SPANISH JOURNAL OF PALAEONTOLOGY

Floras of clastic and peat-forming Pennsylvanian wetlands: are they different? A case study from the Upper Radnice Coal (late Duckmantian), Kladno Coalfield, Czech Republic

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Opluštil, S., Pšenička, J., Šimůnek, Z. & Libertín, M. 2016. Floras of clastic and peat-forming Pennsylvanian wetlands: are they different? A case study from the Upper Radnice Coal (late Duckmantian), Kladno Coalfield, Czech Republic. [Floras de áreas pantanosas de sustrato siliciclástico y de turbera: ¿son diferentes? Estudio de un caso concreto, el Upper Radnice Coal (Duckmantiense superior), cuenca minera de Kladno, República Checa]. *Spanish Journal of Palaeontology*, 31 (1), 145-180.

Manuscript received 26 February 2016
Manuscript accepted 14 April 2016

ISSN 2255-0550

ABSTRACT

Floras of two ecologically and taphonomically different fossiliferous horizons associated with the late Duckmantian Upper Radnice Coal in the Kladno Coalfield are compared. These fossiliferous horizons include the Velká opuka that is a ≥ 10 cm thick volcaniclastic parting embedded in the coal and the Mydlák, which is a laminated mudstone in the roof of the same seam. Observations made in coal mines suggest that the Velká opuka bears autochthonous *in situ* preserved peat-forming vegetation, whereas the Mydlák is a lacustrine sediment that contains mostly drifted allochthonous and locally parautochthonous plant associations derived from coastal mostly clastic wetlands. Material from museum collections and our own field data show that floras of both fossiliferous horizons consist of representatives of the same families and genera but differ in their proportions and to a large part in species composition. This is demonstrated by only 40 % overlap of 89 plant species identified in both horizons. Flora of the Velká opuka is dominated by

RESUMEN

Se comparan las floras de dos niveles fosilíferos ecológica y tafonónicamente diferentes que están asociados con el Upper Radnice Coal, del Duckmantiense superior de la cuenca minera de Kladno. Estos niveles fosilíferos son el horizonte Velká, ≥ 10 cm de volcaniclásticos intercalados en el carbón, y el horizonte Mydlák, una lutita laminada a techo de la capa de carbón. Las observaciones hechas en las minas de carbón sugieren que el horizonte Velká contiene la flora autóctona, que se preservó *in situ* en la turbera, mientras que el Mydlák es un sedimento lacustre que contiene sobre todo restos alóctonos transportados y, localmente, asociaciones parautóctonas procedentes en su mayoría de zonas pantanosas marginales más siliciclásticas. El material de colecciones de museos y nuestras propias observaciones en el campo indican que las floras de ambos horizontes están formadas por representantes de las mismas familias y géneros, auque son diferentes en sus proporciones y en las especies que las componen. Esto se deduce del hecho de que sólo hay un 40

https://doi.org/10.7203/sjp.31.1.17144

lycopsids, either by arborescent lepidodendrids or by the sub-arborescent genus *Omphalophloios*. Co-dominant are sphenopsids and locally common are ferns and cordaitaleans. The Mydlák flora is more diverse and dominated by pteridosperms, whereas the proportion of lycopsids is lower and their composition partly different. Taxa abundant in the Velká opuka and nearly absent in the Mydlák include *Omphalophloios feistmantelii*, *Lepidodendron longifolium* and *L. ophiurus*. Abundant in the Mydlák and mostly missing in the Velká opuka are *Laveineopteris tenuifolia*, *L. bohemica*, *Sphenopteris spiniformis*, *Eusphenopteris nummularia*, *Lepidodendron aculeatum* and *L. mannebachense*. Prevalence of pteridosperms in clastic wetland floras of the Mydlák is in agreement with existing observations.

Keywords: Pennsylvanian, palaeoecology, plant taphonomy, clastic swamp, peat swamp.

% de solapado de las 89 especies identificadas en ambos horizontes. En la flora de Velká predominan las licópsidas, que pueden ser lepidodendraceas arbóreas o géneros subarbóreos como *Omphalophloios*. Las esfenópsidas son co-dominantes y, localmente, los helechos y Cordaitales. La flora de Mydlák es más diversa y con predominio de pteridospermas, mientras que la proporción de licópsidas es menor y su composición parcialmente diferente. Los taxones más abundantes en Velká y prácticamente ausentes en el horizonte Mydlák son *Omphalophloios feistmantelii*, *Lepidodendron longifolium* y *L. ophiurus*. Abundantes en Mydlák y prácticamente ausentes en Velká serían *Laveineopteris tenuifolia*, *L. bohemica*, *Sphenopteris spiniformis*, *Eusphenopteris nummularia*, *Lepidodendron aculeatum* y *L. mannebachense*. El predominio de las pteridospermas en las floras de las zonas pantanosas de sustrato siliciclástico de Mydlák está de acuerdo con las observaciones ya existentes.

Palabras clave: Pensilvánico, paleoecología, tafonomía, áreas pantanosas de sustrato siliciclático, zona de turbera.

1. INTRODUCTION

The Pennsylvanian subperiod is one of the most important coal-bearing intervals in the Earth history. In the tropics of that time, peat-forming wetlands spread from extensive coastal lowlands far into the interior of the Laurussia and China continents. The entire area covered by the wetland ecosystems is estimated to reach several millions of square kilometres (Cleal & Thomas, 2005). High preservation potential of the Pennsylvanian wetland flora, dominated by cryptogamic and early seed plants (DiMichele *et al*., 2010), resulted in its collecting and study since the beginning of systematic coal exploitation in the early 19th century (e.g., Sternberg, 1820-1825; Lindley & Hutton, 1831-1837; Brongniart, 1822, 1828-1838). Mostly taxonomic early studies were later extended to other related topics including stratigraphy, palaeoecology and plant diversity (e.g., White, 1912; Davies, 1929; Gothan & Gimm, 1930; Němejc, 1946; Havlena, 1961; Šetlík, 1977; Wagner, 1984; DiMichele *et al*., 2002; Falcon-Lang, 2004; Cleal, 2005; Cleal *et al*., 2012). The fossil record explored in these studies comprises two basic types: plant compressions preserved in siliciclastic sediments, mostly in mudstones, and in petrifactions represented mostly by coal-balls (Scott *et al*., 1996). Studies of these fossil records revealed long-term ecological stability and conservatism of wetland ecosystems with only minor changes in species composition between individual cyclothems/coal seams during Early to early Middle Pennsylvanian (e.g., DiMichele *et al*., 2002, 2004, 2010; Cleal *et al*., 2012; Tabor *et al*., 2013). Coal-ball studies also showed that tropical peats were dominantly composed of arborescent lycopsids, which comprise 60-90 % of peat volume (Phillips, 1981; Phillips *et al*., 1985). Their decline around the turn of the Middle and Upper Pennsylvanian was confirmed by a drastic decrease in their volume in coal-balls in favour of tree ferns and is expressed in a similar change in composition of compression floras (Cleal *et al*., 2010, 2012) and palynomorphs (Peppers, 1996). Other studies further show that Pennsylvanian tropical wetlands were not stable environments in hundreds of square kilometres but consisted of mosaics of various habitats, which differed in the rate and frequency of sediment input, composition of substrate and its saturation by water expressed by water table height and its fluctuation (DiMichele & Phillips, 1994; Greb *et al*., 2006; Gastaldo & Demko, 2011). A basic subdivision was suggested by Gastaldo (1987) who distinguished between clastic and peat-forming wetlands. The floras of these two major habitats are believed to be basically similar, composed of the same plant genera, but differed in species composition and in the proportion of different plant groups (DiMichele *et al*., 1991, 2010; Cleal *et al*., 2010, 2012). However, differences in the character of these two forms of plant preservation precludes straightforward comparison. Whereas the flora of clastic wetlands is preserved as compressions showing the outer morphology of species, flora of peat swamps can only be studied where plant tissues were permineralised and preserved in histological detail in coal-balls (Galtier, 1997). Direct comparison is possible only where a roof shale flora preserves the final stage of peat swamp development prior its inundation. However, to recognize the relationship between the site of growth of the vegetation and the place of its burial and in turn the relationship between the roof shale flora and an underlying coal (originally peat) requires detailed sedimentological and taphonomical observations (Gastaldo *et al*., 1995; DiMichele & Falcon-Lang, 2011).

