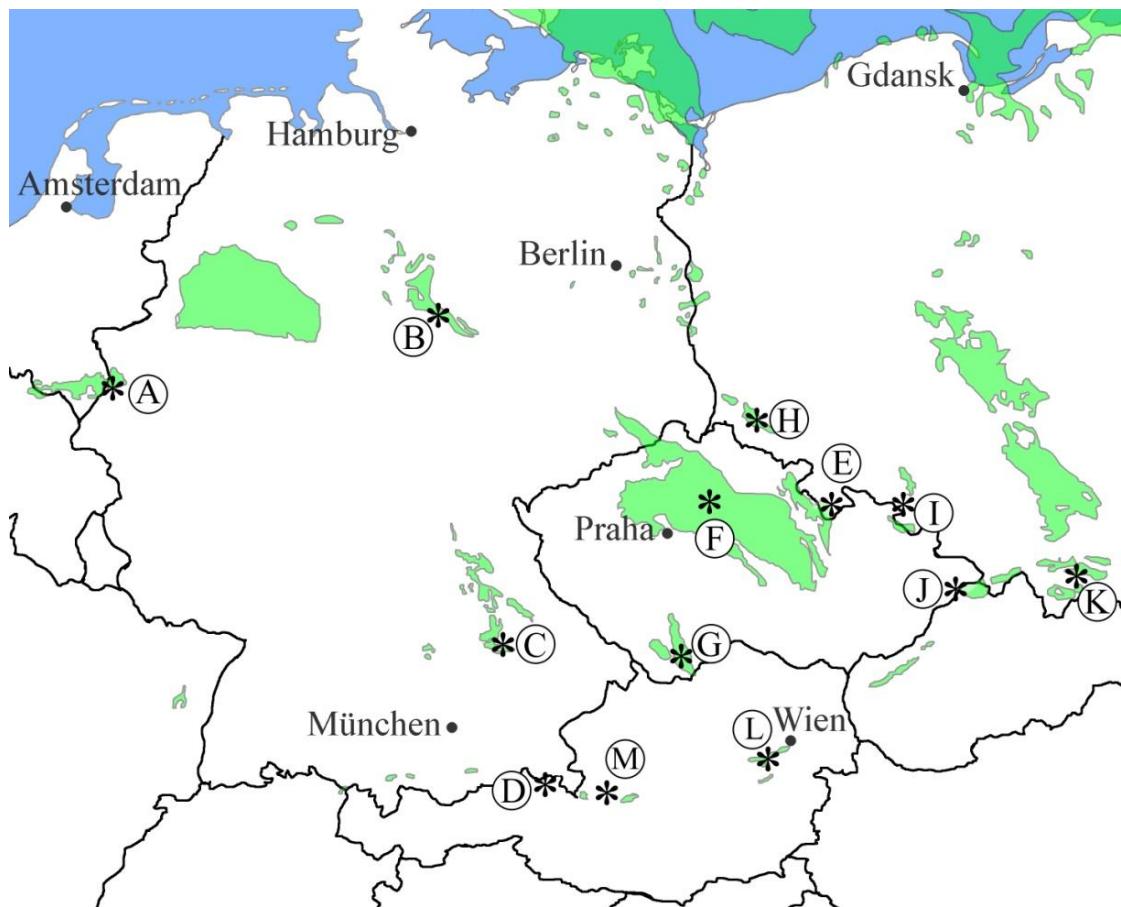


Fig. 1. Geographic distribution of localities. Late Cretaceous deposits highlighted in light grey. A. Aachen area; B. Area of Quedlimburg and Walbeck; C. Amberg-Auerbach area; D. Locality of Kössen, Gosau Series; E. Idików; F. Bohemian Cretaceous Basin; G. South Bohemian Basins; H. Locality Rakowice Małe of North Sudetic Basin; I. Opole Cretaceous Basin; J. Carpathian Flysch of Moravia; K. Locality Rabka-Zaryte of Kanina Formation; L. Neu Welt Basin; M. Salzkammergut Region. Modified from Heřmanová and J. Kvaček (2016).

#### 3.1 Czech Republic

Cretaceous fossil plant material from the Czech Republic comes from two main basins: from the Bohemian Cretaceous Basin and the South Bohemian Basins.

##### Bohemian Cretaceous Basin

The Bohemian Cretaceous Basin, as defined by Čech et al. (1980) and Čech (2011), located in the Bohemian Massif, Middle Europe (Fig. 2), is infilled by Upper Cretaceous freshwater, brackish and marine sediment, Cenomanian to Campanian in age. The Bohemian Cretaceous Basin sensu lato (Fig. 2) encompasses a system of

structural sub-basins filled with deposits of Cenomanian through Santonian age; it formed due to the reactivation of inherited shear zones in basement rocks of the Bohemian Massif during the mid-Cretaceous (e.g., Čech et al. 1980, Valečka and Skoček 1991, Uličný 2001, Herčík et al. 2003, Špičáková et al. 2014). Most of the Bohemian Cretaceous Basin fill consists of shallow-marine deposits, from near-shore and deltaic sandstones to offshore marlstones and local limestones. The basin geometry is asymmetrical, with maximum thickness of sediments at the north-northeastern margin.

The basal-most part of the basin is occupied by the Peruc-Korycany Formation. It is further divided into three units: the Peruc Member (fluvial, marginal marine), the Korycany Member (shallow marine) and the Pecínov Member (offshore marine). The geological terms Peruc and Korycany beds were introduced by Krejčí (1869). The term Pecínov Member was established by Uličný & Špičáková (1996). According to Čech (et al. 1980), Čech (2011) and Špičáková (et al. 2014), the whole formation represents a large body of transgressive sediments, probably with several local regressions. Lower sedimentary bodies are eroded at many places as a result of diachrony; others may expand in thickness, forming very complicated structures. The lowest part of the Peruc Member rich in fossil plants dominated by angiosperms typically includes fluvial sands, pebbly sands, conglomerates and sandstones with mudstone lenses (Uličný & Špičáková 1996, Špičáková et al. 2014). The middle part of the Peruc Member contains mudstones with fossil plants dominated by *Frenelopsis*. It is rich in pyrite concretions. They are products of marginal marine and brackish sedimentation in back swamps and in supratidal marshes. The upper part of the Peruc Member with poor plant fossils consists of cross-bedded sandstones, mudstones and laminites (so called "kanafas"). They are products of sedimentation on a tidal flat crossed by meandering tidal creeks. This sedimentation is well developed in the area of the western part of Central Bohemia (Uličný & Špičáková 1996).

The Korycany Member is built of sandstones containing rich marine fauna and occasionally preserved fossil plants, particularly stems of tree ferns (*Tempskya*), bennettites, conifers and poorly preserved leaf impressions. Intertidal to supratidal mudstones bearing rich megaflora are locally preserved in the uppermost part of the Korycany Member (Pecínov open pit, Uličný 1992, Uličný et al. 1997), reflecting local regression.

The Pecínov Member is a product of deeper offshore sedimentation, and contains glauconite and poorly preserved fauna. Ammonite assemblages from the Pecínov Member (late Cenomanian) are relatively poorly known. Ammonites come predominantly from the *Metoicoceras geslinianum* zone, documented in the higher parts of the Pecínov member (Uličný et al., 1998).

More information dealing with stratigraphy, palaeogeography and palaeontology of the Peruc-Korycany Formation was published by Malkovský in Suk et al. (1984), Uličný & Špičáková (1996), Uličný et al. (1997) and recently by Špičáková et al (2014).

Detailed biostratigraphical studies based on pollen spectra (Pacltová 1977) date the Peruc - Korycany Formation to the upper part of the middle Cenomanian.



**Fig. 2.** Map of the Bohemian Cretaceous Basin (in gray).

#### Březno/Merboltice Formation.

The Březno and Merboltice Formations form the topmost part of the Bohemian Cretaceous Basin (Fig. 2). The Březno Formation ranges from early/middle Coniacian through earliest Santonian in age (Čech, 2011). In northwestern part of the basin it consists of coarse-grained sandstones products of deltaic systems (Nadásky and Uličný 2014) with poorly preserved flora. According to Knobloch and Mai (1986), the plant fossils occur in the lowermost part of the Březno Formation, originally named the Chlomek Beds by Bayer (1886); Halamski and Kvaček (2016) re-described the flora, and indicate its age as Coniacian (Halamski and Kvaček, 2015). The Santonian Merboltice Formation consists mostly of coarse clastics that generally do not yield any plant remains. However, Knobloch and Mai (1986) and Heřmanová (et al. 2016) showed that the regressive, irregularly cyclic, mostly marine sediments of Coniacian to Lower Santonian age yield mesofossil flora (*Caryanthus* spp.). The material comes from boreholes located near the villages of Chřibská, Kerhartice, Markvartice, Mášovice, Stará Huť, Studený, Veselé and Žandov.

## South Bohemian Basins

Mesofossils are particularly common in the Klikov Formation (Coniacian–Santonian age), which is the basal stratigraphic unit of the South Bohemian Basins consisting of two isolated basins - the Třeboň and Budějovice Basins. The formation consists of three lithological types that occur in irregular cyclic sequences: (1) light gray or yellow conglomeratic sandstones; (2) red beds of poorly sorted sandstones, sandy mudstones, or sandy claystones; (3) gray plant-bearing sandstones or claystones with variously distributed coalified plant fragments (Slánská, 1976). The sediments of the South Bohemian Basins are products of fluvial systems (J. Laurin personal communication). Palynological data from Pacltová (1981) suggest Coniacian to Santonian age. Knobloch (1985) suggests Late Turonian–Santonian, based on mesofossils, but this is in contradiction with our data, particularly palaeotemperatures (see below).

## Carpathian Flysch Zone

The Carpathian Flysch Zone represents a complicated unit formed during the Alpine–Carpathian Orogeny. Late Jurassic to early Miocene sediments were transformed by the orogeny, mainly during the middle Miocene, into two groups of nappes of external Western Carpathians. According to Knobloch (1977b) and M. Bubík (personal communication), the mesofossil material (*Caryanthus*) from boreholes Bruzovice Br-4 and Štramberk NJ-50 comes from the Frýdek Formation (Campanian–Maastrichtian). Fossils from the Ráztoka, Řeka and Staré Hamry 3 localities are from the Godula Formation (Coniacian–Campanian). Fossils from Horní Bečva, Horní Bečva–Bůčkový potok, Klín, potok Mečůvka, Staré Hamry 1 & 2 localities are from the Istebská Formation (Campanian–Palaeocene) and the fossils from Rusava locality are from the Soláň Formation (Maastrichtian–Palaeocene).

### 3.2 Czech–Polish border area

Mesofossils from marine sediments of the Opole Cretaceous Basin were extracted from borehole OS-5 near Slezské Pavlovice in Nízký Jeseník. Based on the marine fauna, the plant-bearing sediments are of Late Turonian to Coniacian age. This stratigraphic level corresponds to the Rakowice Wielke Formation of the Opole Cretaceous Basin (Kotański and Radwański, 1977; Voight and Wagreich, 2011). The borehole passes through sediments of Coniacian age with *Inoceramus* cf. *kleinii* G. Müll. and *I. ex gr. Inconstans* Wood (223.3–413.0 m), and through sediments of late Turonian age with *Inoceramus waltersdorffensis* *waltersdorffensis* and *I. striatoconcentricus* *striatoconcentricus* Gümb (413.0–491.5 m) (Knobloch and Mai, 1986).

### 3.3 Poland

The mesofossils studied by Knobloch and Mai (1986) from Rabka-Zaryte locality come from the Kanina Beds, of Campanian age (Bak and Oszczypko, 2000). The specimens from Rakowice Małe locality, Źerkowice Member come from the Rakowice Wielkie Formation and the Czerna Formation including the Nowogrodziec Member, North Sudetic Basin, Coniacian–?Santonian (Leszczyński, 2010). From Knobloch and Mai (1986), it is not clear whether the fossils were picked up from the Czerna or Rakowice Wielkie Formations in quarry at Rakowice Małe. The Cretaceous succession of the North Sudetic Basin comprises marine sediments of marls, limestones, and sandstones (Greguš et al., 2013).

#### Idzikow

The plant material labelled in most collections as Kieslingswalde in German, Idzików in Polish comes from the Upper Nysa Kłodzka Graben, a geological and geographical unit situated in the central part of the Sudetes, the latter being geologically the north-eastern edge of the Bohemian Massif and geographically a mountain range on the border between Poland and the Czech Republic. The Nysa Graben, itself a north-eastern part of the Bohemian Cretaceous Basin, is limited by the Duszniki marginal fault in the north, the Śnieżnik marginal fault in the east, and an unnamed fault in the west (Kędzierski 2002, 2005 and references therein, Don and Wojewoda 2004, Kozdrój 2014). Along these faults, the Nysa Graben is in contact with the Cretaceous Intrasudetic Basin in the north (Góry Stołowe, Stolové hory or Hejšovina) and with two crystalline massifs in the south: the Góry Bystrzyckie (Bystřické hory) to the west and the Śnieżnik Massif (Masyw Śnieżnika, Králický Sněžník) to the east.

The Cretaceous sediments in the Nysa Kłodzka Graben range from the Cenomanian to the Coniacian (Walaszczyk in Voigt et al. 2008). Their total thickness is at least 800 m, according to a minimal estimate by Don and Gotowała (2008), possibly up to 1200 m (Walaszczyk in Voigt et al. 2008). The plant megafossils come nearly entirely from the Idzików Beds. They are defined (Jerzykiewicz 1971) as alternating claystones, sandstones, and conglomerates, overlying a characteristic reference level known as the clinking shales.

They are divided into two following units: 1) The Upper Idzików Beds are composed mainly of littoral sandstones and conglomerates (Jerzykiewicz 1971). Marine macrofauna is abundant there (mostly gastropods and bivalves), and megaflora occurs quite often as well.

2) The Lower Idzików Beds consist of alternating claystones and sandstones (Jerzykiewicz 1971). Its marine fauna is abundant, but megafloral remains are scarce. These beds, however, yielded a rich microflora, composed mostly of marine microplankton, with occasional pollen and spores. Jerzykiewicz & Teissseyre (1974) interpreted the Lower Idzików Beds as flysch sediments. The age of the Lower Idzików Beds has been established as Coniacian, based on the presence of *Scaphites*

*kieslingwaldensis* (Langenhan & Grundey 1891, Rantitsch 1963), *Peroniceras tricarinatum* (Jerzykiewicz 1971) and other fauna.

### 3.4 The Netherlands–Germany border area

Rich charcoalfied mesofossil flora was recovered from the Hergenrath Member (Santonian) of the Aachen Formation from the Liege–Limburg Basin, (Voight and Wagreich, 2011). The Hergenrath Member, 10–35 m in thickness comprises a sequence of alternating light to dark gray, sandy and silty clays, with silty and clayey, light gray fine- to coarse-grained sands, with subordinate fine-grained gravel, silts, minor red clays, and ferruginous horizons (Jagt, 1999). Locally, these beds contain increased amounts of wood debris and root horizons, in parts associated with thin lignite deposits, as well as rich assemblages of autochthonous and parautochthonous gymnosperm and angiosperm fossil remains (Bosma et al., 2009). Where this member rests on a carbonate basement, variegated sandy and silty clays occur at the base. This formation is interpreted as fluvial to limnic in origin, with probable marine ingressions (Jagt, 1999).

### 3.5 Germany

The middle Santonian to early Campanian sediments in the Quedlinburg area have long been known for their spectacular occurrences of leaf impressions, mostly of platanoid affinity (Richter, 1904, 1905; Tschan et al., 2008; Voigt et al., 2004). This locality also yields rich mesofossil flora (Knobloch and Mai, 1986). Cretaceous sediments of this area consist mainly of well-sorted sandstone and intercalated mudstone beds.