Another opportunity to study peat-forming floras is provided by volcanic ash bands either within a coal seam or located in its roof. If they are thick enough, i.e. >10 cm, their deposition over a landscape resulted in severe damage of vegetation and rapid *in situ* burial of fragmented or leveled plant remains by volcanic ash (Burnham & Spicer, 1986; Burnham, 1994; Opluštil *et al*., 2009a, b, 2014). Several examples of such fossil-bearing tuff beds have been described recently from Puertollano, Spain (Wagner, 1989; Wagner & Álvarez-Vázquez, 2015), Döhlen, Germany (Rössler & Barthel, 1998; Barthel, 2016), Wuda, China (Wang *et al*., 2012) and in continental basins of the Czech Republic (Opluštil *et al*., 2007). These tuff beds preserve *in situ* floras that can be compared with similarly preserved floras in the roof of the same coal. This is exactly the case of the Upper Radnice Coal of late Duckmantian age (Early Moscovian) in the Kladno-Rakovník Basin in the central part of the Czech Republic. This up to 10 m thick coal was mined for two centuries and was accompanied by collecting of fossils from intercalated volcanic band and its roof shale during this same time. Extensive collections from both fossiliferous beds provide an excellent opportunity to compare the floras, both of which are preserved as compressions, despite coming from different kinds of environmental settings. Such a comparison contributes to our understanding of whether and how the floras of peat-forming and clastic habitats taxonomically differ.

2. GEOLOGICAL SETTING OF THE KLADNO-RAKOVNÍK BASIN

The Kladno-Rakovník Basin is one of several early post-orogenic continental basins (Fig. 1A), which developed in the Bohemian Massif during Pennsylvanian times (Pešek, 1994). The post-orogenic origin of these basins is demonstrated by sub-horizontally inclined unfolded strata. Deposition in the basin was accompanied by acid explosive volcanism resulting from tectono-thermal activity in the amalgamated Bohemian Massif (Žák *et al*., 2014). As a result a large number of volcaniclastic beds, a few millimetres to >10 m thick are intercalated within sediments (Pešek, 1994). In the northern part of the basin close to volcanic centres over a hundred metres thick ignimbrite bodies occur locally.

Fill of the Kladno-Rakovník Basin reaches up to 1440 m and spans an interval of about 17.1 Ma from late Duckmantian to early Asselian times (Opluštil *et al*., 2016). Basin fill is dominantly of fluvial origin, although lacustrine, lacustrine delta, peat-swamp and colluvial sediments are also present but to a lesser extent (Pešek, 1994). Typical is a basin-wide alternation of grey coal-bearing strata and coal-barren fluvial red beds, the latter with intercalated grey lacustrine horizons in the upper Gzhelian part of the succession (Pešek, 2004; Opluštil *et al*., 2013). This alternation of sediments was used by Weithofer (1896, 1902) for a subdivision into four lithostratigraphic units which are presently called the Kladno, Týnec, Slaný and Líně formations, of which the Kladno and Slaný formations are grey coal-bearing units (Fig. 1B). The Upper Radnice Coal is a part of the Radnice Member (Fig. 1B), the basal unit of the Kladno Formation and the entire basin fill.

2.1. Radnice Member and the Upper Radnice Coal

The Radnice Member is of late Duckmantian-early Bolsovian age and represents the *Paripteris linguaefolia* Zone (Opluštil *et al*., 2016). Sediments of this unit fill a system of fluvial valleys (Fig. 2) either erosionally incised into Late Proterozoic basement with an inherited palaeotopography of up to few hundred metres or provoked by active faults (Opluštil, 2005a, b). This interpretation explains the irregular distribution of its sediments and its variable thickness from 0 to about 250 m with maximum values in tectonically-controlled NNE-SSW striking valleys (Pešek, 1994). Besides the predominantly fluvial facies, colluvial deposits are represented by poorly sorted, clast- to matrix-supported slope breccias derived from local basement palaeohighs. Lacustrine and lacustrine deltaic sediments are rare and represented by up to few metres thick intervals located usually in the roof of major coal seams. Coals developed in those valleys where a low clastic input allowed for long-term peat formations, usually along the valley margins protected by small basement ridges against active fluvial channels; however, some coals spread across the entire valley width (Opluštil, 2005b). Coals of the Radnice Member are arranged into the Pilsen, Radnice and Lubná groups; the Radnice group (late Duckmantian) is the most important of these and is developed in most of the palaeovalleys, now representing individual coalfields. It consists of the Lower and Upper Radnice coals separated by a few tens of centimetres to over 10 m thick Whetstone Horizon which is composed of *in situ* tuff and redeposited volcaniclastic material mixed with siliciclastics (Mašek, 1973; Opluštil *et al*., 2014). In the Kladno-Rakovník Basin the Lower Radnice Coal is usually one or two metres thick and composed of high ash coal. The Upper Radnice Coal is thicker and of better quality. In the Kladno Coalfield, where this comparative study is located, the Upper Radnice Coal is usually 6-8 m thick but reaching locally over 10 m (Opluštil, 2005b).

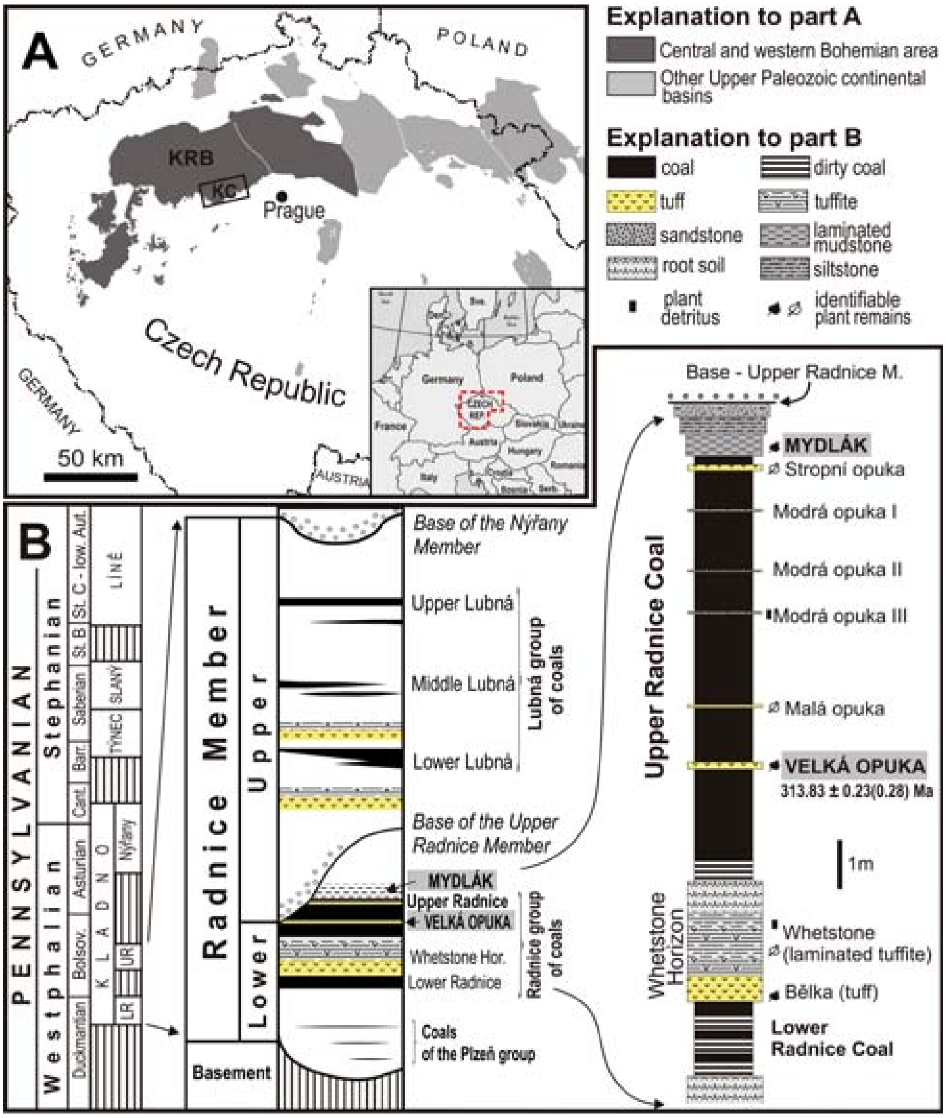


Figure 1. Distribution of Pennsylvanian terrestrial sediments in the Czech Republic and their lithostratigraphic subdivision. **A)** Position of the Kladno-Rakovník Basin (KRB) within the continental basins of central and western Bohemia with location of the Kladno Coalfield (KC) indicated. **B)** Lithostratigraphic subdivision of the Kladno-Rakovník Basin with detail of the Radnice Member and the Radnice coal group.

The coal in this coalfield fills the Kladno Valley, which is the largest palaeovalley of erosional origin in the Kladno-Rakovník Basin. It strikes W-E, is about 25 km long. The economically important Upper Radnice Coal originally covered ~ 19 km of its length (Fig. 2B). However, a base-level drop during the newly identified hiatus between the Radnice and Lubná coal groups resulted in deep erosion of the coal and splitting its area into two parts (Opluštil, 2005a; Opluštil *et al*., 2016). The Upper Radnice Coal covers the 2 to 5 km wide Kladno Valley nearly "from margin to margin". In plan view this distribution is evident from a very irregular outline of the coal, which nearly faithfully traces the edge of basement palaeohighs along the sides of the Kladno Valley (Fig. 2B). Only along western edge of the coal, where increased sediment input from the source areas disturbed peat accumulation, the Upper Radnice Coal grades into carbonacous mudstone and further out to mudstone representing clastic wetlands (Fig. 2B).

Intercalated in the Upper Radnice Coal are whitish or grey volcaniclastic partings, a few millimetres to over 15 cm thick, which are traceable across the entire Kladno Coalfield; thicker of these partings also occur in some other coalfields of the Kladno-Rakovník and Radnice basins (Figs 1B, 3A, 4). These ash beds are called "opuky" and serve as excellent correlation markers in the workings of this thick coal (Fig. 3A; Čepek *et al*., 1936; Orlov, 1942; Mašek, 1973; Mašek & Pešek, 1979). They represent kaolinized, either *in situ* deposited or partly reworked volcanic ash beds. The thickest of these, the Velká opuka, bears rich subaerial plant fragments, generally preserved *in situ* (Opluštil *et al*., 2007). In the roof of the coal, there is laminated mudstone called "Mydlák", which provides also a rich plant fossil record (Fig. 5).

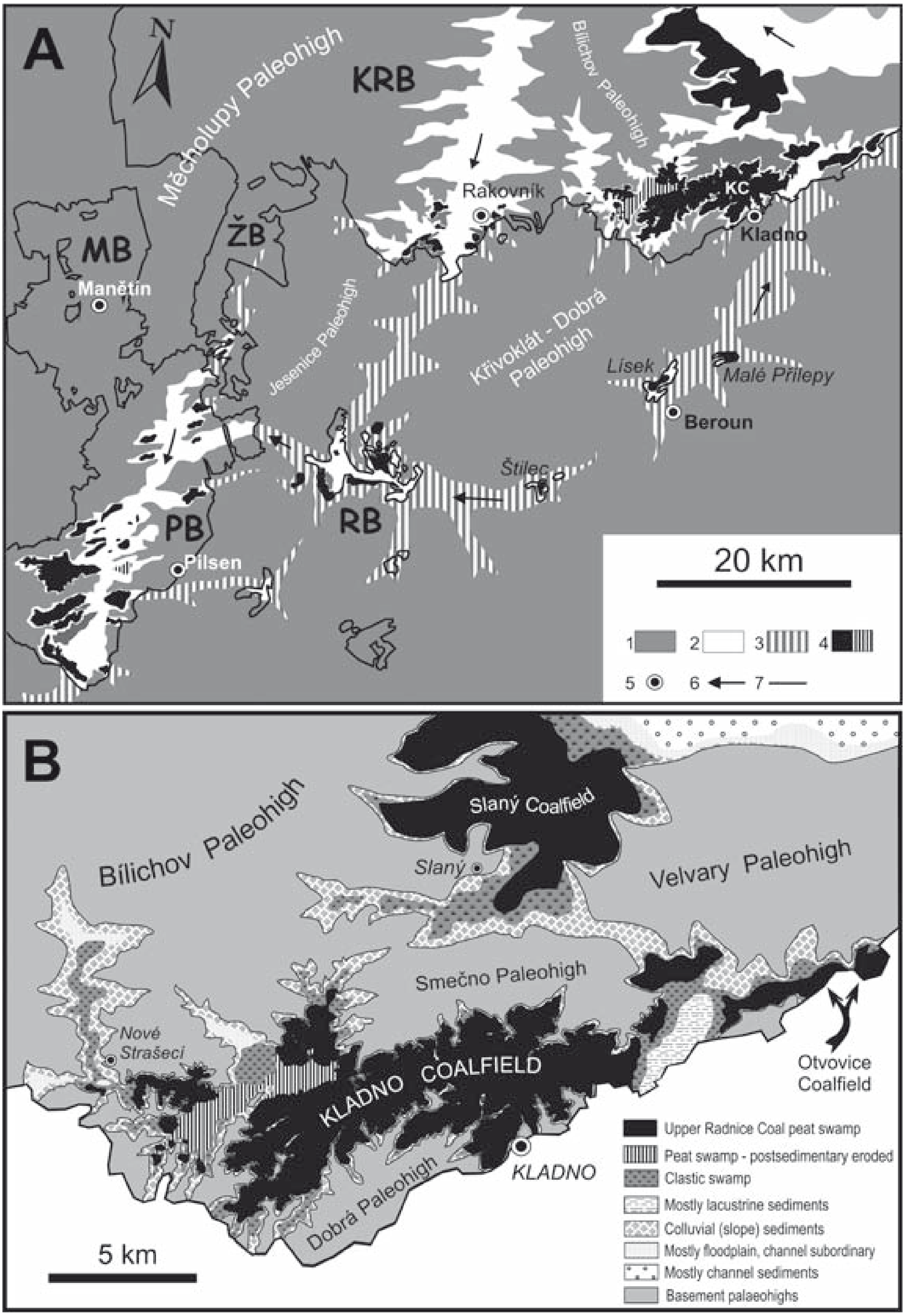


Figure 2. Palaeogeography of the Radnice Member (after Opluštil 2005b, modified). **A)** Palaeogeography of central and western Bohemia during the formation of the Upper Radnice Coal peat swamp. Explanation of abbreviations and symbols: PB – Pilsen Basin, RB – Radnice Basin, MB – Manětín Basin, ŽB – Žihle Basin, KRB – Kladno-Rakovník Basin, KC – Kladno Coalfield, 1 – Basement outcrops, 2 – Current extent of the Lower Radnice Member (LRM), 3 – Assumed distribution of the LRM outside the present-day basin extent, 4 – Upper Radnice Coal peat swamp preserved and eroded post-depositionally, 5 – Towns, 6 – Assumed direction of clastic transport, 7 – Present-day basin margin. **B)** Palaeogeography of the Kladno Coalfield and its surroundings during the same interval.