Material from the Amberg–Auerbach area is geologically a part of the “Upper Danubian” Cretaceous. Sediments occurring near Riggau belong to the so-called Hessenreuther Forst, which is also a part of the ‘Upper Danubian’ Cretaceous. The terrestrial sediments in which fossil plants are found belong to the Parkstein Member. Because of its terrestrial nature, its stratigraphic position has been rather unclear. The first fossils from Riggau were described by Engelhardt (1905), who thought they were Cenozoic in age. Knobloch (1971) was the first to correctly identify the flora from Riggau as Cretaceous, and estimated a Cenomanian–Turonian age. Schweigert (1992) questioned this, and using his own identifications of fossil plants, suggested again a Palaeogene age for the strata. However, later studies (Niebuhr, Pürner & Wilmsen, 2009) argued again for a Cretaceous age, and assigned the sediments to the Turonian–Campanian. The latest study by Niebuhr et al. (2011), using an integrated (sequence) analysis of the whole Danubian Cretaceous, based on borehole sections and surface exposures, correlated the Parkstein Member of the Hessenreuth Formation with the Roding Formation of the Bodenwöhler Senke, which is of Turonian age.

### 3.6 Austria

Fossil plant megafossils and mesofossils from the Gosau Series come from numerous localities in the Austrian Alps. The Gosau Series is divided into six formations, and consists predominantly of continental deposits ranging in age from late Santonian to Eocene (Rasser and Harzhauser, 2011). Megafossils are known from numerous localities south of Vienna from the Grünbach Formation, forming part of the Gosau Group in the Grünbach– Neue Welt Basin in the Eastern Calcareous Alps. Numerous, usually small Gosau basins, widespread in Austrian territory, are filled by predominantly clastic sediments of the synorogenic Gosau Group, which represents a distinct sedimentary cycle (Plöchinger 1961, Summesberger 1997; Summesberger et al. 2000a,b, 2002).

Most plant fossils in the Gossau Formation come from quite high Cretaceous, particularly Campanian. There is one exception: the Tambergau Florula, which is interpreted as coming from the Cenomanian (Tyroff 1984).

The rich shallow-marine fauna of the Campanian-Maastrichtian part of the Gosau Group belongs to the Thetian Realm (Kollmann 2000). The Grünbach – Neue Welt Basin is one of the largest Gosau basins. It represents a syncline (Grünbach Syncline) with an overturned northwest limb (Plöchinger 1961). The Brezova Series in the Little Carpathians (Slovakia) may denote the emerged north-eastern end of the Grünbach – Neue Welt Basin (Summesberger 1997). The predominantly terrigenous clastic infill of the basin (Gosau Group) consists of six lithostratigraphic units of Late Santonian to Eocene age (Summesberger 1997; Summesberger et al. 2002): the Kreuzgraben Formation (Upper Santonian), Maiersdorf Formation (Upper Santonian), Grünbach Formation (Lower Campanian), Piesting Formation (Upper Campanian – Maastrichtian), Zweiersdorf Formation (Danian – Paleocene) and Willendorf Formation (Eocene).

Another important area where the Gosau Group bears plants is in Salzkammergut region. Exposures of plant -bearing Late Cretaceous fine clastic rocks are rather rare in the Salzkammergut. However, Dr. Herald Lobitzer and his colleague, collector Wolfgang Maherndl, from Bad Ischl discovered or re-discovered four localities, from Neualm and Neffgraben in Russbach am Pass Gschütt, from Tiefengraben near St. Wolfgang and from Häuslkogel (correctly Heisslbauerkogel) in Jainzen in the West of Bad Ischl. These localities represent different formations and depositional environments of the Lower Gosau Subgroup.

#### Neualm

Since the classical paper by Moravian geologist Ferdinand Stoliczka (1860), the bright coal-bearing freshwater deposits Southwest of Neualm respectively Northeast of Russbach am Pass Gschütt village are well known. Stoliczka described freshwater gastropods and also a small „dinosaur tooth“ Stoliczka (1860). Much later, Eric Buffetaut (1979) restudied the tooth and discovered that it is a part of the tribodont denture (crushing teeth) of an alligator. The locality has been studied repeatedly from

different points of view, for instance by Rantitsch et al. (1995) in respect of the inorganic geochemistry of the coal.

At present, only scarce evidence of the long-since abandoned small-scale coal mine close to Neualm can be seen. The locality can be reached via a forest road, which comes from the Randograben forest road. In laminated black shales, the lamination probably reflects a seasonal rhythmic sedimentation, which is typical for sapropelic sediments deposited in stagnant „coal swamps“. Small squashed white chalkified gastropods, scarce bivalves and black carbonized plant remains are occasionally enriched on the bedding planes. The latter remained preserved, because they were instantly protected by a thin layer of clayey sediment. Fossil plants include twigs of coniferous foliage of *Pagiophyllum* type with rare conifer ovuliferous cone, fragments of ferns and angiosperm leaves.

The occurrence of coal-bearing fossiliferous freshwater deposits near to Neualm lithologically is attributed to the alluvial fan deposits of the basal Gosau sedimentary cycle of the Kreuzgraben Formation.

### Russbach, Neffgraben

One of the most prominent fossil-localities of the Lower Gosau-Subgroup is the Neffgraben, a creek South of the village Russbach am Pass Gschütt. On top of the conglomerates of the Kreuzgraben Formation, a few hundred meters thick sequence of intercalating marls and sandstones is exposed. The upper part of this sequence is represented by the so called „Hofergrabenmergel“ (Kollmann & Summesberger, 1982), grey sandy marls, which are occasionally rich in macrofossils, in particular of molluses and corals, respectively by corals and hippurites. Fossil plants include leaf impressions of ferns and angiosperms. According to Höfling (1985), the Hofergrabenmergel were deposited in the „middle shelf“; other authors consider them turbid water sediments.

### Tiefengraben near St. Wolfgang

A small and relatively well preserved fossil flora was collected in Tiefengraben, below the farmhouse Holzerbauer near St. Wolfgang. Plants from this locality were already described by Unger (1867). Our material comes from terrigenous, partly laminated and sandy mudstones, and grey marls with comparatively well preserved fossil leaves, associated with thin coal seams. Limnic gastropods (Melaniids) can also be found there. Dark mudstone associated with coal seams contains numerous large fragments of strap-like leaves of fossil pandanus *Pandanites trinervis* (Kvaček and Herman, 2004a). Besides the dominant *P. trinervis*, other fossil plants, particularly angiosperm leaves are present (*Dicotylophyllum* sp., *Dryophyllum* sp.). Laminated sandy claystones to sandstones are exposed cca 5-10 m above the coal seam (5–10 m upstream). They are dominated by fragments of angiosperm leaves. Sandy claystones

are interpreted as possible fluvial deposits bearing flora dominated by angiosperm leaves. Palaeoecology of Tiefenbach / St. Wolfgang is interpreted as a coal swamp with *Pandanites trinervis* as the most important coal-forming plant.

### Heisslbauerkogel west of Bad Ischl

Relatively diverse, but rather poorly preserved fossil angiosperm and gymnosperm flora is known from the North of Jainzen village west of Bad Ischl. The small outcrop is situated in a creek on the slope of Heisslbauerkogel (also „Häuslkogel“), close to the Heisslbauer farmhouse. Strata where fossil plant impressions (angiosperm leaves *Dicotylophyllum* sp.) occur consist of grey, slightly bituminous and partly laminated calcareous pelitic sediments. They are considered to be part of the Kreuzgraben Formation of the Lower Gosau-Subgroup, and overlie with an unconformity Late Triassic Hauptdolomit. The marls are of freshwater origin, and most probably Turonian. Hit with a hammer, they exude a volatile bituminous smell.

Mesofossils of the Gosau Group described from the locality of Kössen near Salzburg (Knobloch, 1975), located in the valley of the Muhlberger brook, come from late Campanian to early Maastrichtian turbiditic sediments (Butt, 1980). Stratigraphy is based on planktonic foraminifera from fine-grained parts of the turbidites. The mesofossils are found in fine to medium sorted gray sandstone, in basal parts of individual cycles.

The mesofossil material from the locality of Wietersdorf (quarry of cement factory near Wietersdorf, north east of Villach, Kärten, Knobloch and Mai, 1986) is assigned to the Campanian of the Krappfel Group (Sanders et al., 2004). Stratigraphy of the group is based on foraminifers (Sanders et al., 2004) and strontium isotope ratios of rudist shells (Steuber, 2001).

## 4 Preservational types

### 4.1 Megafossils

Leaf compression and compressions are the most frequent megafossils in Late Cretaceous. Permineralised wood and stems occur rarely in particular strata in the Korycany Sandstone or Gosau Group.

#### 4.1.1 Leaf Impressions

Leaf impressions are probably the most frequent preservations of fossil plants. Fossils plant remains show impressed external morphologies of leaves and usually their venation. Although quite common they provide only limited amount of characters. Particularly entire-margined leaves lacking venation which are usually prevailing in the

Cretaceous strata are difficult to be characterised and assigned to particular genus or family. They are described as morphotypes and used particularly for CLAMP analysis (Wolfe and Spicer 1999). However even there we have a good chance to distinguish major plant groups as pteridophytes, conifers and angiosperms. Angiosperm leaves are seemingly similar to recent genera as at first determined by Velenovský (1882-1885a). This fact was particularly in Cretaceous floras challenged by various authors (e.g. Upchurch and Dilcher 1990, Herman and Kvaček 2010). Despite these difficulties e.g. presence of intramarginal vein or perpendicular tertiary veins and other characters can help us to assign taxa at least to fossil genera.

#### 4.1.2 Leaf compressions

Study of leaf compressions provide much more details. Fossil leaves in such a case are fossilised including their cuticle. Internal tissues are transformed into coal, while cuticle thanks to its very stable waxy nature survives fossilisation processes. It usually provides preserved epidermal pattern which can be studied using light, fluorescence or electron microscopes. Cuticle analysis provides details of epidermal leaf anatomy (for more information see Jones and Rowe 1999), which can help us to assign fossil leaves to taxa with higher precision (Upchurch and Dilcher 1993). We can at least identify larger plant groups, e.g. distinguishing cycads and bennettits (Kvaček 1995). The most important for identification are stomata and their type. Resin bodies present in mesofil are also useful for identification, they are typical for lauroids Chloranthaceae and obviously for conifers. Apart of type of stomata, presence or absence of indumentum, cuticle provides information about palaeoecology. Thickly cutinised taxa with frequent occurrence of papillae are typical for xerophytic to mesophytic or halophytic environments. Thin cuticles are typical for hydrophilous and deciduous plants.

## 4.2 Mesofossils

Fruits and seeds in Cretaceous of Central Europe were documented by Knobloch et Mai (1986). Although the monograph is now more than 30 years old with brief descriptions, this work is still valid and serves as a good starting point for studies of Late Cretaceous mesofossils. Within the monograph small amount of mesofossils is described from the Bohemian Cenomanian. Their number was remarkably increased by studies of Eklund and Kvaček (1998), Kvaček and Eklund (2003), Kvaček and Friis (2010) and Kvaček (et al. 2016). Mesofossil are preserved as lignified or charcoalified fossil: megaspores, seeds, fruits, inflorescences, infructescences, flowers, wood, cones, and fragments of leaves. Particularly charcoal, which is very common in the Cenomanian of Central Europe suggests presence of regularly occurring fires. Mesofossils preserve number of details including pollen *in situ*. In combination with megafossils, leaves, inflorescences, and wood they serve as an important source of fossil data for whole plant reconstructions. e.g. bilobed structures frequently occurring isolated in association with reproductive structures earlier described as *Ceratostrobus squamosus*, later separated

from the conifer species (*Brachyphyllum squamosum*). They can be interpreted as parts of angiosperm inflorescence/infructescence *Mauldinia bohemica*. They were found attached to leaves *Grevilleophyllum constans*. Mesofossils help us in understanding of the angiosperm reproductive structure *Myricanthium*. Its systematics was changed using mesofossils and is interpreted as close to Chloranthaceae. Study of well preserved material from Praha-Hloubětín and Brník were resulted in description of a new genus *Zlatkocarpus*

Large amount of mesofossils was described by Knobloch and Mai (1986) from the Turonian-Santonian of the South Bohemian Basins. Two key genera were currently revised. *Budvaricarpus* consisting of three unified fruits was interpreted as an infructescence (Heřmanová et al. 2011), while *Caryanthus* remained as separate fruits / flowers (Heřmanová and Kvaček 2012, 2016). Both genera are assigned to plants of Normapolles complex.

## 5 Palaeofloristics

This chapter describes key Late Cretaceous floras of the Central Europe. The Peruc Flora is revised herein, the Klikov, Idzików and Grünbach floras were revised in papers by Váchová and Kvaček (2009), Herman and Kvaček (2010) and Halamski and Kvaček (2015).

### 5.1 Peruc Flora

The Peruc Flora comprises a high number of mega- and meso-fossils. It is characterised by a high percentage of angiosperms, particularly early angiosperms – chloranthoids, magnoliids and early eudicots - platanooids. However, there is still a comparatively high number of relict taxa surviving from the Early Cretaceous and Jurassic (*Sagenopteris*, *Nilssonia*, *Anomozamites*, *Cycadeoidea*, *Nilssoniopteris*, *Zamites*, *Eretmophyllum*). After revision of most of the important taxa, there are 255 species representing: Lycopodiophyta (1 species), Polypodiophyta (48 species), Gymnospermophyta, Caytoniales (1 species), Cycadales (7 species), Bennettitales (8 species), Ginkgoales (4 fossil species belonging to one natural species), Pinales, (62 species), Erdmanithecales (1 species) and Angiospermophyta (123 species). Additionally, there is a group of 20 fossil plant species of unknown or problematic affinity. The larger part of fossil angiosperms (66 species) are dicot leaves, which were used for CLAMP analysis.

The revised taxa are listed in the following (Table 1). They are accompanied by their occurrences in most rich and known localities.

## Table of Peruc Flora.

**Explanation of abbreviations:** A. Praha-Hloubětín, B. Praha-Hloubětín- Hutě, C. Vyšehořovice, D. Kounice, E. Mělník, F. Lanšperk, G. Bohdánkov, H. Lipenec, I. Peruc, J. Mšeňé-Lázně, Lidice, L. Otruby, M. Praha-Vidoule,, N. Praha-Malá Chuchle, O. Touchovice, P. Pecínov, Q. Praha-Klíčov, R. Praha-Slivenec, S. Lázně Bělohrad, T. Rudka, U. Kunštát, V. Starý Maletín, W. Horoušany, X. Brník, Y. Velké Opatovice, partly after Frič and Bayer 1901).