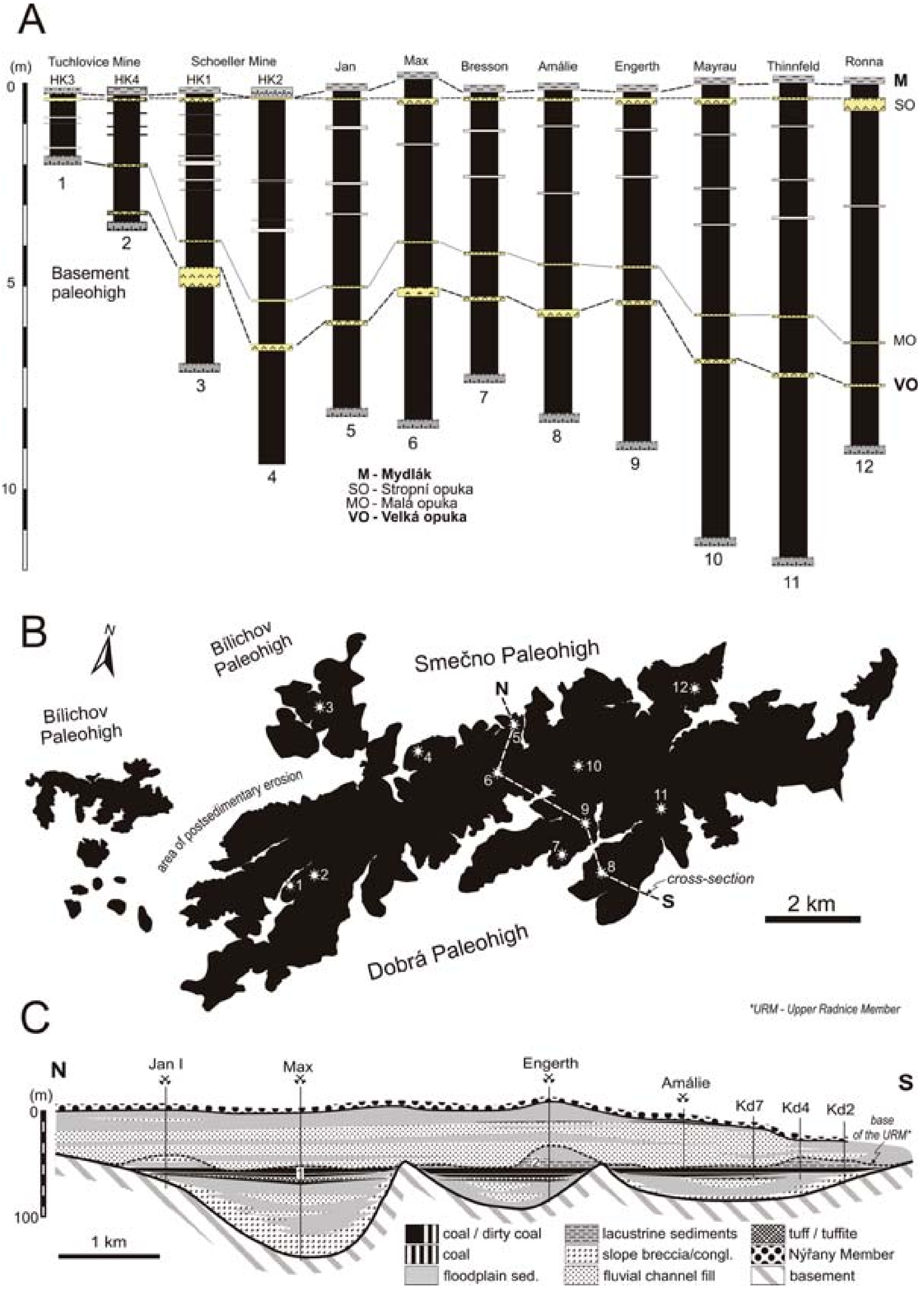


Figure 3. Kladno Coalfield. **A)** Sections of the Upper Radnice Coal in selected coal mines with location of major sedimentary and volcanic (opuky) partings indicated. For location of sections see numbers in Fig. 3B. **B)** Present-day extent of the Upper Radnice Coal. **C)** Cross-section of the Radnice Member in the Kladno Coalfield. Note the prominent pre-existing palaeotopography.

3. MATERIAL AND METHODS

Although the plant fossils preserved in the Upper Radnice Coal roof shale and the Velká opuka were collected in various coalfields (~ palaeovalleys) of central and western Bohemia (= central and western Czech Republic), characterization and comparison of the two floras is restricted only to the Kladno Coalfield. This is because this coalfield provided the largest collections from both fossiliferous horizons.

This study is based on extensive field activities of the authors as well as a systematic re-examination of plant fossils in institutional and private collections. Field studies include observations of sedimentological characters of the studied horizons in coal mines since the early 1980s until the closure of coal mining in 2002. Several tens of excursions into galleries allow conclusions with regard to sedimentology and taphonomy as related in the following chapters. The second part of our field activities included collecting of fossils from these easily identifiable beds on coal mine dumps since the late 70ties until shortly after mine closure. Such long-lasting collecting activity allowed the authors to judge the character and composition of plant fossils in both fossiliferous horizons. Surprisingly, there are some amateur collectors, who successfully continue collecting until present, providing additional material.

For the purpose of our floral studies we have examined several large collections stored in the Chlupáč Museum of Earth History at the Faculty of Science, Charles University in Prague, the National Museum in Prague, West Bohemian Museum in Pilsen, Sládeček Museum in Kladno, and the private collection of Mr. J. Haldovský from Pchery near Kladno. In addition to these primary data from plant collections, we made also a literature search. This included mostly papers of the famous Czech palaeobotanist Prof. F. Němejc (1901/1976), who collected fossils in the Kladno Coalfield for several decades.

Because the main aim of this contribution is to describe the composition of floras and their diversity, not all the morphospecies have been listed. Instead we focused on plant organs which best characterize original biological species. As a result, only one morphotaxon is selected for each biological species. This excludes taxonomic inflation and, thus, expresses more adequately the original plant diversity (Cleal, 2005; Cleal *et al.*, 2012).

The abundance of individual species was estimated only semi-quantitatively as rare, common or abundant since no counts were made in the field.

4. ORIGIN OF THE “VELKÁ OPUKA” AND “MYDLÁK” AND THE FLORAL TAPHONOMY

The Velká opuka and Mydlák are two major plant-bearing horizons associated with the Upper Radnice Coal in the Kladno Coalfield of the Kladno-Rakovník Basin. They are of contrasting origin and their fossil records differ in taphonomical history.

4.1. Velká opuka

The Velká opuka is a name used by miners and geologists for ~ 10-20 cm thick, sharply-based whitish-grey volcaniclastic band intercalated in the lower part of the Upper Radnice Coal and laterally persistent across all coal-mining areas in the Kladno-Rakovník and the Radnice basins (Fig. 4). It is situated usually ~ 2 m above the base of the coal; however, this position increases to over 4 m in the centre of the coalfield, whereas this band can be absent where the lower part of the coal wedges on basement palaeohighs (Fig. 3A). Zircons separated from the Velká opuka provided the CA-ID-TIMS age of 313.83 ± 0.23 (0.28) Ma, which corresponds to the latest Duckmantian (Opluštil *et al.*, 2016). Mašek & Pešek (1979) interpreted the Velká opuka as a massive argilized vitro-crystallic tuff generated by volcanic ash fall. Its upper part may be locally redeposited as indicated by lamination and the presence of plant detritus in areas of increased to anomalous thickness up to ~ 1 m, where unconsolidated volcanic ash was washed down from the surrounding basement palaeohighs.

It is estimated that the current thickness is about one half or even one third of the original uncompacted volcanic ash bed, covering the landscape (Bohor & Triplehorn, 1993). Observations of modern volcanic eruptions show that volcanic ash beds of such thickness (~ 50 cm) are sufficient to bury the herbaceous groundcover and heavily damage shrubs and trees (Burnham & Spicer, 1986; Burnham, 1994). Such observations are consistent with the presence of large plant fragments concentrated near the base in the case of herbaceous species (Opluštil *et al.*, 2014). These remains represent a temporally instantaneous, pre-eruption coal-forming flora preserved *in situ* and in some cases even in growth position as suggested by stumps rooted in coal below the tuff. Upright calamitalean stems show signs of regeneration as indicated by the presence of roots in originally (prior to volcanic ash fall) subaerial part of the stem (Opluštil *et al.*, 2007). Only where the upper part of the ash bed was redeposited and thickened, usually along valley margins in the proximity of basement palaeohighs, it also contains drifted plant detritus with only sparse identifiable plant remains of a compositionally distinct possibly upland flora. Where the thickness of the Velká opuka is not increased by redeposition, it is usually

Figure 4. Upper Radnice Coal as exposed in the Tuchlovice **(A)** and Max **(B)** mines of the Kladno Coalfield. Arrows indicate several volcaniclastic partings called "opuka". Figure 4B provided by Josef Seifert.

heavily penetrated by stigmarian rhizomorphs and their appendices, and less frequently by some other types of rooting systems of the post-eruption flora that recolonized the buried peat swamp.

Palynological analysis of the Upper Radnice Coal indicates a transition from the Lycospore to Densospore phases around the level of the Velká opuka (Opluštil *et al*., 1999). This implies the existence of two contrasting plant associations, the former dominated by *Lycospora*-producing lepidodendrid lycopsids and the latter by the sub-arborescent lycopsid *Omphalophloios feistmantelii* (Bek *et al*., 2015). This is in agreement with macroflora collected from the Velká opuka in various mines across the entire Kladno Coalfield.

4.2. Mydlák

The Mydlák is a name given by miners to an irregularly laminate grey mudstone which overlies the roof of the Upper Radnice Coal in the Kladno Coalfield (Fig. 5) with a sharp contact. Contrary to the Velká opuka, the Mydlák is interpreted as a lacustrine sediment (Opluštil, 2003, 2005a, b). It is of variable thickness ranging from a few tens of centimetres to ~ 7 m (Havlena, 1964) and irregularly grades upward into fine-grained ripple-bedded sandstone terminated by an erosional surface of regional extent followed by fluvial channel sandstone and/or conglomerates (Fig. 3C). Locally these conglomerates are deeply incised into the Mydlák and even the Upper Radnice Coal below (Opluštil, 2005a). The whole coarsening-up sequence from the base of the Mydlák to the erosional surface is interpreted as a lacustrine delta complex filling the lake formed due to a rise in relative base level (Opluštil, 2005a). Absence of benthic fauna suggests either a high sedimentation rate or anoxic bottom conditions. The contact of Mydlák and the Upper Radnice Coal is sharp and no indications of interruption of deposition have been observed. Roots are absent in the Mydlák except for the marginal areas of the Upper Radnice Coal – deposits of the original lake shallow near the basement palaeohighs. Here, the roots and aerial part of plants occur together and lamination is usually poorly developed or absent. With increasing distance from the lake margin, however, roots disappear and only drifted plant remains occur (Opluštil, 2003). The Mydlák becomes dark grey to grey, thinly bedded and often irregularly laminate mudstone with plant compressions on the bedding planes (Fig. 5). The plant remains consist mainly of identifiable plant fragments of various sizes and lacking any sorting; massive stems being usually crudely- and the fragile foliage finely fragmented. Most plant remains are concentrated in the basal few centimetres, where they often cover bedding planes densely; up-section their density decreases significantly. In the few basal millimetres at the contact of the Mydlák with the underlying coal, the plant fossils often cover most of the bedding plane; however, their coalified remains are usually separated from each other by thin sediment layers. This kind of preservation indicates a transport and coeval deposition of mud from suspension (Gastaldo *et al*., 1995). Compressions are mainly flat lying. Stems that penetrate sediments diagonally and upright stems are rare. Typical plant assemblages found in the Mydlák consists of cm – dm (or even larger) fragments of prostrate calamite stems, pteridosperm and fern axes associated with foliage of the different plant groups. Remains of arborescent lycopsids are usually subordinate elements, represented by isolated leaves, fructifications or fragments thereof, as well as leafy shoot, branch or stem fragments.

Based on our taphonomical and sedimentological field observations the Mydlák is interpreted as a lake sediment, which terminated the formation of the Upper Radnice Coal (Opluštil, 2005a, b). Except for marginal areas, the lake was deep enough to prevent its colonization by plants as indicated by the absence of roots. Alternating deposition of mud and silt from suspension dominated across most parts of the lake except the marginal areas where deposition from density flows as well as traction currents resulted in the deposition of ripple-bedded sand lenses, laminae or even decimetres thick, fairly complex sand bodies (Fig. 5B).

The sharp contact between the coal and the Mydlák suggests relatively fast but probably not catastrophic inundation of the peat swamp as is also suggested by the rare occurrences of upright stems (Gastaldo *et al*., 1995; DiMichele & Falcon-Lang, 2011). Differences in coal thickness between the Stropní opuka and the Mydlák (Fig. 3A) as well as between some other isochronous volcanic partings embedded in coal, may indicate an irregular rate of peat accumulation prior to the isochronous inundation of entire peat swamp or a gradual onset of inundation under more or less spatially even peat accretion. Possible explanation is also a palaeotopography of mire with presence of raised-mire areas separated by low-lying topography peat swamp. Currently, no clear data allow a preference for either one of these hypotheses. No evidence of any interruption of deposition between the peat and the Mydlák has been observed. However, the beginning of lacustrine flooding of the peat swamp is traceable back into the coal where a palynological change is observed several tens of centimetres below its roof; this is marked by a transition from a densospore to a lycospore phase (unpublished data of J. Bek and S. Opluštil).