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	
<b>LYCOPODIOPHYTA:</b>																										
Selaginella dichotoma VELENOVSKÝ			x														x									
<b>PTERIDOPHYTA:</b>																										
Acrostichum cretaceum VELENOVSKÝ			x					x																		
Acrostichum tristaniaeophyllum BAYER																x										
"Acrostichum" touchovicense KNOBLOCH																	x									
Adiantites sp.																							x			
Anemia fremontii KNOWLTON																x						x	x			
Asplenium dicksonianum HEER																					x					
Asplenium foersteri DEBEY & ETTINGSHAUSEN			x	x																						
Cladophlebis cf. albertsii (DUNKER) BRONGNIART		x													x	x	x							x		
Cladophlebis frigida (HEER) SEWARD		x	x	x					x	x	x												x			
Dipteriphyllum cretaceum (VELENOVSKÝ) KRASSER		x										x														
Drepanolepis cretacea VELENOVSKÝ & VINIKLÁŘ																			x				x			
Drepanolepis triloba VELENOVSKÝ & VINIKLÁŘ															x											
Filicophyllum dentatum VELENOVSKÝ & VINIKLÁŘ												x									x					
Gleichenia acutiloba HEER						x															x					
Gleichenia crenata VELENOVSKÝ	x	x																								
Gleichenia delicatula HEER	x	x			x	x					x	x			x	x										
Gleichenia fricci BAYER																	x				x					
Gleichenia integra VELENOVSKÝ & VINIKLÁŘ												x														
Gleicheniaceaephylloides kurrianum (HEER) GREGUŠ & J. KVAČEK																					x	x				
Gleichenia multinervosa VELENOVSKÝ	x								x			x			x		x									
Gleichenia rotula HEER			x																							
Gleichenia sternbergii VELENOVSKÝ & VINIKLÁŘ				x																						
Gleichenia vidovagensis MARÍK															x											
Gleichenia votrubensis BAYER													x			x		x	x	x		x	x			
Gleichenia zippei (CORDA) HEER	x	x	x			x		x	x	x	x	x		x	x	x	x	x	x		x	x				
Gymnogramme bohemica BAYER						x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x		

TAXON	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y		
<i>Jeanpaulia carinata</i> VELENOVSKÝ			x	x										x	x					x							
<i>Konijnenburgia bohemica</i> J.KVAČEK et al.			x																								
<i>Phlebopteris dunkeri</i> (SCHENK) SCHENK	x		x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				x			
<i>Marattia cretacea</i> VELENOVSKÝ				x																							
<i>Marsilia cretacea</i> BAYER		x				x																					
<i>Matonia pussila</i> VELENOVSKÝ & VINIKLÁŘ													x														
<i>Matonidium weisneri</i> (KRASSER) SEWARD															x			x			x						
<i>Monheimia</i> cf. <i>aquisgranensis</i> DEBEY & ETT.							x							x			x										
<i>Nathorstia fascia</i> (BAYER) NATHORST	x	x									x	x		x	x		x	x		x	x						
<i>Oncopteris nettwallii</i> DORMITZER			x																								
<i>Onychiopsis capsulifera</i> (VELENOVSKÝ) SEWARD	x	x	x	x	x						x		x	x		x		x		x		x		x			
<i>Onychiopsis cretacea</i> (VEL. & VINIKLÁŘ) KNOBLOCH																											
<i>Osmundophyllum</i> sp.															x												
<i>Osmundophyllum cretaceum</i> VELENOVSKÝ						x									x												
<i>Pecopteris minor</i> VELENOVSKÝ													x			x											
<i>Raphaelia lobifolia</i> (CORDA) KNOBLOCH									x																		
<i>Protopteris maletinensis</i> GREGUŠ & J. KVAČEK		x																			x						
<i>Protopteris punctata</i> (STERNBERG) STERNBERG	x	x																									
<i>Schizaeopsis ekrtii</i> J. KVAČEK et al.																					x						
<i>Sphenopteris cretacea</i> VELENOVSKÝ & VINIKLÁŘ									x					x	x												
<i>Tempskya varians</i> (CORDA) VELENOVSKÝ												x					x				x						
<i>Viniklaria cenomanica</i> KNOBLOCH													x			x											
<b>GYMNOSPERMOPHYTA, CAYTONIALES:</b>																											
<i>Sagenopteris variabilis</i> (VELENOVSKÝ) VELENOVSKÝ													x		x							x					
<b>GYMNOSPERMOPHYTA, CYCADALES:</b>																											
<i>Dioonites cretosus</i> (REICH) SCHIMPER																		x		x							
<i>Jirusia jirusii</i> (BAYER) DOMIN	x																										
<i>Mesenea bohemica</i> (CORDA) J. KVAČEK		x	x	x					x	x	x	x	x	x	x												
<i>Microzamia gibba</i> (REUSS) CORDA	x	x							x	x	x	x									x						
<i>Nilssonia bohemica</i> VELENOVSKÝ								x				x													x		
<i>Nilssonia holyi</i> KVAČEK et Knobloch																x								x			
<i>Pseudoctenis babinensis</i> J. KVAČEK												x															
<b>GYMNOSPERMOPHYTA, BENNETITALES:</b>																											
<i>Anomozamites</i> sp. 1																									x		
<i>Anomozamites</i> sp. 2																					x						
<i>Cycadeoidea</i> sp.													x														

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<i>Nilssoniopteris pecinovensis</i> J. KVAČEK																x									
<i>Nilssoniopteris</i> sp.																								x	
<i>Velenovskia opatovicensis</i> KNOBLOCH																								x	
<i>Zamites bayeri</i> J. KVAČEK															x										
<i>Zamites</i> cf. <i>bayeri</i> J. KVAČEK																			x				x		
<b>GYMNOSPERMOPHYTA, GINKGOALES:</b>																									
<i>Eretmophyllum obtusum</i> (VELENOVSKÝ) J. KVAČEK	x	x					x		x						x							x			
<i>Ginkgoxylon gruettii</i> PONS & VOZENIN-SERRA																	x								
<i>Nehvizdyella bipartita</i> J. KVAČEK et al.																						x			
<i>Pecinovicladus kvacekii</i> FALCON-LANG															x										
<b>GYMNOPSERMOPHYTA, PINALES:</b>																									
<i>Abies chuchlensis</i> VELENOVSKÝ														x											
<i>Alvinia bohemica</i> (VELENOVSKÝ) J. KVAČEK		x				x								x											
<i>Araucariopsis cretacea</i> VELENOVSKÝ & VINIKLÁŘ																x					x				
<i>Brachiphyllum squamosum</i> (VELENOVSKÝ) PALIBIN	x														x		x				x				x
<i>Cephalotaxites perucensis</i> VELENOVSKÝ & VINIKLÁŘ	x					x			x																
<i>Ceratostrobus echinatus</i> VELENOVSKÝ	x			x										x	x										
<i>Ceratostrobus sequoiaphyllus</i> VELENOVSKÝ						x			x																
<i>Chamaecyparis cretacea</i> VELENOVSKÝ & VINIKLÁŘ													x												
<i>Chamaecyparites charonis</i> VELENOVSKÝ						x	x					x													
<i>Cunninghamites johannae</i> J. KVAČEK				x																					
<i>Cunninghamites lignitum</i> (PRESL) J. KVAČEK	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Cunninghamites ubaghsii</i> DEBEY																						x			
<i>Cyparissidium minimum</i> VELENOVSKÝ	x				x																				
„ <i>Dammara</i> “ <i>borealis</i> HEER	x	x	x	x	x	x	x	x	x	x						x	x	x	x						
<i>Dammarites albens</i> PRESL in STERNBERG	x	x	x		x			x		x	x														
<i>Dammarophyllum striatum</i> (VEL.) VEL. ex J. KVAČEK						x								x			x		x				x		
<i>Dammarophyllum</i> sp.																					x				
<i>Distroichostrobus pussilus</i> VELENOVSKÝ & VINIKLÁŘ													x												
<i>Elatocladus macilenta</i> (HEER) SEWARD		x				x		x							x	x									
<i>Elatocladus velenovskyi</i> J. KVAČEK	x	x	x		x	x	x	x	x									x	x			x	x		
<i>Ephedropsis otrubensis</i> VELENOVSKÝ & VINIKLÁŘ											x														
<i>Ephedropsis strobilifera</i> VELENOVSKÝ & VINIKLÁŘ		x	x				x				x	x			x	x		x							

TAXON	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	
<i>Frenelopsis alata</i> (FEISTMANTEL, K.) KNOBLOCH	x		x			x	x					x		x	x	x							x			
<i>Geinitzia reichenbachii</i> (GEINITZ) HOLLICK & JEFFREY									x			x		x	x	x	x			x	x	x				
<i>Inolepis imbricata</i> HEER			x							x								x								
<i>Microlepidium striatum</i> VELENOVSKÝ	x						x																			
<i>Masculostrobus</i> sp. 1																							x			
<i>Masculostrobus</i> sp. 2																						x				
" <i>Picea</i> " <i>cretacea</i> VELENOVSKÝ		x																								
<i>Pinus belohradensis</i> BAYER																			x							
<i>Pinus kettneri</i> VELENOVSKÝ & VINIKLÁŘ			x																							
<i>Pinus landsbergensis</i> J. KVAČEK				x																						
<i>Pinus protopicea</i> VELENOVSKÝ		x																								
<i>Pinus quenstedtii</i> HEER		x			x								x	x	x					x						
<i>Pinus vyserovicensis</i> VELENOVSKÝ & VINIKLÁŘ		x																								
<i>Pinus</i> sp.													x	x					x			x				
<i>Pityospermum pecinovense</i> KNOBLOCH & MAI													x			x										
<i>Plutonia cretacea</i> VELENOVSKÝ		x	x			x							x													
<i>Podocarpus cretacea</i> VELENOVSKÝ			x										x													
<i>Podocarpus mucronatus</i> VELENOVSKÝ & VINIKLÁŘ																			x							
<i>Podozamites bohemicus</i> VELENOVSKÝ & VINIKLÁŘ		x		x									x													
<i>Podozamites eichwaldii</i> (SCHIMPER) HEER													x													
<i>Podozamites lanceolatus</i> (LINDLEY & HUTTON) HEER					x	x							x						x			x		x		
<i>Podozamites latipennis</i> HEER		x			x								x			x										
<i>Podozamites longipennis</i> VELENOVSKÝ					x								x													
<i>Podozamites major</i> VELENOVSKÝ & VINIKLÁŘ							x							x												
<i>Podozamites pusillus</i> VELENOVSKÝ													x			x			x							
<i>Quasisequoia crispa</i> (VELENOVSKÝ) J. KVAČEK	x					x			x	x	x		x	x	x											
" <i>Sequoia</i> " affinis VELENOVSKÝ & VINIKLÁŘ													x													
" <i>Sequoia</i> " elongata BAYER		x																								
" <i>Sequoia</i> " fastigiata (STERNBERG) HEER								x											x	x	x					
" <i>Sequoia</i> " cylindrica VELENOVSKÝ & VINIKLÁŘ									x									x								
" <i>Sequoia</i> " major VELENOVSKÝ	x	x	x			x			x			x			x			x								
" <i>Sequoia</i> " minor VELENOVSKÝ		x							x										x							
" <i>Sequoia</i> " rigida HEER					x				x																	
" <i>Sequoia</i> " sp.														x				x			x			x		
<i>Sequoiopsis perucensis</i> VELENOVSKÝ & VINIKLÁŘ	x														x				x							
<i>Sphenolepis pecinovensis</i> J. KVAČEK														x				x								
<i>Taxodium boheticum</i> KNOBLOCH & MAI													x													

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<i>Thuites alienus</i> STERNBERG												x			x								x		
<i>Widdringtonia graminea</i> (STERNBERG) KNOBLOCH	x	x	x	x	x	x	x	x	x	x	x				x	x	x	x	x	x	x	x	x		
<i>Widdringtonites otrubensis</i> VELENOVSKÝ & VINIKLÁŘ											x														
<b>GYMNOSPERMOPHYTA, ERDMANITHECALES</b>																									
<i>Bayeritheca hughesii</i> J.KVAČEK & PACLOVÁ			x																						
<b>ANGIOSPERMOPHYTA, MAGNOLIOPSIDA:</b>																									
<i>Antohocephale chuchlensis</i> KVAČEK												x													
„Aralia“ cf. <i>saportanea</i> LESQUEREAUX			x												x										
<i>Araliphyllum anisolum</i> (VELENOVSKÝ) VELENOVSKÝ						x																			
<i>Araliphyllum daphnophyllum</i> (VELENOVSKÝ) VELENOVSKÝ	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x								
<i>Araliphyllum decuurrens</i> (VELENOVSKÝ) VELENOVSKÝ		x																				x			
<i>Araliphyllum dentiferum</i> (VELENOVSKÝ) VELENOVSKÝ												x				x									
<i>Araliphyllum formosum</i> (HEER) VELENOVSKÝ	x					x	x	x			x	x								x	x	x			
<i>Araliphyllum kowalewskianum</i> (SAPORTA) VELENOVSKÝ		x	x			x																x			
<i>Araliphyllum minor</i> (VELENOVSKÝ) VELENOVSKÝ		x																							
<i>Araliphyllum propinquum</i> (VELENOVSKÝ) VELENOVSKÝ		x	x													x									
<i>Araliphyllum transitivum</i> (VELENOVSKÝ) VELENOVSKÝ		x	x												x	x									
<i>Araliphyllum trilobum</i> (VELENOVSKÝ) VELENOVSKÝ		x													x										
<i>Asterocelastrus cretaceus</i> VELENOVSKÝ & VINIKLÁŘ												x							x						
<i>Banksicarpus cretaceus</i> VELENOVSKÝ & VINIKLÁŘ		x																							
<i>Banksiphyllum pusillum</i> (VELENOVSKÝ) VELENOVSKÝ						x									x										
<i>Bombacophyllum argillaceum</i> (VEL.) VELENOVSKÝ		x	x					x	x												x				
<i>Bombacophyllum coriaceum</i> VELENOVSKÝ & VINIKLÁŘ		x																							
<i>Bresciphyllum cretaceum</i> VELENOVSKÝ											x	x			x										
<i>Budvaricarpus serialis</i> KNOBLOCH & MAI			x																						
<i>Butomites cretaceus</i> VELENOVSKÝ	x	x	x		x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x		
<i>Callistemon cretaceum</i> VELENOVSKÝ		x																							
<i>Callistemophyllum bruderii</i> ENGELHARDT			x												x			x							
<i>Caryanthus triasseris</i> (KNOBLOCH) KNOBLOCH & MAI		x																							
<i>Ceratoxylon laterale</i> VELENOVSKÝ & VINIKLÁŘ		x																x							

TAXON	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	
<i>Cissophyllum exulum</i> (VELENOVSKÝ) VELENOVSKÝ	x		x														x									
<i>Cissophyllum vitifolium</i> VELENOVSKÝ													x													
<i>Coccophyllum cinnamomeum</i> (VELENOVSKÝ) VELENOVSKÝ	x	x					x	x									x									
<i>Conospermites hakeaefolius</i> ETTINGSHAUSEN							x	x	x		x	x	x	x	x	x										
<i>Cupulicarpus fechteri</i> VELENOVSKÝ & VINIKLÁŘ																			x							
<i>Cussoniphylum partitum</i> (VELENOVSKÝ) VELENOVSKÝ		x			x																					
<i>Daphnophyllum slivenense</i> VELENOVSKÝ & VINIKLÁŘ																			x							
<i>Debeya coriacea</i> (VEL.) KNOBLOCH	x	x	x			x	x	x	x		x	x	x	x	x	x	x						x			
<i>Debeya pentaphylla</i> (VELENOVSKÝ) KNOBLOCH					x						x	x														
<i>Diceras cenomanicus</i> VELENOVSKÝ		x																								
<i>Dicotylophyllum araliopsis</i> (VELENOVSKÝ & VINIKLÁŘ) KNOBLOCH		x									x															
<i>Dicotylophyllum macrophyllum</i> (HEER) GREGUŠ & J.KVAČEK																				x						
<i>Dicotylophyllum velenovskyi</i> KNOBLOCH																			x				x			
<i>Diospyrophylum provectum</i> (VELENOVSKÝ) VELENOVSKÝ			x	x									x													
„ <i>Diospyros</i> “ cretacea VELENOVSKÝ & VINIKLÁŘ	x																x					x				
<i>Diplophyllum cretaceum</i> VELENOVSKÝ & VINIKLÁŘ							x																			
<i>Diplophyllum primigenium</i> (SAPORTA) KNOBLOCH		x	x																							
<i>Diplostrobus stupeckyanus</i> VELENOVSKÝ & VINIKLÁŘ		x																		x				x		
“ <i>Dryandra</i> ” bayeri VELENOVSKÝ & VINIKLÁŘ									x				x		x											
“ <i>Dryandra</i> ” cretacea VELENOVSKÝ	x			x						x			x		x			x		x	x	x				
<i>Ettingshausenia bohemica</i> (VEL.) J.KVAČEK & VÁCHOVÁ		x	x	x											x			x					x			
<i>Ettingshausenia cuneifolia</i> (BRONN) STIEHLER									x	x								x		x	x	x	x			
<i>Ettingshausenia laevis</i> (VEL.) J. KVAČEK & VÁCHOVÁ		x	x	x							x		x		x		x		x							
„ <i>Eucalyptus</i> “ harrachii BAYER	x																									
„ <i>Ficus</i> “ perunii VELENOVSKÝ	x	x																								
„ <i>Ficus</i> “ stylosa VELENOVSKÝ		x							x																	
„ <i>Ficus</i> “ suspecta VELENOVSKÝ	x																x									
„ <i>Grevillea</i> “ dvorakii BAYER										x		x		x		x										
<i>Grevilleophyllum constans</i> (VELENOVSKÝ) VELENOVSKÝ	x	x	x	x					x	x	x		x	x	x		x									
<i>Grevilleophyllum tenerum</i> (VELENOVSKÝ) VELENOVSKÝ					x																					
<i>Halyserites elegans</i> (VELENOVSKÝ) KNOBLOCH	x	x															x	x						x		
<i>Halyserites reichii</i> STERNBERG		x						x					x		x		x		x							
<i>Hederaephyllo</i> sp.																	x									