From a taphonomic point of view, the plant fossils preserved in rootless laminate mudstones represent allochthonous flora, drifted in from a relatively short distance of ~ 2 km maximum from the lake shore, where roots are common. These rooted shoreline "facies" of the Mydlák bear autochthonous to parautochthonous subaerial plant remains *sensu* Bateman (1991). The roots provide

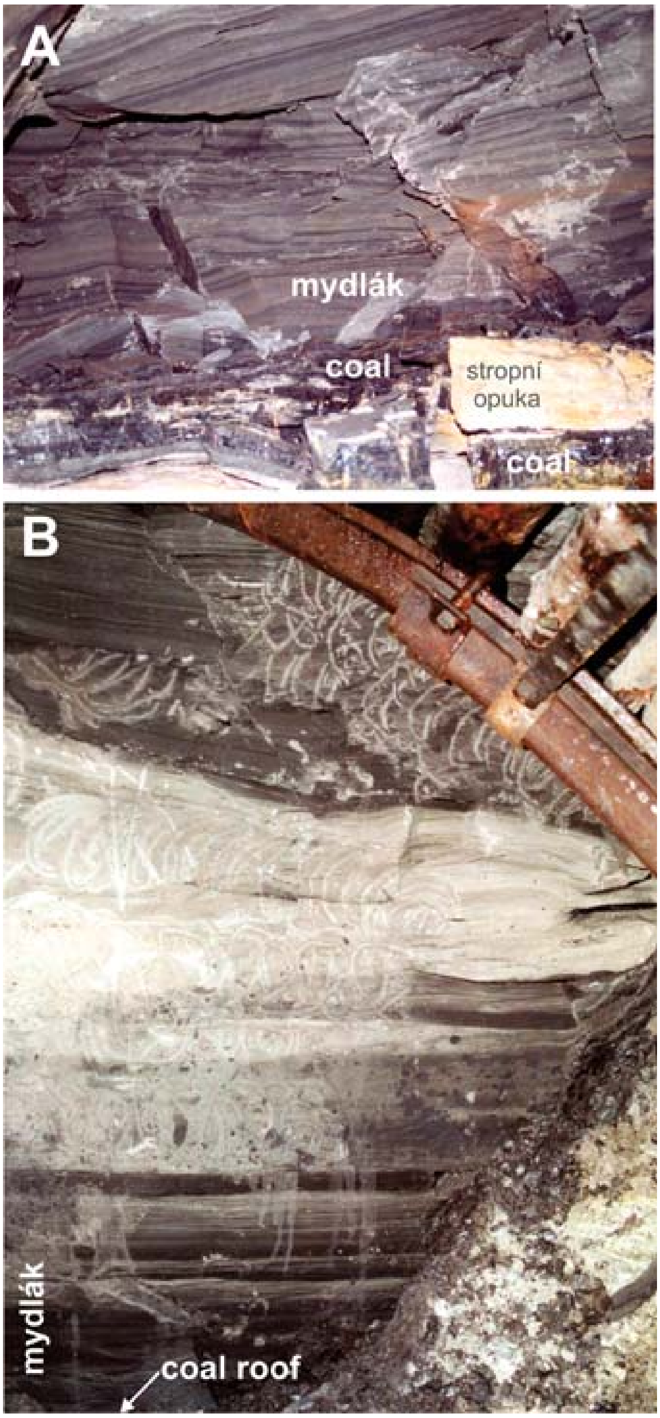


Figure 5. Mydlák horizon in the roof of Upper Radnice Coal. **A)** Irregularly laminated mudstone overlying the coal with intercalated Stropní (= roof) opuka tonstein, Tuchlovice Mine. Central part of palaeovalley. **B)** About 3 m thick part of the overburden of the Upper Radnice Coal as exposed in a gallery of the Tuchlovice Mine close to the margin of palaeovalley. Note the sharp-based thick sand body representing a sudden clastic influx into a lake close to palaeovalley margin.

evidence that at least part of the plant remains preserved in the Mydlák is derived from these coastal clastic wetlands, although the presence of relictual plant fossils from the terminal drowning phase of the peat swamp, preserved at or near the contact of the Mydlák and coal, cannot be excluded. However, differences in the species composition of the plant association in the Mydlák and that preserved in the intra-coal Velká opuka suggest drowning of the peat swamp and the gradual establishment of mineral-rich wetlands bordering the lake. The fossil-plant assemblages of these new peri-lacustrine habitats are dominated by sphenopsids, pteridosperms and ferns with subordinate arborescent lycopsids of species that are rare or absent in the Velká opuka.

Decrease in plant fossil content up-section suggests diminishment of wetlands, possibly due to increased clastic input, as the lake was gradually filled in. This is suggested by coarsening of the Mydlák up the section into ripple-bedded fine-grained sandstone followed by the regional erosional surface marking base level drop (Opluštil, 2005a).

5. PLANT SYSTEMATICS AND BIODIVERSITY

In all, 89 biological species have been recognized in the Velká opuka and Mydlák together. 59 species of these occur in the Velká opuka and 67 in the Mydlák (Figs 6, 7, 8). Both plant-bearing horizons have 37 species in common, which makes for ~ 42 % overlap in species composition. This overlap varies between the different plant groups (Figs 7, 9). The highest is among sphenopsids, both within calamites and sphenophylls, where about 83 and 80 % overlap exists respectively. In contrast, the lowest number of species in common between the two fossiliferous horizons was found among pteridosperms. Here the overlap within the entire group is ~ 32 %; however, in the case of medullosaleans specifically, this decreases to 22 % (Figs 7, 9). Low or no overlap exists in case of low-diversity plant groups represented by Noeggerathiales, Cordaitales and Dicranophyllales. They are, however, represented only by one or few species and except for cordaitaleans, their remains are rare. Two or three species of *Cordaites* were identified based on venation pattern; however, recent cuticular studies of this plant group (Šimůnek & Haldovský, 2015) have revealed much greater diversity than previously suspected.

A semi-quantitative estimate of frequency of occurrence of the most common species in both fossiliferous horizons shows that their abundance varies significantly between these two horizons (Fig. 6). Besides the common species there are also species that are unique or nearly so for one of the horizons examined. In the Velká opuka the highest percentage of species restricted to this band is among ferns (especially Filicales), making up ~ 28 % and c. 20 % for lycopsids. An anomalously high value of 80 % in the case of cordaitaleans is inflated by the systematic cuticular study of their leaves from the Velká opuka (Šimůnek & Haldovský, 2015) and the absence of such a study in the Mydlák.

There is also a similar set of species unique to the Mydlák. The highest number of species occurring exclusively in this fossiliferous horizon is among pteridosperms with 13 species, making up to 52 %. Detailed examination of this group reveals that the Mydlák contains ~ 78 % of medullosaleans taxa, 80 % of Lyginopteridales and 100 % of Callistophytales. A relatively high percentage of species unique to the Mydlák is found among the lycopsids (36 %), with the highest diversity corresponding to arborescent lycopsids where 7 of 19 species (37 %) were identified only from the Mydlák (Figs 6, 7, 8, 9). The diversity within the individual plant groups is described below.

5.1. Lycopsida

Lycophytes in the Velká opuka and Mydlák are mainly represented by arborescent lepidodendrids (Bek & Opluštil, 2004, 2006). Identified so far are the following species: *Lepidodendron aculeatum* Sternberg, *L. mannebachense* Presl *in* Sternberg, *L. longifolium* Presl *in* Sternberg, *L. lycopodioides* Sternberg, *L. ophiurus sensu* Němejc, 1954 (non Brongniart), *L. simile sensu* Němejc, 1954 (non Kidston), *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner, *Lepidophloios laricinus* (Sternberg) Sternberg, *Lepidophloios acerosus* Lindley & Hutton, *Lepidophloios macrolepidotus* Goldenberg, and *Bothrodendron minutifolium* Boulay (Figs 6, 10, 11).

Identification of individual species is based on the morphology of leaf cushions on stem and branches, and where possible, also on the morphology of leaves, cones and their spore contents. Based on these characteristics, the lepidodendrids can be split into several groups, which at least partly correspond to anatomically defined genera as described from coal balls (Bateman *et al*., 1992; DiMichele & Bateman, 1992). They include *Lepidodendron aculeatum* and *L. mannebachense* with leaf cushions that have infrafoliar parichnos, representing *Lepidodendron sensu stricto* as understood by Bateman *et al*. (1992). Leaves of these two species are long and grass-like. Rarely attached microsporangiate cones (Bek & Opluštil, 2004) bear *Lycospora* and belong to the genus *Lepidostrobus*. *Lepidodendron aculeatum* and *L. mannebachense* are abundant in the Mydlák, whereas the former species is absent and the latter very rare in the Velká opuka of Kladno Coalfield and elsewhere.

Another long-leaved species, *L. longifolium* has raised diamond-shaped leaf cushions without infrafoliar parichnos; its leafy shoots often contain cones described by Němejc (1954) as *Lepidostrobus cernuus* Sternberg. They are either microsporangiate and bear *Cappasporites distortus* or megasporangiate, containing *Cystosporites diabolicus* (unpublished data of J. Bek). Anatomically preserved cones with such spores are assigned to the genus *Achlamydocarpon* (see Bateman *et al*., 1992). Plants, bearing these cones belong to the anatomically defined genera *Synchysidendron* and *Diaphorodendron* (DiMichele & Bateman, 1992). *Lepidodendron* (*Synchysidendron*) *longifolium* is abundant in the Velká opuka and probably absent from or very rare in the Mydlák.

Leaf cushions of two other species, *Lepidodendron simile* and *Bergeria dilatata* are flat and lack infrafoliar parichnos and a differentiated leaf scar. Nearly always attached to stems and branches are short leaves, providing additional character for the recognition of species. Commonly in organic connection to leafy shoots are narrow cylindrical cones of *Lepidostrobus lycopodites* type (Němejc, 1954), with both megaspores and microspores (Bek & Opluštil, 1998 and unpublished data). These belong to the genus *Flemingites*. All these characters fit perfectly the polycarpic genus *Paralycopodites* Morey & Morey. *Bergeria dilatata* and *Lepidodendron simile* are quite common in both the Velká opuka and Mydlák (Figs 10, 11).

Another short-leaved species with flat leaf cushions lacking infrafoliar parichnos is *Lepidodendron lycopodioides*. Its slender cones resemble those of *Flemingites*. However, spores remain unrecorded; it is, therefore, currently impossible to prove this generic attribution. This species is very rare in both fossiliferous horizons.

Lepidodendron ophiurus sensu Němejc (1947) is a short-leaved species, bearing short arch-like leaves and small cylindrical microsporangiate cones, *Lepidostrobus ronnaensis* Bek & Opluštil, with *Lycospora rotunda* (Bek & Opluštil, 2004). The genus *Lepidophloios* Sternberg is represented by three species: *L. laricinus*, *L. acerosus* and *L. macrolepidotus*. Their remains are common in the Velká opuka as well as in the Mydlák.

Specimens of *Sigillaria* are generally much less common in comparison to lepidodendrid lycopsids. However, they are quite diverse. Their identification is based solely on bark compressions/impressions and encompasses the following species: *Sigillaria diploderma* Corda, *S. pachyderma* Brongniart, *S. trigona* Sternberg, *S. mamillaris* Brongniart, *S. feistmantelii* Geinitz, *S. deutschii* Brongniart and *S. polleri* Brongniart. Their distribution and “abundance” in individual horizons is expressed in Figure 6.

Common in the Velká opuka but very rare in the Mydlák are the remains of the subarborescent lycopsid *Omphalophloios feistmantelii* (Bek *et al*., 2015). Locally

	Plant groups			**Species**	**Upper Radnice Coal**	
					VO	**M**
1	Lycopsida	Arborescent		*Lepidodendron aculeatum*	0	XX
2				*Lepidodendron mannebachense*	x	XX
3				*Lepidodendron longifolium*	XXX	x
4				*Lepidodendron ophiurus*	XX	x
5				*Bergeria dilatata*	XX	XX
6				*Lepidodendron simile*	XX	X
7				*Lepidodendron lycopodioides*	x	x
8				*Lepidophloios acerosus*	X	X
9				*Lepidophloios laricinus*	X	XX
10				*Lepidophloios macrolepidotus*	0	x
11				*Bothrodendron minutifolium*	0	X
12				*Sigillaria diploderma*	X	X
13				*Sigillaria polleri*	0	X
14				*Sigillaria* cf. *deutschii*	0	X
15				*Sigillaria scutellata*	0	X
16				*Sigillaria feistmantelii*	X	0
17				*Sigillaria mamillaris*	x	X
18				*Sigillaria pachyderma*	X	X
19				*Sigillaria trigona*	X	0
20		Subarborescent		*Omphalophloios feistmantelii*	XXX	x
21				*Spencerites chalonerii*	X	0
22				*Polysporia robusta*	X	0
23				*Polysporia rothwellii*	0	x
24		Herbaceous		*Selaginella* sp.	0	x
25				*Selaginella labutae*	x	0
26	Sphenopsida	Calamitaceae	Leafy shoots	*Annularia radiata*	x	XXX
27				*Annularia pseudostellata*	X	X
28				*Asterophyllites grandis*	XXX	XXX
29				*Asterphyllites charaeformis*	0	XXX
30				*Asterophyllites equisetiformis*	X	XX
31				*Asterophyllites longifolius*	XX	XX
32		Sphenophyllales		*Sphenophyllum priveticense*	XX	XXX
33				*Sphenophyllum myriophyllum*	X	XXX
34				*Sphenophyllum cuneifolium*	X	XX
35				*Sphenophyllum pseudoaquense*	XX	0
36				*Sphenophyllum taylorii*	XX	X
37	Pteridopsida	Marattiales		*Pecopteris abbreviata*	0	X
38				*Pecopteris miltonii*	0	X
39				*Pecopteris aspidioides*	XX	XXX
40				*Pecopteris incerta*	0	X
41		Zygopteridales		*Desmopteris alethopteroides*	X	0
42				*Desmopteris longifolia*	XX	x
43				*Corynepteris sternbergii*	XXX	X
44				*Corynepteris coralloides*	0	x

45	Pteridopsida	Filicales	Tedeleaceae	*Senftenbergia pennaeformis*	0	X
46				*Senftenbergia plumosa*	XX	XXX
47			Sermayaceae	*Oligocarpia gutbieri*	X	X
48				*Oligocarpia lindsaeoides*	XX	0
49			Incertae sedis	*Hymenotheca globullifera*	X	0
50				*Renaultia rotundifolia*	0	x
51				*Discopteris vuellersii*	x	0
52				*Sphenopteris (Boweria) schatzlarensis*	XX	XX
53				*Zeilleria delicatula*	0	XX
54				*Sphenopteris (Zeilleria) haidingerii*	x	0
55	Pterido-spermopsida	Medullosales		*Alethopteris distantinervosa*	0	X
56				*Alethopteris* cf. *serlii*	0	X
57				*Laveineopteris loshii*	x	x
58				*Laveineopteris bohemica*	0	XXX
59				*Laveineopteris tenuifolia*	0	XXX
60				*Macroneuropteris scheuchzeri*	0	X
61				*Havlenaea "Mixoneura" praeovata*	0	x
62				*Linopteris neuropteroides* f. *major*	x	X
63				*Paripteris linguaefolia*	0	XX
64		Callistophytales		*Mariopteris muricata*	0	x
65				*Fortopteris radnicensis*	0	x
66		Lyginopteridales		*Eusphenopteris nummularia*	x	XXX
67				*Eusphenopteris obtusiloba*	0	XX
68				*Eusphenopteris neuropteroides*	0	x
69				*Eusphenopteris sauveurii*	0	X
70				*Eusphenopteris schumannii*	0	x
71		Incertae sedis		*Palmatopteris furcata*	XX	XX
72				*Sphenopteris spiniformis*	x	XXX
73				*Sphenopteris spinosa*	x	X
74				*Sphenopteris mixta*	X	XX
75				*Sphenopteris pulchrior*	XX	0
76				*Sphenopteris flexuosissima*	XXX	x
77	Progymno-spermopsida	Noeggerathiales	Noeggerathiaceae	*Noeggerathia foliosa*	x	x
78				*Noeggerathia intermedia*	x	0
79			Discinitaceae	*Palaeopteridium macrophyllum*	x	0
80				*Palaeopteridium reussii*	0	x
81				*Rhacopteris elegans*	x	0
82				*Rhacopteris bipinata*	x	0
83				*Rhacopteris speciosa*	x	0
84	Pinopsida	Cordaitales	Cordaitaceae	*Cordaites kladnoensis*	XX	0
85				*Cordaites latus*	X	0
86				*Cordaites theodorii*	X	0
87				*Cordaites wartmannii*	XXX	0
88				*Cordaites* sp.	X	XX
89		Dicranophyllales	Dicranophyllaceae	*Dicranophyllum dominii*	X	0
Estimated number of biological species					**59**	**67**
Estimated number of biological species (without very rare and uncertain)					**40**	**48**
Total number of biological species in both horizons					**89**	