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<i>Hederaephyllum credneriaeefolium</i> (VELENOVSKÝ) VELENOVSKÝ			x	x																					
<i>Hederaephyllum primordiale</i> (SAPORTA) VELENOVSKÝ			x	x			x										x				x				
<i>Hymenaeophyllum elongatum</i> VELENOVSKÝ																	x								
<i>Illiciphyllum deletum</i> VELENOVSKÝ							x																		
<i>Ingophyllum latifolium</i> (VELENOVSKÝ) VELENOVSKÝ			x																						
<i>Kalinaia decatepala</i> BAYER			x								x														
<i>Laramisamen hypericoides</i> KNOBLOCH & MAI												x													
<i>Laurophyllum acuminatum</i> (GOEP.) HALAMSKI & J.KVAČEK				x																					
„Laurus“ plutonia HEER						x			x			x													
<i>Leptospermum cretaceum</i> VELENOVSKÝ			x																						
<i>Liriodendropsis simplex</i> (NEWBERRY) NEWBERRY											x	x			x		x		x		x		x		
<i>Magnoliaephyllum alternans</i> (HEER) GREGUŠ & J.KVAČEK			x	x	x	x				x		x		x			x	x		x	x				
<i>Magnoliaephyllum</i> sp.																	x	x		x		x			
<i>Mauldinia bohemica</i> EKLUND & J.KVAČEK		x															x								
<i>Menispermophyllum celakovskii</i> VELENOVSKÝ											x							x							
„Myrica“ decidua VELENOVSKÝ & VINIKLÁŘ											x								x						
„Myrica“ fragiliformis (ZENKER) ENGELHARDT			x									x	x		x	x		x	x						
„Myrica“ indigena KRASSER																				x	x				
<i>Myricanthium amentaceum</i> VELENOVSKÝ	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
<i>Myricophyllum denticulatum</i> VELENOVSKÝ & VINIKLÁŘ			x	x																					
<i>Myricophyllum glandulosum</i> VELENOVSKÝ											x														
<i>Myricophyllum serratum</i> (VELENOVSKÝ) VELENOVSKÝ	x	x		x	x										x	x		x							
<i>Myricophyllum zenkeri</i> (ETTINGSHAUSEN) VELENOVSKÝ	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Myrsinophyllum</i> variant VELEN.									x	x															
<i>Myrtophyllum angustum</i> (VELENOVSKÝ) KNOBLOCH	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Myroidea geinitzii</i> (HEER) J.KVAČEK & GREGUŠ	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Oreodaphne cretacea</i> VELENOVSKÝ								x									x								
Paraphyllanthoxylon aff. utahense THAYN et al.																		x							
<i>Pecinovia annonoides</i> J.KVAČEK & EKLUND																		x			x	x		x	
Platanus sp.											x				x		x	x		x			x		
<i>Platanus purkynei</i> VELENOVSKÝ & VINIKLÁŘ																	x								
<i>Pragocladus lauroides</i> J.KVAČEK & EKLUND	x																x								

TAXON	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<i>Proteoides acuta</i> HEER																x									
<i>Proteoides reussii</i> ENGELHARDT								x							x										
<i>Proteophyllum cissiforme</i> VELENOVSKÝ & VINIKLÁŘ												x						x							
<i>Proteophyllum coriaceum</i> VELENOVSKÝ											x														
<i>Proteophyllum cornutum</i> VELENOVSKÝ							x			x															
<i>Proteophyllum decorum</i> VELENOVSKÝ										x	x					x									
<i>Proteophyllum dichotomum</i> VELENOVSKÝ & VINIKLÁŘ											x			x											
<i>Proteophyllum enervium</i> VELENOVSKÝ & VINIKLÁŘ											x														
<i>Proteophyllum laminarum</i> VELENOVSKÝ										x	x														
<i>Proteophyllum minutum</i> VELENOVSKÝ & VINIKLÁŘ	x										x														
<i>Proteophyllum paucidentatum</i> VELENOVSKÝ											x														
<i>Proteophyllum productum</i> VELENOVSKÝ	x						x			x									x						
<i>Proteophyllum saportaneum</i> VELENOVSKÝ		x								x	x				x										
<i>Proteophyllum subtile</i> BAYER		x								x			x			x									
<i>Proteophyllum trifidum</i> VELENOVSKÝ										x															
<i>Proteopsis proserpinæ</i> VELENOVSKÝ		x																							
<i>Pseudoasterophyllites cretaceus</i> O. FEISTMANTEL ex VELENOVSKÝ	x							x							x										
<i>Rutaecarpus quadrilobus</i> VELENOVSKÝ & VINIKLÁŘ										x			x												
<i>Saliciphyllum perucense</i> (VELENOVSKÝ) VELENOVSKÝ		x	x																						
<i>Sapindophyllum apiculatum</i> (VELENOVSKÝ) VELENOVSKÝ		x	x												x				x						
<i>Juglandiphylloides pelagicus</i> (UNGER) HERMAN et J.KVAČEK		x	x																						
<i>Sapotophyllum obovatum</i> VELENOVSKÝ										x				x											
<i>Sparganiocarpus terminalis</i> VELENOVSKÝ & VINIKLÁŘ															x				x						
<i>Stachyura spicata</i> VELENOVSKÝ & VINIKLÁŘ																x									
„ <i>Sterculia</i> “ <i>geinitzii</i> ENGELHARDT														x			x								
<i>Sterculiphylloides limbatum</i> (VELENOVSKÝ) VELENOVSKÝ										x	x														
<i>Sterculiphylloides</i> sp.														x			x								
<i>Terminaliphylloides rectinerve</i> (VELENOVSKÝ) VELENOVSKÝ				x																					
<i>Ternstroemiophyllum crassipes</i> (VELENOVSKÝ) VELENOVSKÝ			x																						
<i>Triphyllum fechteri</i> VELENOVSKÝ & VINIKLÁŘ												x													
<i>Triplicarpus purkynei</i> VELENOVSKÝ & VINIKLÁŘ			x																						

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
<i>Viniklaria cenomanica</i> KNOBLOCH & MAI			x																						
<i>Zlatkocarpus brnikensis</i> J.KVAČEK & FRIIS																									x
<i>Zlatkocarpus pragensis</i> (J.KVAČEK & EKLUND) J.KVAČEK & FRIIS	x																								
<b>INSERTAE SEDIS:</b>																									
<i>Ancoraecarpon cristatum</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Anthodium involucratum</i> VELENOVSKÝ & VINIKLÁŘ			x																						
<i>Carpolithus nyssiformis</i> KNOBLOCH & MAI																		x							
<i>Carpolithus ovalis</i> KNOBLOCH & MAI																		x							
<i>Carpolithus pecinovensis</i> KNOBLOCH & MAI																		x							
<i>Ceratocarpus fendrichii</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Dichandrium cretaceum</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Distroichostrobus pussilus</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Drepanolepis cretacea</i> VELENOVSKÝ & VINIKLÁŘ															x	x				x					
<i>Drepanolepis triloba</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Eolirion primigenium</i> VELENOVSKÝ & VINIKLÁŘ		x																		x					
<i>Epacridiphyllum quinquenervium</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Ginkgophyllum chuchlense</i> BAYER																x									
<i>Globocarpon otrubense</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Involucrum tripterum</i> VELENOVSKÝ & VINIKLÁŘ															x										
<i>Phyllites bipartitus</i> VELENOVSKÝ & VINIKLÁŘ		x																							
<i>Pseudoginkgo bohemica</i> VELENOVSKÝ & VINIKLÁŘ															x				x						
<i>Spermatostrobus suspectus</i> VELENOVSKÝ & VINIKLÁŘ		x														x					x				
<i>Strobilanthes cretaceus</i> VELENOVSKÝ & VINIKLÁŘ																				x					
<i>Strobilanthes minor</i> VELENOVSKÝ & VINIKLÁŘ																				x					

**Table 1. Peruc Flora.**

## 5.2 Klikov Flora

The Klikov Flora includes a smaller amount of plant megafossils (23 leaf dicot taxa used for CLAMP), but a large number of meso-fossils. It is characterised by presence of plant remains of Normapolles complex (*Caryanthus*, *Budvaricarpus*). These were recently revised (Heřmanová et al. 2011, 2016). A number of seeds and fruits of unknown affinity were described by Knobloch and Mai (1986), some of which are definitely not remains of plants. Particularly *Palaeoaldrovanda*, and some species of *Spirella*, formerly described as seeds, have recently been shown to be eggs of insects (Heřmanová and Kvaček 2010, Heřmanová et al. 2013).

Apart from megafossils from surface outcrops in the Klikov Flora, there is material from a large number of boreholes. For the present study, only material from the following boreholes was used: Branišov GB-3, Branišov Br 21, Břidlice L-XIII, České Budějovice ČB-4, Haklový Dvory ČB-2, Hluboká nad Vltavou, GB-5, Lomnice nad Lužnicí V-10, Nedabyle TsV-6, Opatovice Hl-1, HP-VI, Třebeč Tj-4a, Třebeč TSv-5, Petrovice GB-10, Vráto Vo-38-Vo-66. In the Klikov Flora, there were identified members of: Bryophyta (1 species), Sphenophyta (1 species), Polypodiophyta (6 species), Gymnospermophyta, Pinales (5 species) and Angiospermophyta (24 plant megafossils species, 26 meso-fossil species) and 29 of unknown affinity (Knobloch et Mai (1986). Partly revised taxa are listed in Table 2, including their occurrences.

TAXON	A - Branišov GB - 3	B - Břidlice L - XIII	C - Borek u Českých Budějovic	D - České Budějovice, Roudné ČB-4	E - České Budějovice - Budvar	F - Drahotěšice	G - Haklový dvory- Branišov Br21	H - Haklový dvory ČB2	I - Hluboká nad Vltavou, GB-5	J - Hnětov	K - Klikov	L - Lomnice n. L. V-10	M - Nedabyle TsV - 6	N - Opatovice Hl - 1, HP-VI	O - Třebeč Tj - 4a	P - Třebeč TSv- 5	Q - Petrovice, GB-10	R - Výškov	S - Vráto Vo - 38 - Vo - 66	T - Zliv - Řídká Blana	
<b>Bryophyta</b>																				x	
<i>Notothylacites filiformis</i> Němejc & Paclosová																				x	
<b>Sphenophyta</b>																				x	
<i>Equisetum</i> sp.																				x	
<b>Polypodiophyta</b>																				x	
<i>Filicites</i> sp. 1																				x	
<i>Filicites</i> sp. 2																				x	
<i>Filicites</i> sp. 3																				x	
<i>Filicites</i> sp. 4																				x	
<i>Filicites</i> sp. 5																				x	
<i>Filicites</i> sp. 6																				x	
<b>Gymnospermophyta, Pinales</b>																				x	
<i>Brachyphyllum squamosum</i> (Velenovský) Palibin						x														x	
<i>Geinitzia reichenbachii</i> (Geinitz) Hollick & Jeffery	x									x										x	
" <i>Dammara</i> " <i>borealis</i> Heer		x																		x	
<i>Podozamites cf. lanceolatus</i> (Lindley & Hutton) Heer																				x	
<i>Pityophyllum</i> sp.																				x	
<b>Angiospermophyta</b>																				x	
<i>Araliophyllum elongatum</i> Němejc									x											x	

TAXON	A - Braníšov GB - 3	B - Brdílice L - XIII	C - Borek u Českých Budějovic	D - České Budějovice, Roudné ČB-4	E - České Budějovice - Budvar	F - Drahotěšice	G - Haklov dvory- Braníšov Br21	H - Haklov dvory ČB2	I - Hluboká nad Vltavou, GB-5	J - Hnutov	K - Klikov	L - Lomnice n. L. V-10	M - Nedabyle TsV -6	N - Opatovice Hl - 1, HP-VI	O - Třebeč Tj - 4a	P - Třebeč TjSv- 5	Q - Petrovice, GB-10	R - Výškov	S - Vráto Vo - 38 - Vo - 66	T - Zliv - Řídká Blana	
<i>Coccophyllum extinctum</i> (Vel.) Němejc & Kvaček																			x	x	x
<i>Debeya cf. coriacea</i> (Velenovský) Knobloch																			x	x	x
<i>Debeya haldemiana</i> (Saporta & Marion) Knobloch									x										x	x	x
<i>Debeya insignis</i> (Hosius & Marck) Knobloch	x								x										x	x	x
<i>Debeya lusitanica</i> (Teixeira) Knobloch									x										x	x	x
<i>Dicotylophyllum saliciforme</i> Němejc									x										x	x	x
<i>Laurophylum acuminatum</i> J.Kvaček & Halamski Velenovský									x	x								x	x	x	x
<i>Dicotylophyllum</i> sp. A																			x	x	x
<i>Dicotylophyllum</i> sp. B										x									x	x	x
<i>Dicotylophyllum</i> sp. C																			x	x	x
<i>Dicotylophyllum</i> sp. D									x										x	x	x
<i>Dicotylophyllum</i> sp. E										x									x	x	x
<i>Dicotylophyllum</i> sp. F											x								x	x	x
<i>Dicotylophyllum</i> sp. G											x								x	x	x
<i>Dicotylophyllum</i> sp. H												x							x	x	x
<i>Ettingshausenia cf. laevis</i> (Vel.) J.Kvaček & Váchová										x								x	x	x	x
<i>Ettingshausenia senonensis</i> (Knob.) J. Kvaček & Vách.		x	x						x									x	x	x	x
<i>Myricophyllum serratum</i> (Velenovský) Velenovský									x	x									x	x	x
<i>Proteophyllum laminarium</i> Velenovský									x	x	x							x	x	x	x
<i>Proteophyllum lanceolatum</i> Němejc & Kvaček										x								x		x	x
<i>Quercophyllum pseudodrymejum</i> (Vel.) Němejc										x									x		x
<i>Qurecophyllum triangulodentatum</i> Knobloch											x							x			
mesofossils																					
<i>Liriodendron papilliformis</i> Knobloch & Mai		x													x		x				
<i>Padragutia haasii</i> Knobloch & Mai															x		x				
<i>Klikovispermum bohemicum</i> Knobloch & Mai															x						
<i>Klikovispermum facettale</i> Knobloch & Mai															x					x	
<i>Klikovispermum hurnikii</i> Knobloch & Mai				x	x		x	x						x		x	x			x	
<i>Klikovispermum malechii</i> (Knobloch)Knobloch & Mai	x	x		x	x		x	x	x	x				x	x	x	x	x	x	x	x
<i>Klikovispermum micromalechii</i> Knobloch & Mai						x								x	x		x				
<i>Klikovispermum senonicum</i> Knobloch & Mai							x							x							
<i>Klikovispermum velenovskyi</i> Knobloch & Mai														x							

TAXON	A - Braníšov GB - 3	B - Brdíčce L - XIII	C - Borek u Českých Budějovic	D - České Budějovice, Roudné ČB-4	E - České Budějovice - Budvar	F - Drahošice	G - Haklový dvory- Braníšov Br21	H - Haklový dvory ČB2	I - Hluboká nad Vltavou, GB-5	J - Hrutov	K - Klikov	L - Lomnice n. L. Vz-10	M - Nedabyle TsV - 6	N - Opatovice Hl - 1, HP-VI	O - Třebeč Tj - 4a	P - Třebeč TjSv - 5	Q - Petrovice, GB-10	R - Vyškov	S - Vráto Vo - 38 - Vo - 66	T - Zliv - Řídká Blana		
<i>Klikovispermum verrucosum</i> Knobloch & Mai													x	x	x	x						
<i>Klikovispermum vratense</i> Knobloch & Mai			x										x	x	x	x	x	x	x	x		
<i>Moroidea cretacea</i> Knobloch & Mai													x									
<i>Bohmeria cyrokii</i> (Knobloch) Knobloch & Mai	x	x x		x x x			x	x x x	x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x		x			
<i>Bohmeria reticulata</i> Knobloch & Mai													x x								x	
<i>Memorialis verrucosa</i> (Knobloch) Knobloch & Mai			x		x								x x		x x							
<i>Urticoidea cucurbitoides</i> (Vangerow) Knobloch & Mai												x										
<i>Urticoidea minutissima</i> Knobloch & Mai														x								
<i>Urticoidea pedicellata</i> Knobloch & Mai								x				x	x x		x x x							
<i>Calathiocarpus minimus</i> Knobloch & Mai		x x		x x							x									x		
<i>Calathiocarpus hollandicus</i> Knobloch & Mai									x													
<i>Caryanthus communis</i> Knobloch & Mai	x x		x x		x x x		x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x	
<i>Caryanthus deltoides</i> (Knobloch) Knobloch & Mai	x		x x		x x x		x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x		
<i>Caryanthus microtriasseri</i> Knobloch & Mai	x		x x		x x		x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x		
<i>Caryanthus trebecensis</i> Knobloch & Mai	x x		x x		x x		x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x	
<i>Caryanthus triasseri</i> (Knobloch) Knobloch & Mai	x x		x x		x x		x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	
<i>Budvaricarpus serialis</i> Knobloch & Mai	x x		x x		x x		x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x	
<i>Manningia crassa</i> Friis													x									
<i>Protovisnea reticulata</i> Knobloch & Mai	x x		x x		x x		x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x	
<i>Protovisnea tetragonalis</i> Knobloch & Mai													x									
<i>Protovisnea zahajensis</i> Knobloch & Mai			x x		x x		x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x		
„ <i>Saurauia</i> “ <i>alena</i> Knobloch & Mai	x x						x			x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x	
„ <i>Saurauia</i> “ <i>antiqua</i> Knobloch & Mai													x x	x x	x x	x x	x x	x x	x x	x x		
<i>Epacridicarpum cretaceum</i> (Jung) Knobloch & Mai					x								x x	x x	x x	x x	x x	x x	x x	x x		
<i>Shrubsolea trebecensis</i> Knobloch & Mai												x			x			x				
<i>Sapindospermum nitidum</i> Knobloch & Mai															x			x				
<i>Sabia menispermoides</i> Knobloch & Mai				x																		
<i>Icacinicarya budvarensis</i> Knobloch & Mai			x																			
<i>Bicameria holyi</i> Knobloch & Mai	x		x x		x x		x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x	x x x		

TAXON	A - Braníšov GB - 3	B - Brdílice L - XIII	C - Borek u Českých Budějovic	D - České Budějovice, Roudné ČB-4	E - České Budějovice - Budvar	F - Drahotěšice	G - Haklov dvory- Braníšov Br21	H - Haklov dvory ČB2	I - Hluboká nad Vltavou, GB-5	J - Hnutov	K - Klikov	L - Lomnice n. L. V-10	M - Nedabyle TsV -6	N - Opatovice Hl - 1, HP-VI	O - Třebeč Tj - 4a	P - Třebeč TjSv- 5	Q - Petrovice, GB-10	R - Výškov	S - Vráto Vo - 38 - Vo - 66	T - Zliv - Řídká Blana	
<i>Bicameria orbicularis</i> Knobloch & Mai	x				x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Bicameria zborovicensis</i> Knobloch & Mai			x		x																
<i>Incertae sedis</i>																					
<i>Carpolithus achaenoides</i> Knobloch & Mai															x						
<i>Carpolithus kleinii</i> Knobloch & Mai															x						
<i>Carpolithus rufeflei</i> Knobloch & Mai															x						
<i>Carpolithus rzehakovae</i> Knobloch & Mai	x				x									x							
<i>Costaeccarpus pterocarpus</i> Knobloch & Mai											x			x							
<i>Laramisamen bohemicum</i> Knobloch & Mai		x												x						x	
<i>Laramisamen branisoviense</i> Knobloch & Mai	x		x											x							
<i>Laramisamen faboides</i> Knobloch & Mai			x											x							
<i>Laramisamen mammilosum</i> Knobloch & Mai				x										x							
<i>Laramisamen microcanaliculatum</i> Knobloch & Mai			x	x		x	x	x						x	x	x	x	x		x	
<i>Laramisamen microgranulatum</i> Knobloch & Mai					x	x								x	x						
<i>Laramisamen moravicum</i> Knobloch & Mai						x	x							x							
<i>Laramisamen mrazekii</i> Knobloch & Mai														x							
<i>Laramisamen multivaleculosum</i> Knobloch & Mai															x						
<i>Laramisamen opatovicense</i> Knobloch & Mai														x							
<i>Laramisamen rothii</i> (Knobloch) Knobloch & Mai														x	x					x	
<i>Laramisamen rotundatum</i> Knobloch & Mai														x	x						
<i>Laramisamen rugosissimum</i> Knobloch & Mai								x						x			x				
<i>Laramisamen stigmosum</i> Knobloch & Mai														x							
<i>Laramisamen verrucatum</i> Knobloch & Mai														x							
<i>Orthonucella minima</i> Knobloch & Mai														x	x					x	
<i>Saccospermum trebecense</i> Knobloch & Mai									x	x					x						
<i>Vangerovia tricornuta</i> (Knobloch) Knobloch & Mai	x			x	x		x	x						x	x	x	x	x		x	
<i>Walbeckia fricii</i> Knobloch & Mai		x		x	x		x	x						x	x	x				x	
<i>Walbeckia guttaeformis</i> (Knobloch) Knobloch & Mai	x							x	x					x						x	

TAXON	A - Braníšov GB - 3	B - Brdíčce L - XIII	C - Borek u Českých Budějovic	D - České Budějovice, Roudné ČB-4	E - České Budějovice - Budvar	F - Drahotěšice	G - Haklový dvory- Braníšov Br21	H - Haklový dvory ČB2	I - Hluboká nad Vltavou, GB-5	J - Hrutov	K - Klikov	L - Lomnice n. L. V-10	M - Nedabyle Tsv-6	N - Opatovice Hl - 1, HP-VI	O - Třebeč Tj - 4a	P - Třebeč TjSv- 5	Q - Petrovice, GB-10	R - Vyškov	S - Vráto Vo - 38 - Vo - 66	T - Zliv - Řídká Blana	
<i>Walbeckia hlubocensis</i> Knobloch & Mai	x																				
<i>Walbeckia libusae</i> Knobloch & Mai																		x			
<i>Wetersdorffia cyperoides</i> Knobloch & Mai																		x			

**Table 2. Klikov Flora**, modified from Knobloch and Mai 1985, Váňová and J. Kvaček 2009.

### 5.3 Idzików Flora

The Idzików Flora is described from the Upper Nysa Klodzka Graben in Poland. Although completely allochthonous (coming from marine sandstones), it is quite rich in fossil plant taxa. There were recorded 24 leaf dicot taxa, used for CLAMP analysis, two monocots, 5 ferns and 4 conifers. The flora was recently revised by Halamski and Kvaček (2015). Due to poor preservation, as only impressions, a number of leaves are assigned to formal groups. It was impossible to get more detailed information, particularly about their cuticle and associated reproductive organs, which are necessary for understanding their natural systematic affinity.

Completely revised flora including occurrences is listed in Table 3 derived from Kvaček and Halamski (2015).

TAXON	Idzików	Nowy Waliszów	Stary Waliszów	Krośnowice	Stary Wielisław
<b>Polypodiopsida</b>					
<i>Nathorstia fascia</i> (BAYER) NATHORST	X				
<i>Monheimia</i> sp.	X				
cf. <i>Anemia fremontii</i> KNOWLTON	X				
<i>Sphenopteris</i> cf. <i>ungeri</i> J. KVAČEK & HERMAN	X				
<i>Sphenopteris</i> sp.	X				
<b>Gymnospermophyta, Pinales</b>					
<i>Frenelopsis</i> aff. <i>alata</i> (K. FEISTMANTEL) KNOBLOCH	X				
<i>Geinitzia reichenbachii</i> (GEINITZ) HOLICK & JEFFREY	X	X	X		

TAXON	Idzików	Nowy Waliszów	Stary Waliszów	Krośnówice	Stary Wielisław
<i>Geinitzia cf. schlotheimii</i> KUNZMANN, KNOLL & GAIPL	X				
<i>Conago</i> sp.	X				
<i>Angiospermophyta</i>					
<i>Dryophyllum geinitzianum</i> (GOEPPERT) HALAMSKI & J. KVAČEK	X	X			
<i>Juglandiphyllites cf. pelagicus</i> (UNGER) HERMAN & J. KVAČEK	X	X			
<i>Dalbergites atavius</i> (VELENOVSKÝ) HALAMSKI & J.KVAČEK	X	X			
<i>Dalbergites</i> sp. 1	X				
<i>Debeya</i> sp.	X	X			
<i>Cinnamomoides extinctus</i> (VELENOVSKÝ) HALAMSKI & J. KVAČEK	X	X			
<i>Laurophyllum acuminatum</i> (GOEPPERT) J. KVAČEK & HALAMSKI	X	X			
<i>Laurophyllum</i> sp. 1	X	X			
<i>Laurophyllum</i> sp. 2	X				
<i>Magnoliphylum emarginatum</i> (GOEPPERT) HALAMSKI & J. KVAČEK	X				
<i>Ficonium silesiacum</i> (VEL.) HALAMSKI & J. KVAČEK	X				
<i>Ettingshausenia onomasta</i> (BAYER) J. KVAČEK & HALAMSKI	X				X
<i>Ettingshausenia</i> sp.	X				
<i>Amelanchites cerasiformis</i> (VELENOVSKÝ) HALAMSKI & J. KVAČEK	X				
<i>Dryandrodes geinoglypha</i> BAYER	X	X			
<i>Apocynophyllum fractum</i> (VELENOVSKÝ) J. KVAČEK & HALAMSKI	X				
<i>Salicites petzelianus</i> GOEPPERT	X	X			
<i>Dicotylophyllum montis-nivium</i> HALAMSKI & J.KVAČEK	X				
<i>Dicotylophyllum thaddaei-guniae</i> HALAMSKI & J.KVAČEK	X				
<i>Dicotylophyllum</i> sp. 1		X			
<i>Dicotylophyllum</i> sp. 2	X	X			
<i>Dicotylophyllum</i> sp. 3				X	
<i>Dicotylophyllum</i> sp. 4	X				
<i>Dicotylophyllum</i> sp. 5	X				
<i>Pandanites cf. spinatissimus</i> PETRESCU & DUSA ex POPA et al.	X	X			
<i>Smilacites panartius</i> (BAYER) HALAMSKI & J. KVAČEK	X				

**Table 3. Idzików Flora,** from Kvaček Halamski (2015).

#### 5.4 Grünbach Flora

The Campanian Grünbach Flora is described from the Neuwelt Basin of the Gosau Group in Austria. The flora differs from the earlier-mentioned floras in high percentage of monocots. Some, *Pandanites* in particular, were very probably coal-forming plants. Herman and Kvaček (2010) identified 51 species of vascular plants representing: Equisetophyta (1 species), Polypodiophyta (11 species), Gymnospermophyta, Cycadales (1 species), Pinales (4 species), Angiospermophyta (34 species, out of the 6

monocots). The larger part of the fossil angiosperms (27 species) are dicot leaves, which were used for CLAMP analysis. The revised list of taxa is presented in the Table 4 following largely Herman and Kvaček (2010).

TAXON	Grünbach	Dreistätten	Muthmannsdorf	Frankenhof	Höflein	Felbering	Maiersdorf
Equisetophyta							
<i>Equisetites</i> sp.	x						
Polypodiophyta							
<i>Cladophlebis gosauensis</i> J. Kvaček & Herman	x		x				
<i>Coniopteris</i> sp.	x						
<i>Gosauopteris danaeoides</i> J. Kvaček & Herman	x	x	x	x			
<i>Marsileaceaephyllum campanicum</i> J. Kvaček & Herman	x						
<i>Microphyllopteris austriaca</i> J. Kvaček & Herman	x		x				
<i>Monheimia ungerii</i> J. Kvaček & Herman	x		x				
<i>Raphaelia lobifolia</i> (Corda in Reuss) Knobloch	x				x		
<i>Sphenopteris gruenbachiana</i> J. Kvaček & Herman	x						
<i>Sphenopteris heterophylla</i> (UNGER) J. Kvaček & Herman			x				
<i>Sphenopteris ungerii</i> J. Kvaček & Herman	x						
<i>Sphenopteris</i> sp.	x						
Gymnospermophyta, Cycadales							
<i>Nilssonia</i> cf. <i>holyi</i> J. Kvaček & Knobloch	x						
Gymnospermophyta, Pinales							
<i>Lindleycladus lanceolatus</i> (Lindley & Hutton) Harris	x						

TAXON	Grünbach	Dreistätten	Muthmannsdorf	Frankenhof	Höflein	Felbering	Maiersdorf
<i>Geinitzia formosa</i> Heer	x						
<i>Geinitzia reichenbachii</i> (Geinitz) Hollick & Jeffrey	x			x			
<i>Pagiophyllum</i> sp.	x						
<i>Angiospermophyta</i>							
<i>Brasenites krasseri</i> Herman & J. Kvaček	x						
<i>Orontiophyllum austriacum</i> (J.Kvaček & Herman) J. Kvaček & Smith	x						
<i>Pandanites trinervis</i> (Ettingshausen) J. Kvaček & Herman	x	x	x	x			
<i>Gruenbachia pandanoides</i> J. Kvaček & Herman	x		x				
<i>Sabalites longirhachis</i> (UNGER) J. Kvaček & Herman	x		x		x	x	
<i>Theiaiphyllum kollmannii</i> Herman & J. Kvaček	x						
Monocotyledon gen. & sp. indet	x						
<i>Celastrophylloides johannae</i> Herman & J. Kvaček	x		x				
<i>Celastrophylloides</i> sp.	x						
<i>Compositiphylloides serratum</i> Herman & J. Kvaček	x						
<i>Debeya insignis</i> (Hosius & Marck) Knobloch	x						
<i>Ettingshausenia gruenbachiana</i> Herman & J. Kvaček	x					x	
<i>Ettingshausenia</i> cf. <i>laevis</i> (Velenovský) Herman & J. Kvaček	x						
<i>Ettingshausenia</i> sp.	x						
<i>Gebenkiella europeica</i> Herman & J. Kvaček	x						

TAXON	Grünbach	Dreistätten	Muthmannsdorf	Frankenhof	Höflein	Felbering	Maiersdorf
<i>Juglandiphyllites pelagicus</i> (Unger) Herman & J. Kvaček	x	x	x				
<i>Leguminosites mucronata</i> Herman & J. Kvaček	x						
<i>Menispermites ettinghausenii</i> Herman & J. Kvaček	x						
<i>Menispermites summesbergerii</i> Herman & J. Kvaček	x						
<i>Myricophyllum serratum</i> (Velen.) Velenovský	x						
<i>Myricophyllum</i> cf. <i>zenkeri</i> (Ettingshausen) Heer	x						
<i>Quereuxia angulata</i> (Newberry) Kryshlofovich	x						
<i>Rogersia</i> sp.	x						
<i>Ternstroemites</i> (?) <i>neuwestensis</i> Herman & J. Kvaček	x						
<i>Viburniphyllum austriacum</i> Herman & J. Kvaček	x						
<i>Viburniphyllum ermannii</i> Herman & J. Kvaček	x						
<i>Dicotylophyllum proteoides</i> (Unger) Herman & J. Kvaček	x		x	x			
<i>Dicotylophyllum</i> sp. 1	x						
<i>Dicotylophyllum</i> sp. 2	x						
<i>Dicotylophyllum</i> sp. 3	x						
<i>Dicotylophyllum</i> sp. 4	x						
<i>Dicotylophyllum</i> sp. 5	x						
<i>Dicotylophyllum</i> sp. 6	x						
<i>Dicotylophyllum</i> sp. 7	x						
<i>Ceratoxylon</i> sp.	x						

**Table 4. Grünbach Flora**, modified from Herman and J.Kvaček 2010.

## **6 Whole-plant concept and reconstructions**

One important obstacle in studies of fossil plants is that the fossil record consists mainly of plant fragments. This contrasts sharply with living plants, which are usually collected as flowering or fruiting specimens of whole plants, or their parts. Fossil plants occur with individual organs detached in most cases. From the very beginning of paleobotanical research, scientists dealing with plant fossils have attempted to combine knowledge, at least from foliage and fruits, to get a more complete reconstruction of the original living plant (e.g. Velenovský 1889). The whole-plant concept was introduced by Z. Kvaček (2004, 2008) for leaves and reproductive organs. Sakala (2004) incorporated association of wood.

New studies of fossil plants, particularly angiosperms, reiterate the importance of the whole-plant concept for a full understanding of fossil plants. Although this can be a risky undertaking, reliable reconstructions can be accomplished by the use several reliable lines of evidence (studies of pollen and cuticles *in situ*, co-occurring wood, foliage, fruits, etc.). Experience shows that such reconstructions contribute to a more complete understanding of fossil plant evolution, and can help correct errors in the systematic interpretation of previously described plant fossils (Z. Kvaček 2008).

In reconstructing whole Cretaceous plants, we face different problems than when undertaking such a process for Cenozoic plants. In Tertiary floras, particularly the Neogene, all parts of plants usually have one name, because their similarity to recent plants is obvious (fossil *Taxodium dubium* is very similar to living *T. distichum*), leaving no doubt that the association of all parts of the plant belong to one species. The situation for the Mesozoic and Palaeozoic is completely different. With only a few exceptions, Mesozoic and Palaeozoic plants are extinct.

Cretaceous palaeobotany deals with extinct plants, but also with a number of plants having living relatives. The nearest living relatives of Cretaceous plants are usually relict plants that survived extinction, and typically are not the most representative of the plant group. In the worst cases, there is no surviving “relative” of the group, as in the case of cheirolepidaceous conifers or Bennettitales. In studying Cretaceous plants, we usually do not find plant organs attached, but only in association. However, if the association repeats in several localities, or if there is a clear association of several

organs in a monodominant taphocenosis, there is a clear argument for association of the two organs.

In the fossil plant record, including the Cretaceous, a number of plants have very similar foliage (e.g. angiosperm *Myrtoidea geinitzii* (Heer) Kvaček et Greguš earlier known as *Myrtophyllum* or *Eucalyptus geinitzii*). This occurs also among conifers (*Geinitzia reichenbachii*) that associate / belong to more than one reproductive structure. Importance of foliage for identification of natural genera is usually secondary, while knowledge of reproductive structures is very important. Their reliable associations can be achieved in various ways. The most secure is direct connection of leaves and reproductive structures (*Mauldinia*, *Anthocephale*, unpublished). Quite secure is association of leaves and reproductive structures in monodominant taphocenoses (*Alvinia* Kvaček 2000a, *Nehvizdyella* Kvaček et al. 2005, *Pseudoasterophyllites* Kvaček et al. 2016). Another, although less accurate indicator is repeated association of leaves and reproductive structures in different localities (*Zlatkocarpus* Kvaček et Friis 2010).

Due to the fact that frequently, each fossil plant organ has its own name, the whole-plant concept requires particular attention. The fragmentary nature of plant fossils and their preservation requires its own terminology. Cleal and Thomas (2010a,b) introduced clear distinction of: “plant fossils—fragmentary remains of extinct plants—and fossil plants—the individual extinct plant as it appeared in life or, more accurately, as it is now perceived to have appeared in life.” For fragmentary plants fossil organs term ‘morphotaxa’ was used in the *St Louis Code* (Greuter & et al. 2000) and ‘fossil taxa’ in the *Vienna Code* (McNeill et al. 2006). Whereas ‘fossil taxon’ is defined as “any taxon whose type is a fossil” (footnote to Preamble 7), ‘morphotaxon’ is a category within the broader category of fossil taxon “that can only include fossils of the same plant-part, life-history stage or preservational state as represented by the type” (Art. 1.2). Given this definition, any taxon for which greater knowledge subsequently becomes available (e.g., two formally named “plant-parts” are shown to be conjoined) is no longer a morphotaxon.

Bateman and Hilton (2010) declared correctly that in the *Vienna Code* there is no category complementary to ‘morphotaxon’ and introduced terms: „**Organ-species:** Any morphologically delimited category of disarticulated organ. **Form-species (shared organ-species):** Morphologically delimited category of disarticulated organ that, within the context of a particular comparative study, is perceived to lack unique charakter

states (and thus is assignable to multiple whole-plant species). **Autapo-species (unshared organ-species):** Morphologically delimited category of disarticulated organ that, within the context of a particular comparative study, is perceived to possess at least one unique character state (and thus is assignable to a single whole-plant species)“.

In the case of the ginkgoalean plant *Nehvizdyella*, we use the following succession of names of organ species: autapo-species *Eretmophyllum obtusum* (Velenovský) J. Kvaček for leaves, autapo-species *Nehvizdyella bipartita* Kvaček et al. for female reproductive structures, form-species *Cycadopites* sp. for pollen *in situ*, autapo-species *Pecinovicladus kvacekii* Falcon Lang for short shoots, form-species *Ginkgoxylon gruettii* Pons and Vozenin-Serra for trunk wood. All these names represent one plant, with male organs yet to be described. On the other hand, under the autapo-species *Pseudoasterophyllites cretaceous*, all sterile leaves with axes bearing male and female reproductive structures are associated (except pollen, which is form-species *Tucanopollis* sp.).

Bateman and Hilton (2010) also introduced a category “**Whole-plant species:** Morphologically delimited conceptual aggregate of all of the organ-species required to complete the relevant template, including at least one autapo-species.“

Naming of a whole plant is therefore an issue. Nomenclatural requirements for whole plants are not solved by Bateman and Hilton (2010), but we need to name reconstructed plants. Therefore, this paper introduces informal names in terms of nomenclature following the author's personal communication with W. Challoner in 2008. Only one rule is suggested here for names of whole plants: the first name should be autapo-species name characterising the plant (typically the name of a reproductive organ, or the organ bearing the most differential characters, see Kvaček 2008), followed by the word **plant** e.g. *Nehvizdyella bipartita* plant. Examples of more completely known Late Cretaceous taxa are listed below:

***Konijnenburgia bohemica* plant:** *Konijnenburgia bohemica* (fertile leaves) - *Nathorstia* (sterile leaves) - *Matonisporites* (pollen).

***Monheimia ungeri* plant:** *Monheimia ungeri* (fertile and sterile leaves) - *Matonisporites* (pollen).

***Dammarites albens* plant:** *Dammarites albens* (trunk) – *Kranneria* (leaves).

***Nehvizdyella bipartita* plant:** *Nehvizdyella bipartia* (ovuliferous organ) - *Eremophyllum* (leaves) - *Cycadopites* (pollen) – *Pecinovicladus* (short shoot wood)-*Ginkgoxylon* (trunk wood).

***Alvinia bohemica* plant:** *Alvinia bohemica* (ovuliferous cone) - *Frenelopsis alata* (sterile shoots) – *Classostrobus* (pollen cone)-*Classopolis* (pollen).

***Pseudoasterophyllites cretaceus* plant:** *Pseudoasterophyllites cretaceus* (sterile and fertile parts) - *Tucanopollis* (pollen).

***Zlatkocarpus pragensis* plant:** *Zlatkocarpus pragensis* (female reproductive structure)-*Dicotylophyllum araliopsis* (leaves) - *Retimonocolpites* (pollen).

***Zlatkocarpus brnikensis* plant:** *Zlatkocarpus brnikensis* (female reproductive structure) - *Araliphyllum formosum* (leaves)-*Retimonocolpites* (pollen).

***Myricanthium amentaceum* plant:** *Myricanthium amentaceum* (reproductive structure) - *Debeya coriacea* (leaves).

***Mauldinia bohemica* plant:** *Mauldinia bohemica* (inflorescence) - *Grevilleophyllum constans* (leaves) – *Paraphyllantoxylon* (wood).

***Antocephale chuchlensis* plant:** *Antocephale chuchlensis* (inflorescence) – *Myrtoxylon angustum* (leaves) - *Paraphyllantoxylon* (wood).

***Pragocladus laurooides* plant:** *Pragocladus laurooides* (inflorescence) – *Pandemophyllum* (leaves) - *Paraphyllantoxylon* (wood).

***Platananthus* plant:** *Platananthus* (inflorescence) - *Ettingshausenia* (leaves) – *Icacinoxylon* (wood) – *Retitricolpites* (pollen).

## 7 Plants indicating climate and palaeoenvironment

Plants are generally good climate and environmental indicators because their physiognomy and morphology is strongly influenced by climate (Spicer et al. 1994).

### 7.1 Fossil plants as climate indicators

Basic distribution of fossil plants in global scale in Cretaceous was defined by Vakhrameev (1991). Vegetationl types were defined by Graham (2011) for general orientation in the Cretaceous. However, if more detailed studies are carried out, we need more detailed information. Classification of modern vegetation is based on presence of particular plant taxa, termed index taxa (Chytrý et al. 2001). They are more sensitive than other plants to moisture, temperature and substrate.

As climate indicators are used classical stenotermic taxa, like palms and pandans (Kvaček and Herman 2004), but also other plants. One of them is *Glenrosa*, a conifer

which seems to be quite sensitive to temperature. This taxon is found in Cretaceous strata in southern Europe, but in Central Europe it has been found only in the Turonian (actually its very closely related or identical plant *Sedites*, compare Kunzmann 2010), from the time of the hothouse period.

*Nilssonia* and platanoids are generally accepted as members of Boreal Realm (Vakhrameev 1991), while araucarians and other amber producers, additionally angiosperms lauroids and chloranthoids are interpreted as representatives of Tethyan Realm. Massive amber producers are missing in the Cenomanian of Central Europe, but present in southern Europe. On the other hand, lauroids and chloranthoids were present in both southern and central Europe during the Cretaceous. Presence of *Nilssonia* indicates cooler climate in Central Europe in Cenomanian and Campanian (Kvaček 1994, Kvaček and Knobloch 1997, Herman and Kvaček 2010).

Plants as climate indicators are used in the method of the Nearest Living Relative (NLR) co-existence approach. Particularly higher up in the Cretaceous, we find more and more taxa that could be used for this coexistence method and NLR, as it was successfully used in Klikov and Grünbach Floras (Váčová and Kvaček 2009, Herman and Kvaček 2007). In the case of Klikov, the following taxa were used for NLR method: *Liriodendron*, *Platanus*, *Sauraia*, and *Sabia* (Váčová and Kvaček 2009). In Grünbach Flora we used palms (*Sabalites*), pandans (*Pandanites*), Schizaeaceae (spores *Leiotriletes*, *Appendicisporites* and *Cicatricosisporites*) Matoniaceae (*Monheimia*) (Herman and Kvaček 2007).

## 7.2 Fossil plants as environment indicators

Fossil plants are good indicators of palaeoenvironment. In the case of palynology, we have signals from larger scale; in case of mega- and meso-fossil, we get usually locally focused fossil record. As today, also in past particular plants are associated with particular biotopes. Their occurrence is used in classification in phytocenology (e.g. Chytrý et al. 2001). Similar situation was definitely in past and is reflected in plant fossil record. Generally accepted examples of indicator plants are given below.

Lycophytes and their megaspores are indicators of humid palaeo-environments. Their reproduction is generally possible in highly humid substrates. Lycophyte megaspores are frequently reported in Late Cretaceous near-shore facies, particularly swamps and back swamps and are virtually missing in sediments of braided rivers.

Ferns in the Late Cretaceous are of two groups:

- 1) ferns with thin and light cutinisation are typical for humid habitats. Particularly tree ferns (*Protopteris*, *Oncopteris*) with their foliage *Cladophlebis*, tree fern *Tempskya* and herbaceous ferns (*Anemia*, *Schizaeopsis*, *Monheimia*) are all hydrophytic.

2) heavily cutinised ferns with sporangia covered with large indusia (e.g. *Konijnenburgia*, *Nathorstia*) are typical for xerophytic open habitats characterised as fern steppe.

Gymnosperms, particularly cycads are sensitive to stability of the substrate. They are long-growing plants with a long life cycle. They prefer growing in well drained but stable parts of flood plains. Bennetites are generally accepted as growing in meso- to xerophytic conditions. Their stems are equipped with protection against fires; leaves have stomata with papillae.

In the Late Cretaceous, *Frenelopsis* and its pollen *Classopollis* are characteristic elements of taphocoenoses produced in halophytic environments (Uličný et al. 1997). Large branches of *Frenelopsis* are good indicators of its autochthonous/parautochthonous origin. However, *Classopollis* pollen can be transported long distances upstream in tidally influenced rivers Uličný (et al 1997). As already mentioned, only a few plants, prevailingly gymnosperms, were able to cope with halophytic environments in the Late Cretaceous. The conifer *Frenelopsis*, ginkgoaceous *Nehvizdyella* (with leaves *Eretmophyllum*) and *Dammarites*. There are only two angiosperms in this environment, both occurring infrequently: “*Diospyros*” *cretacea* and *Pseudoasterophyllites cretaceus*.

Platanoid and lauroid angiosperms are indicators of flood plains. During the entire Late Cretaceous, platanoids were an important part of the flood plain forests. However, as we know from Cenomanian braided rivers studied in the Pecínov Quarry, they avoided the immediate vicinity of braided river canals, since such braiding cause rapid changes in the local environment and substrate, a condition unacceptable for platanoids. Such disturbed biotopes are characterised by the presence of two lauroid genera: *Mauldinia* and *Pragocladus*, associated with leaves *Grevilleophyllum* and *Pandemophyllum*.

In contrast with braided rivers, meandering rivers in the Cenomanian are characterised by platanoids (*Ettingshausenia bohemica*), lianas (*Hederophyllum primordiale*), lauroids of *Antocephale* type (with foliage *Myrtoidea*, earlier *Myrtophyllum*), chloranthoids (*Debeya coriacea*), juglandoids (*Juglandiphyllites pelagicus*) and angiosperms of unknown affinity (*Araliaephylgium kowalewskianum*, “*Ternstroemia*” *crssipes*, *Cissophyllum exulum*). This taphocenosis is typical for the locality of Vyšehořovice, Břežany, Černíky.

### 7.3 Plants of disturbed habitats

Disturbance is one of the most important factor controlling plant diversity. Usually plants are sensitive to stability of their habitat, since they are unable to relocate. Therefore, high diversity in the plant fossil record is associated with the stable habitats, particularly in nutrient rich flood plains of meandering rivers. In the Bohemian Cretaceous Basin, it is the case of the Peruc Flora from the Cenomanian locality Vyšehořovice.

However facing disturbance is a strategy of particular plant groups. Disturbed habitats are difficult for most long-lived gymnosperms. Their strategy is to grow long time on one place where they can grow large surviving fire, grazing of herbivores or flooding and substrate unsatbility. A perennial strategy is typical for herbaceous pteridophytes (e.g. genus *Gleichenia*) and angiosperms. Both groups show diversification during Late Cretaceous.

Disturbance is the major reason why surroundings of the Cenomanian braided rivers were covered by shrubby angiosperm vegetation of low diversity. This environment is well documented from the Cenomanian locality Pecínov (Uličný et al. 1997). Entire-margined lanceolate leaves of *Grevilleophyllum* and *Pandemophyllum* associated with reproductive structures *Mauldinia* and *Pragocladus* are the most frequent fossils there. Even ferns are very rare in this taphocenosis.

Important and frequently overlooked type of disturbance in Cretaceous was grazing of dinosaurs. It is important to stress that herbivorous dinosaurs were one of the most important disturbance factors. Particularly large herbivorous dinosaurs had to have devastating influence on Cretaceous forests. Destruction of modern forest caused by elephants is well known (Ssali et al. 2012, Tweheyo et al. 2013). Larger herbivorous dinosaurs were sometimes ten times larger than modern elephants and they had to cause ten times larger devastation in the forest. Rather simplifying, that is possible to say, dinosaurs helped keep Cretaceous forests open and ready for penetration of angiosperms. We propose a hypothesis that disturbed habitats, regularly destructed by dinosaurs, were the first habitats of early angiosperms.

Fires were important disturbance factor particularly in seasonal climates of Central Europe (Falcon-Lang et al. 2001). CLAMP analysis (Tab. 5) shows clearly periods of draught with very limited amount of precipitation. This type of Mediterranean climate is very prone for fires. Frequent charcoalified mesofossils, particularly fragments of heavy cutinised pinnae of ferns coming from fern steppe are typical for the Cenomanian Peruc Flora. Even more frequent, charcoal is found in the Klikov Formation documenting very frequent fires which experienced Klikov Flora during Santonian-Coniacian. On the other hand the Grünbach Flora coming from coal swamp conditions was not influenced by fires (Kvaček and Herman 2004a).

#### 7.4 Plants of xerophytic and halophytic habitats

For many reasons, the “taphonomy window” to xerophytic habitats in the Cretaceous (the same as for other periods) remains closed for us. For studies of xerophytic environments, we can indirectly use Cretaceous salt marsh and mangrove habitats. It is known from recent mangroves and salt marshes that part of the halophytic taxa come from and have their relatives in xerophytic habitats (Tomlinson 1994, Hogarth 1999). Good examples are in the families Acanthaceae (*Acanthus*), Chenopodiaceae (*Salicornia*), Fabaceae (*Cesalpina*). Xerophytic plants are equipped with mechanisms to survive drought, and in a similar way, they can face secondary drought caused by salt.

Certainly, there are other halophytic plants having their relatives in freshwater wetlands (e.g. *Acrostichum*, Tomlinson 1994), but their fossil record would be known to us (wetland plants have the highest potential for fossilisation). In that way, *Frenelopsis* in the Lower Cretaceous is reported from xerophytic habitats (e.g. Upchurch and Doyle 1981), and in the Cenomanian from salt marshes and mangroves (Uličný et al. 1997). One plant from salt marsh calls special interest in that way. This is *Pseudoasterophyllites* – an herbaceous halophytic plant showing unique inconspicuous flowers and reduced, needle-like leaves. According to a new investigation of its morphology and phylogeny (Kvaček et al. 2016), it represents a member of very early evolving clade of angiosperms. Its herbaceous succulent habitus makes it a good candidate for a model of early angiosperms, which developed in open mesophytic-xerophytic habitats of Early Cretaceous and during mid-Cretaceous secondarily switched to grow in halophytic environments. We can even estimate when this happened. Palaeobotanical studies of Albian strata in Cantabria, Spain showed dominance of *Frenelopsis* in salt marshes/mangroves, but revealed no *Pseudoasterophyllites*. However, the Cenomanian strata in the same locality already contained *Pseudoasterophyllites* plant remains (author's unpublished data). So we can assume *Pseudoasterophyllites* became a part of the salt marsh vegetation by Cenomanian. The unique case of *Pseudosaterophyllites* may be a key for understanding the palaeophytography and phylogeny of very early evolving angiosperms.

Other sources of information about xerophytic habitats are charcoalfied and lignified mesofossils found in allochthonous taphocoenoses. There are numerous fragments of fern indusia, fern pinnulae, charcoalfied coniferous cones, seeds and fruits and small leaves of angiosperms with well-developed papillae (Uličný et al. 1997).

## 8 Fossil plant habitats

Plant ecosystems are parts of the Earth biomes recognizable by distinctive combinations of plant communities, climate and geological features. Graham (2011) suggested a suitable system, originally designed for the New World, but useful also for Europe. He defined eight major plant assemblages for the Cretaceous: *Polar broad-leaved deciduous forest*, *Notophyllous broad-leaved evergreen forest*, *Paratropical rain forest*, *Tropical forest, aquatic assemblages*, *Herbaceous freshwater bog/marsh/swamp*, *Mangrove Beach/strand/dune environment* Graham (2011). The classification by Graham (2011) is used here (Chapter 9) in combination with the classification by Peel (et al. 2007), who modified the Köppen classification of global climates (Köppen 1918).

The studied Central European floras differ in terms of palaeoenvironment, age, and in plant content. As indicated by some studies environmental conditions in Central Europe remained similar in course of Late Cretaceous (e.g. Kvaček and Herman 2004a, Kvaček et al. 2015). This ecological stability resulted in only gradual changes of the flora and occurrence of number of Lower Cretaceous and even Jurassic relict taxa (Kvaček 1999) in European Late Cretaceous. Due to this fact fossil plants, particularly in Late

Cretaceous are not very good stratigraphic index fossils. They could be however used for reconstruction of palaeovegetation, palaeoenvironment, and palaeoclimate. In the following text there are listed the most characteristic Late Cretaceous types of vegetation recorded in Central Europe.

## 8.1 Aquatic habitats

Generally Late Cretaceous aquatic plant assemblage is represented by two index water plants: *Brasenites* and *Quereuxia*. *Brasenites* has round or elliptic, entire-margined, peltate, floating leaves with well-developed aerenchyma. *Quereuxia* is represented by small triangular or elliptic leaves forming leaf rosettes. This plant assemblage is known from the Cretaceous of Grünbach (Herman and Kvaček 2010) where aquatic plant remains are abundant, suggesting the presence of an extensive shallow water environment.

## 8.2 Swamp habitats

Cretaceous swamp plant communities in Central Europe are distinguished in two basical types the back swamp coniferous forest and coal forming *Pandanites* swamp.

### Coal swamp

Semiaquatic plant assemblage of coal forming *Pandanites* swamp in Late Cretaceous of Europe is dominated by woody monocots - pandans. *Pandanites trinervis* is characterised by strap-like, parallel-veined, typically armed leaves. These plants probably formed monodominant stands in a swampy environment and constituted the main coal-forming biomass in Gosau coals (localities Grünbach, St. Wolfgang, Kvaček and Herman 2004a, Kvaček et al. 2007). It is probable that the assemblage also included semi-aquatic herbaceous monocots (*Orontiophyllum* etc.), horsetails *Equisetites* and ferns. Palm trees with *Sabalites* leaves may occur there, forming groups similar to recent *Sabal* or hardwood hammocks in Florida. These plant communities occur in Gosau Group (Grünbach, St. Wolfgang) in the Campnain of Austria and in the Maastrichtian of the Hateg Basin in Romania (Popa et al 2014, 2016).

### Back swamp habitats

This plant assemblage of the back swamp coniferous forest is dominated by large cupressaceous trees. Most common species is *Cunninghamites lignitum* or *C. oxycedrus*. These cupressaceous conifers have long needles sitting on small leaf cushions. Their large ovuliferous cones have typically four seeds per scale. Other elements of this plant assemblage are *Elatocladus velenovskyi* and *Quasisequoia crista*. In some particular cases (Pecínov unit 5) there are recorded other cupressaceous conifers such as *Spenolepis pecinovensis*. These back swamp forests had relatively poor understorey of herbaceous lycophytes and ferns. This assemblage was probably original place of

growth of the fern *Tempskya varians*. Back swamps occurred in near shore lowlands and in flood plains of rivers. Cretaceous back swamp communities are typical for the Bohemian Cenomanian (particularly localities Pecínov, Prague –Hloubětín, Hutě, Horoušany–Kamenná Panna), the Peruc Korycany Formation (Uličný et al. 1997). These palaeoenvironments could be compared with *Taxodium* swamps of Florida.

### 8.3 River flood plain habitats

There are two main types of flood plain associations in the Late Cretaceous: the braided river associations and meandering river associations. Cenomanian and Campanian plant communities of flood plains differ quite largely in plant content. Cenomanian flood plain associations are dominated by lauraceous angiosperms, while Santonian and older plant communities are dominated by plants of Normapolles group.

#### Braided rivers

Cenomanian braided river flood plain associations are formed by two major lauraceous plants *Mauldinia bohemica* with leaves of *Grevilleophyllum constans* and *Pragocladus laurooides* with leaves *Pandemophyllum*. Typical braided river plant communities are characteristic in low diversity and absence of understorey - ferns and cycads. More stable parts of river flood plains were more diversified. These transitional communities are characteristic in presence of *Platananthus* and its foliage *Ettingshausenia*, further *Myricophyllum zenkeri*, *Araliophyllum formosum*, *Debeya coriacea*. There are more common cycads (*Pseudoctenis*, *Nilssonia*) and ferns (*Gleichenia*).

#### Meandering rivers

Riparian forests of meandering rivers belong to the most nutrients richest habitats. They are more stable hosting remarkably diversified plant communities. Their content differs gradually from Cenomanian to Campanian and Maastrichtian. Lauraceous plants are dominant in Cenomanian, plants of Normapolles complex are dominant since Turonian-Coniacian.

Cenomanian: Plant communities are dominated by Lauraceae and Platanaceae (*Antocephale* and leaves *Myrtoidea*) and *Platananthus* with large leaves *Ettingshausenia bohemica*. There are more characteristic plants: pentalobed leaves *Araliophyllum kowalewskianum*, probably liana foliage *Hederophyllum primoridiale*, dentate leaves of *Myricophyllum zenkeri*, bilobate leaves of *Hymenophyllum primigenium*, infructescences *Proteopsis proserpinae*, peltately compound leaves *Debeya coriacea*, ferns *Gleichenia* sp., *Cladophlebis frigida*, large leaved cycads *Jirusia jirusii*, *Mesenea bohemica*.

Coniacian: The platanoid genus *Ettingshausenia* is characteristic for flood plain assemblage reconstructed in Idzików (Halamski and Kvaček, 2015). It may also be hypothesised that the numerically most common leaf taxa (*Laurophyllum* and *Dryophyllum*) belong to plants having grown in the same palaeocommunity. The

riparian assemblage probably also included other angiosperms as *Debeya* and *Salicites*. Lianas (leaves *Smilacites*) and tree ferns, found in dispersed sporomorph spectra (Kvaček et al. 2015), were probably accessory elements of the riparian assemblage.

Campanian: Riparian wetland forests in Campanian were dominated by plants having leaves of *Juglandiphyllites*, palms *Sabalites* and conifers *Geinitzia*. Fossil *Juglandiphyllites* leaflets are rarely attached forming compound leaves. Leaves of *Sabalites* occurring in the same type of sediment as *Juglandiphyllites* could not be transported for long distances: usually they, being heavy, fall close to the trees and could have become fragmented before (and during) transport. *Geinitzia formosa* shows rigid shoots with falcate keeled leaves. Ferns of possibly marattiaceous affinity were a typical component of this plant assemblage. This plant assemblage was probably taxonomically the most diverse and included species of ferns, such as *Microphylopteris*, *Monheimia*, *Cladophlebis*, *Onychiopsis* and angiosperms *Myricophyllum*, *Menispermites* etc. (Herman and Kvaček 2010).

## 8.4 Salt marsh/mangrove habitats

Salt marsh/mangrove environment is typical for various stratigraphic horizons of the European Late Cretaceous. The best documented and preserved it is in the Peruc-Korycany Formation of the Bohemian Cretaceous Basin (Uličný et al. 1997, Kvaček et al. 2006). This association is presently well exposed in the Pecínov quarry in unit 3 (as defined by Uličný et al. 1997). The most common and index plant fossil is there *Frenelopsis alata*. It occurs with both male and female reproductive structures. Female reproductive structures are deascribed as *Alvinia bohemica* (J. Kvaček 2000a). The second common element is a ginkgophyte *Eretmophyllum obtusum* with female reproductive structures *Nehvizdyella bipartita*. The other gymnosperm present in this association is still not enough understood *Dammarites albens*. Two angiosperms occur in this plant association: *Pseudoasterophyllites cretaceus*, and “*Diospyros“ cretacea*. *Pseudoasterophyllites cretaceus* represents one of the most basal angiosperm representing a relict already in Cenomanian (Kvaček et al. 2016).

In Europe there is a clear trend, from the Early Cretaceous where this salt tolerant environment is relatively rich in ginkgophytes (*Tritaenia*, *Eretmophyllum*, *Pseudotorrelia*), the ginkgophytes are gradually disappearing in younger strata. *Tritaenia* (*Mirovia*) and *Eretmophyllum* (*Nehvizdy*) are present in the Albian of Spain (Gomez 2000, 2003), but only *Eretmophyllum* as the last representative of ginkgos is known from Cenomanian strata of France (Pons, Boureau et Broutin 1976) and the Czech Republic (Kvaček 1999, Kvaček et al. 2005). By the Turonian *Eretmophyllum* seems to be absent in Central Europe. The most hardy plant of this environment is *Frenelopsis* which survives in central Europe till Coniacian e.g. in Idzikow Halamski et Kvaček 2015), but in Spain it is present till Maastrichtian (Villalba-Breva et al. 2016). It is interesting to observe *Frenelopsis* as a stable and the most prominent plant being typically xerophytic in Early Cretaceous and halophytic in the Late Cretaceous.

## 8.5 Upland habitats

Upland plant vegetation of the Late Cretaceous of Central Europe is known very fragmentarily as already mentioned. Its is known particularly from the Peruc-Korycany Formation of the Bohemian Cretaceous Basin. Most important localities are Praha, Malá Chuchle, Praha Hloubětín-Hutě, Bohdánkov and Pecínov, unit 1 (Uličný et al. 1997). This environment is characterised by presence of Caytoniales: *Sagenopteris variabilis*, Bennettitales: *Zamites*, *Anomozamites*, conifers: *Dammarophyllum*, Pinaceae – *Pinus*, *Pityostrobus*, small and papillate angiosperm leaves (*Dicotylophyllum*), and accessoric ferns (Matoniaceae – *Konijnenburgia*. To upland plant we can assign also *Araucaria* described from the Coniacian of the Březno Formation within the Bohemian Cretaceous Basin (Kunzmann 2007).

## 9 Palaeoclimatic interpretations

### 9.1 Methods

The Climate Leaf Analysis Multivariate Program (CLAMP) is a widely used multivariate statistical technique for obtaining quantitative palaeoclimatic information (Wolfe, 1990, 1993; Kovach and Spicer, 1995; Kenedy et al., 2002; Hayes et al., 2006; Kvaček and Teodoridis, 2007; Herman and Kvaček, 2010; Teodoridis et al., 2011a,b; Fletcher et al., 2014). CLAMP is a multivariate statistical technique for quantitatively determining a range of palaeoclimate variables based on the leaf physiognomy of woody dicotyledonous flowering plants. It was initially introduced by Wolfe (1993) and later refined, mainly by Wolfe and Spicer (1999), Spicer et al. (2004) and Spicer (2000, 2007), Spicer et al. (2009), and Teodoridis et al. (2011a). In its most widely used form, CLAMP employs 31 different leaf physiognomic characteristics to estimate 11 climatic parameters, i.e., MAT (mean annual temperature), WMMT (warmest month mean temperature), CMMT (coldest month mean temperature), GROWSEAS (length of the growing season), GSP (growing season precipitation), MMGSP (mean monthly growing season precipitation), 3-WET (precipitation during 3 consecutive wettest months), 3-DRY (precipitation during 3 consecutive driest months), RH (relative humidity), SH (specific humidity) and ENTHAL (enthalpy). This quantitative palaeoclimate proxy is based on canonical correspondence analysis (Ter Braak, 1986); a direct ordination method used to order site, leaf character and environmental data simultaneously in a multidimensional space: <http://clamp.ibcas.ac.cn>. In its most widely used form, calibration is based on CLAMP physiognomic datasets from 144, 173 and 189 modern sites, relevant modern gridded meteorological datasets (i.e., Physg 3br, Physg 3ar and PhysgAsia1; GRIDMet3b, GRIDMet3a and GRIDMetAsia1), and an updated version of the special tools developed by Teodoridis et al. (2011a,b) and Teodoridis et al. (2012). All the mentioned reference files and datasets are free to download from the CLAMP website: <http://clamp.ibcas.ac.cn/Clampset2.html>. Recently, a new automatic

application “CLAMP analysis online” has been made accessible on the CLAMP website (Yang et al., 2011). This application was used in parallel with our own calculations. We have not found any significant difference between results produced by the two methods. For the present floras, dataset Physg3arcAZ from 144 modern sites, and relevant modern gridded meteorological datasets GRIDMet3brAZ were used.

## 9.2 Evolution of climate

The floras of Central European Late Cretaceous contain rich dicot leaf assemblages, which allowed application of CLAMP analysis for calculating approximate palaeoclimatologic data. Physiognomic analysis of four key floras using the CLAMP technique is based on their revised taxonomy (Kvaček and Váchorová 2006, Herman and Kvaček 2010, Halamski and Kvaček, 2015, Kvaček J. unpublished data). The scored results (percentage of characters) are presented in Table 5.

Flora	MAT in °C	WMMT in °C	CMMT in °C	GROW SEAS	GSP in mm	MMGSP in mm	3-WET in mm	3-DRY in mm	RH in %	SH in %	ENTHAL
Peruc	16.54	28.12	7.60	9.70	127.86	15.76	65.11	16.65	68.82	8.33	32.21
Klikov	14.92	26.20	4.89	8.25	127.14	16.21	74.82	11.30	54.41	5.59	30.99
Idzikow	17.10	25.33	9.59	9.29	145.01	16.15	75.13	16.36	67.69	8.55	32.35
Grünbach	13.20	25.20	2.28	7.55	119.92	17.40	69.36	15.46	65.20	6.24	31.80

Table 5. Climate data for Cenomanian - Campanian floras of Central Europe.

### 9.2.1 Cenomanian

CLAMP analysis of the Peruc Flora using the above-described datasets (Physg3arcAZ\_GRIDMet3brAZ) yielded a MAT of 16.5 °C, a WMMT of 28.1 °C, a CMMT at 7.6 °C, a LGS of 9.7 months, a GSP 127 mm, a MMGSP 15.8 mm, 3-WET 65 mm, 3-DRY 17 mm, a RH of 68.8, a SH of 8.3 and enthalpy 32.2 (Table 5). This data suggests that Peruc Flora experienced a warm temperate, seasonally dry type of climate. Precipitation of 17 mm during the three driest months (3-DRY) and GSP of 127 mm indicate very dry seasonal temperate climate. Based on palaeotemperatures, Peruc vegetation was reconstructed as dry temperate seasonal forest, experiencing hot summers with a short dry season. The presence of false rings indicates in some years the occurrence of successive droughts late and early in the growing season (Falcon Lang et al. 2001). Here the modified Köppen classification of global climates is used (Peel et al., 2007), defining the seasonal warm temperate climate as a “warm temperate rainy climate having the mean temperature of the coolest month below 18 °C, but above 0 °C. The mean temperature of the warmest month is over 22 °C”. The MAT 16.5 °C and the high WMMT (28 °C) and low CMMT, together with presence of plants like tree ferns in the Peruc flora indicate warm temperate to tropical seasonally dry climate. According to Graham (2011), this plant assemblage can be classified as a notophyllous broad-leaved forest with conspicuous evergreen component.

### **9.2.2 Turonian**

Turonian floras in Central Europe are fragmentarily preserved. However, even working with these fragmented floras of the Bohemian Cretaceous Basin, one can reach conclusions about palaeofloristic shifts, reflecting temperature increases. Particularly important is the occurrence of *Sedites rabenhorstii*, which represents a conifer extremely similar, and very probably identical to the genus *Glenrosa* (compare Kunzmann 2010). This conifer is a typical representative of salt marsh/mangrove environments of Tethyan Realm (Moreau et al. 2015). It occurs in the Cenomanian of France (Moreau et al. 2015) and Spain (Gomez et al. 2001), but is virtually missing in Bohemian Cenomanian flora. Its presence in the Turonian of the Bohemian Cretaceous Basin (Geinitz 1842, Kunzmann 2010) clearly indicates its Turonian expansion northward due to optimal climate conditions driven by the Cretaceous hothouse effect. Similar occurrence shift is suggested for the genus *Araucaria*. This genus is typical for the Southern Hemisphere, but in the Cretaceous, it also occurred in Europe. Its occurrence in the Bohemian Cenomanian has not been recorded, but later, in the Turonian – Coniacian, its present there indicates its expanding occurrence northward. Ovuliferous cone-scales of *Araucaraia* are known from the Turonian and Coniacian of the Bohemian Cretaceous Basin (Kunzmann 2007, JK unpublished data), and from the Santonian in Aachen (Kunzmann 2007). High temperatures in the Turonian are documented from the Bohemian Cretaceous Basin by El-Shazly et al. 2011), who documented very high sea surface temperatures of 24.5 to 31.5 °C for the Late Cenomanian, and 32.9 to 34.7 °C for the Early Turonian.

### **9.2.3 (Late Turonian) Coniacian-Santonian**

The age of the Klikov Flora was suggested by Pacltová (1981) and Knobloch (1985), based on carpology and palynology, as Late Turonian to Santonian. In the context of revision of the Klikov Flora and Turonian hothouse effect, we have had to revise this estimate. Palaeotemperatures calculated for the Klikov Flora using CLAMP provide quite uniform climatic conditions in context with other Late Cretaceous floras, without any extremes. Therefore, the Klikov Flora does not seem to come from the Turonian period influenced by hothouse effect (compare El Shazly et al. 2011), but from the Coniacian-Santonian.

CLAMP analysis of the Klikov Flora using the above-described datasets yielded a MAT of 14.9 °C, a WMMT of 26. °C, a CMMT at 4.9 °C, a LGS of 8.3 months, a GSP 127 mm, a MMGSP 16 mm, 3-WET 75 mm, 3-DRY 11 mm, a RH of 54, a SH of 6 and enthalpy 31 (Physg3arcAZ\_GRIDMet3brAZ). This proxy data suggests that the Klikov Flora experienced a warm temperate, seasonally dry type of climate. Precipitation of 11 mm during the three driest months (3-DRY) and GSP of 127 mm indicate an extremely dry seasonal temperate climate. Based on palaeotemperatures, Klikov vegetation is reconstructed as very dry temperate seasonal forest to semi-desert, experiencing hot summers, with a very dry season of dormancy. According to the modified Köppen classification of global climates (Peel et al., 2007), Klikov Flora experienced seasonal

warm temperate climate, similarly to that of Peruc Flora. However, it is important to note that values of precipitation for the three driest months (3DRY) and mean annual precipitation (MAP about 175 mm) of the Klikov flora are so low, that Klikov Flora is very near precipitation values indicative for an arid climate (threshold 150 mm). In the sense of this information, we can reconstruct the Klikov vegetation as a forest dense near rivers, but patchy, alternating with steppe in particularly exposed locations.

The present work also revised the preliminary results of CLAMP by Herman et al. (2002) and more detailed results by Váčová and Kvaček (2009). Earlier published CLAMP data by Herman et al. (2002), based on a dataset of 103 modern vegetation sites, and in the case of Váčová and Kvaček (2009), based on a dataset of 177 modern vegetation sites, shows lower temperatures and very high precipitation rates. The new interpretation of higher temperatures and lower precipitation rates is probably caused by better approximation, particularly in terms of precipitation, of the newly developed modifications of CLAMP analysis.

#### **9.2.4 Coniacian**

CLAMP analysis of the Idzików Flora using the above-mentioned datasets (Physg3arcAZ\_GRIDMet3brAZ) yielded a MAT of 17.2 °C, a WMMT of 25.2 °C, a CMMT well above freezing at 8.8 °C, a LGS of 9.4 months, a GSP 841 mm, a MMGSP 135 mm, 3-WET 484 mm, 3-DRY 100 mm, a RH of 68.5, a SH of 8.9, and enthalpy 32.57 (Table 5). It can therefore be concluded that Idzików flora experienced a warm temperate seasonally dry type of climate. Precipitation of 100 mm during the three driest months (3-DRY) and GSP of 841 mm indicate seasonally dry temperate climate (Peel et al., 2007). Based on palaeotemperatures, Idzików reconstructed vegetation was probably a warm temperate seasonal forest, experiencing hot summers and a short relatively dry season. Here we use the modified Köppen classification of global climates (Peel et al., 2007), defining the seasonal warm temperate climate as a “warm temperate rainy climate having the mean temperature of the coolest month below 18 °C but above –3 °C. The mean temperature of the warmest month is over 10 °C”. The MAT 17.2 °C and the high WMMT and CMMT, together with presence of typically wet tropical plants like pandans and tree ferns in the Idzików flora underpin warm temperate to tropical seasonally dry climate. According to Graham (2011), this plant assemblage can be classified as a notophyllous broad-leaved evergreen forest to paratropical rain forest.

#### **9.2.5 Campanian**

CLAMP analysis of the Grünbach Flora using the above-mentioned datasets (Physg3arcAZ\_GRIDMet3brAZ) yielded a MAT of 13.2°C, a WMMT of 25.2°C, a CMMT well above freezing at 2.3°C, a LGS of 7.6 months, a MMGSP of 17.4 mm, 3-WET of 69.3 mm and 3-DRY of 15.5 mm (Table 5). Therefore, it is suggested that the Grünbach Flora grew in conditions of hot seasonally dry type of climate, quite similar to the Peruc Flora, but with lower mean temperatures in the coldest month to dropping to

2°C. It also falls in the category of „Notophyllous broad-leaves evergreen forest“ in classification by Graham (2011). In terms of temperatures, there are very similar results to the earlier analyses done by Herman and Kvaček (2002), and Herman and Kvaček (2010). However in terms of precipitation, it is quite different. Earlier, the climate of the Grünbach Flora was reconstructed as humid, subtropical and frost-free, with hot summers and short, relatively dry, but not arid, seasons (Herman and Kvaček 2007). In light of the new analysis providing relatively low values of precipitation, this must be reconsidered. The climate of the Grünbach Flora is reclassified as warm temperate seasonally dry.

## 10 Discussion

Discussing climate fluctuations in Late Cretaceous we need to consider the above-described four floras from Central Europe characterize short intervals within the entire Late Cretaceous, and cannot provide detailed information about climate evolution of the whole period. However, the four floras cover all the Late Cretaceous and provide enough data for comparison.

In terms of MAT, the highest temperatures are calculated for Coniacian Idzików Flora (17.1°C), while the coldest MAT 13.2°C is calculated for Campanian Grünbach Flora. The highest values for WMMT come from the Cenomanian Peruc Flora (28.12°C), while the lowest values of WMMT were calculated for Grünbach Flora (25.2°C). The highest values of CMMT were obtained for Idzików Flora, which experienced milder temperature extremes over the course of the year. The lowest values of CMMT calculated for Grünbach Flora were 2.3°C, which does not preclude the possibility of some days when the temperature dropped below 0°C. The longest growing season was reconstructed for the Peruc Flora (9.7 month), the shortest growing season is suggested for Grünbach Flora (7.6 months). The Peruc and Klikov Floras provided nearly identical GSP. This similarity can be caused by the fact that both floras come from very similar locations. The highest GSP (145 mm) was obtained for the Idzików Flora. The highest values for MMGSP come from the Grünbach Flora (17.4 mm). Peruc and Grünbach floras have relatively smaller differences between 3-DRY, indicating relatively balanced delivery of precipitation within the year. The greatest differences between 3-WET and 3-DRY were calculated for Klikov Flora, perhaps indicating position of the flora further inland on the island.

The Idzików vegetation experienced very similar climate conditions to the geographically and stratigraphically similar flora of the Klikov Formation. We recalculated the data used in a paper by Váňová and Kvaček (2009), and found quite similar MAT values of 17.2 °C for Idzików and 15.7 °C for Klikov, but rather different precipitation (GSP) estimates (GSP for Idzików 841 mm, GSP for Klikov 282 mm). The difference is probably caused by location of the source vegetations for each of the taphocenoses. The interior of a large island where the freshwater Klikov Formation was deposited was probably much drier than in Idzików, where vegetation grew near the sea

shore. The presence of mesophytic to subxerophytic environments in the Klikov Formation is supported by red beds occurring in sediment cycles within the formation (Slánská, 1974, 1976). The difference between the Idzików and Klikov floras is similar to that between two localities analysed in the Cenomanian Peruc flora, as documented by Herman et al. (2002). The Peruc flora from the locality Praha, Malá Chuchle (where taxa of a mesophytic forest prevail) showed similar estimates for temperature, but lower estimates for precipitation, whereas the Peruc Vyšehořovice fossil flora was interpreted as growing along a flood plain meandering river margin, and yielded higher precipitation estimates. Generally, the Peruc Flora of the Bohemian Cretaceous Basin shows a very similar palaeoclimate to the Idzików Flora: MAT 17.3 °C, WMMT 22.7°C, CMMT 11.6 °C, MAP 1468 mm, and MGSP 1033 mm (Herman et al., 2002). We can suggest that the climate within the northern Tethys, where all the Central European Cretaceous floras grew on various islands, was quite stable and perhaps uniform from Cenomanian to Coniacian.

Climatic indicators discussed above argue for a quite stable environment in the Late Cretaceous in central Europe. Occurrence of some indicative taxa *Sedites* (*Glenrosa*) in the Turonian argue for higher temperature during that period. (Unfortunately, we were not able to prepare CLAMP analysis for the Turonian, due to lack of rich dicot floras.) Occurrence of boreal taxa (*Nilssonia*) in the Cenomanian and again in the Campanian may reflect a vegetational reaction to cooling of climate.

## 11 Summary

Late Cretaceous floras provide important insights to the palaeoecology of terrestrial ecosystems, and the climate in which they flourished in Central Europe. The first chapters of the present work summarise the history of the study, localities and fossil plant material. Diversity of Late Cretaceous flora is documented by four selected key floras. A floristic list of the Peruc Flora provides the first comprehensive and critical summary of recently distinguished taxa and their current names. The Peruc Flora consists of 275 taxa, and is one of the richest Cretaceous floras in the world. Other lists are compiled from earlier publications (Knobloch and Mai 1986, Váňová and Kvaček 2009, Herman and Kvaček 2010, Halamski and Kvaček 2015). Detailed studies of particular taxa of these floras provide important insights in their morphology, anatomy and phylogeny. There are seven research papers attached as appendices to the present work documenting the above-mentioned floras.

The first appendix deals with *Pseudoasterophyllites*. It is focused on a description of sterile and fertile parts of the plant that are important for interpretation of its role in the evolution of early angiosperms. The paper on ginkgoaceous *Nehvizdyella* (Kvaček et al. 2005) is a good example of well-understood organs of one whole plant. The paper

contains description of its wood, leaves and reproductive structures, including pollen. A paper introducing the new genus *Zlatkocarpus* (Kvaček and Friis 2010) provides important arguments for chloranthaceous affinity of *Zlatkocarpus* reproductive structures. Two species are described: *Zlatkocarpus brnikensis* and *Z. pragensis*. Interpretation of the genus *Myricanthium* is also discussed. The paper on Campanian monocots from Grünbach dealing with *Sabalites* and *Pandanites* genera illustrates monocot diversity in the Campanian of Austria. The orontiod Araceae is discussed in more detail in the paper by Kvaček and Smith (2015), where the new genus *Oronciophyllum* is introduced. A monograph on Grünbach flora (Herman and Kvaček 2010) is included in the appendix, due to its comprehensive treatment of this important Campanian flora, describing its diversity, palaeoecology and palaeoclimate. Finally, the paper dealing with palaeoecology of the Idzikow Flora by Kvaček and Halamski (2015) is included. This paper represents a summary of the flora more broadly described by Halamski and Kvaček (2015), with the first interpretation of its palaeoecology and palaeoclimatology.

The seven publications from the appendix represent only a selection of papers where the present author and his colleagues fully describe the relevant floras. Beside those, there are more than 50 publications of the author and his co-authors fully documenting the discussed topics on Late Cretaceous floras of Central Europe. They are papers by Kvaček (2007, 2013a,b, 2014, 2015), Kvaček and Dašková (2010), Kvaček and Friis (2010) Kvaček et al. (2005, 2007, 2012, 2016), Bosma et al. (2012), Greguš and Kvaček (2015), Greguš et al. (2013), Kvaček and Herman (2004), documenting Peruc Flora; Herman and Kvaček (2007ab), Kvaček and Herman (2005), Kvaček and Lobitzer (2010), Kvaček and Smith (2015) Hradecká et al. (2007, 2008), Szente et al. (2010) documenting Austrian and German floras; Kvaček and Váchová (2006), Heřmanová and Kvaček (2010, 2012), Heřmanová et al. (2011, 2013), Váchová and Kvaček (2009) documenting and interpreting Klikov Flora; Halamski and Kvaček (2013, 2015), Kvaček et al. (2015) described and interpreted Idzików Flora. Additional papers are focused on whole European Cretaceous (Coiffard et al. 2008, 2009).

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### **13 List of appendices**

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## **14 Appendices**