Relative frequency of occurrence: XXX – abundant, XX – common, X – rare, x – very rare or exceptional.

Figure 6. List of species identified so far in the Velká opuka and Mydlák and an estimation of their relative abundance.

common in this volcanic parting are also representatives of the genera *Spencerites* (Scott) and *Polysporia* Newberry (Drábková *et al*., 2004; Bek *et al*., 2009a). On the other hand, herbaceous lycopsids are very rare in both plant-bearing horizons. They are represented by the genus *Selaginella* (Bek *et al*., 2009b and unpublished data).

5.2. Sphenopsida

Sphenophytes of the studied horizons are represented by calamitaleans and sphenophylls (Fig. 6). Species diversity of calamitaceans seems to be best estimated from their foliage, although cone and stem species were also identified (Figs 12, 13). The following species of calamite leafy shoots were identified: *Annularia radiata* (Brongniart) Sternberg, *A. pseudostellata* Potonié, *Asterophyllites grandis* (Sternberg) Geinitz, *A. charaeformis* (Sternberg) Unger, *A. equisetiformis* Brongniart and *A. longifolius* (Sternberg) Brongniart. The number of foliage taxa is comparable with "stem" taxa as well as with diversity of calamite cones (Němejc, 1953). There is an apparent overlap in species diversity between the Velká opuka and Mydlák; except for *Asterophyllites charaeformis*, all species occur at both horizons. *Calamites* are known by their extensive range of ecological adaptability ranging from clastic to peat substrates (e.g., DiMichele, 2014), and including stressful habitats.

Herbaceous sphenophytes are represented by the genus *Sphenophyllum* Brongniart. Identified were following species: *Sphenophyllum cuneifolium* (Sternberg) Zeiller, *S. priveticense* Libertín *et al*., *S. myriophyllum* Crépin, *S. taylorii* Bek *et al.* and *S. pseudoaquense* Libertín *et al.* (Fig. 6). Four of these are common for both horizons, whereas only *S. pseudoaquense* has been so far found in the Velká opuka.

5.3. Pteridopsida

Ferns of the studied horizon are represented by eusporangiate as well as leptosporangiate forms. They belong to the following groups: Marattiales, Zygopteridales and Filicales (Figs 6, 7, 14, 15). Eusporangiate ferns have been identified following artificial foliage species assigned to the Marattiales: *Pecopteris abbreviata* Brongniart, *P. miltonii* (Artis) Brongniart, *P. aspidioides* Sternberg and *Pecopteris incerta* Corsin. *Pecopteris incerta* is probably identical with *Pecopteris aspidioides* but this can be confirmed only by detailed systematic revision in the future. Similarly *Pecopteris miltonii* and *P. aspidioides* show very similar pinnules, which make their correct identification problematic, especially if only fragments of ultimate pinnae are available. Both species had large fronds with a considerable amount of morphological variation that has not been precisely documented up to date as mentioned by Wagner & Álvarez-Vázquez (2016). It results in lot of confusions in understanding of both species. Pšenička *et al.* (2009) strictly separated both species and assigned them within the genus *Lobatopteris* whereas Wagner & Álvarez-Vázquez (2016) synonymized both species and putted them to the genus *Pecopteris*. This concept, however, is based only upon assumptions rather than exact data. The holotype of *Pecopteris aspidioides* comes from the Radnice Basin and Wagner & Álvarez-Vázquez (2016) unfortunatelly ignored additional material from the type locality, where hundred of specimens, even large than the holotype and including fertile material, are available. These specimens show large pinnule variability depending on position on frond. The main difference can be found in venation, where pinnules of *P. aspidioides* show besides once to twice bifurcated lateral veins also simple veins, while pinnules of *P. miltonii* show twice (rarelly once) bifurcated veins. Another important difference is in shape of proximal part of penultimate pinna, which is acute in case of *P. miltonii*, while *P. aspidioides* has acuminate tip of pinna. Mentioned should be also different type of synangia; *P. aspidioides* bears 4-5 (commonly 5) sporangia per synangium while *P. miltonii* bears only 3-4 (commonly 4) sporangia per synangium. Based on these facts we keep *P. miltonii* and *P. aspidioides* as separate species. Nevertheless, detailed taxonomic revision is necessary in future. Marattialean foliage of the studied horizons thus probably represents only three biological species of the subfamily Miltonoide with typical lobatopterid venation pattern (Wagner, 1958; Pšenička & Bek, 2009). Marattialean ferns are interpreted as colonizers of wet substrates (Lesnikowska, 1989; DiMichele & Phillips, 2002) as well as moderately well-drained soils (DiMichele & Phillips, 2002). Marattialean ferns are known from the Velká opuka and Mydlák, but only *P. aspidioides* is abundant in both horizons. In the Velká opuka consists a part of an *in situ* preserved, pre-eruption, peat-forming phytocoenosis. In contrast, an allochthonous association of *P. abbreviata*, *P. aspidioides* and *P. miltonii* in the Mydlák is derived from lake-margin wetlands where they likely colonized various habitats.

Zygopterids are represented by *Desmopteris alethopteroides* (Ettingshausen) Stur, *Desmopteris longifolia* (Sternberg *in* Goeppert) Stur, *Corynepteris sternbergii* (Ettingshausen) Zeiller and *Corynepteris coralloides* (Gutbier) Zeiller (Fig. 6). These differ from filicalean as well as marattialean ferns in architecture, anatomy and reproductive organs (Phillips & Galtier, 2005). There is a nomenclatural and taxonomic problem with *Corynepteris angustissima* and *Asplenites* (*Corynepteris*) *sternbergii*. *Pecopteris* (*Corynepteris*) *angustissima* was established by Sternberg (1825) based on material from Svinná locality (tuff bed at the base of the Whetstone Horizon, Radnice Member). Later, Ettingshausen (1854) established a new species *Asplenites* (*Corynepteris*) *sternbergii* based on material from the same locality and

Species ▼ / Horizons ►	**Number of species**	**Velká opuka**			**Mydlák**			**Common species**	**%**
		Total	**Only VO**	**%**	**Total**	**Only Mydlák**	**%**		
Arborescent lycopsids	19	13	2	10,5	17	6	31,6	11	57,9
Sub-arborescent lycopsids	4	3	2	50,0	2	1	25,0	1	25,0
Herbaceous lycopsids	2	1	1	50,0	1	1	50,0	0	0,0
Lycopsida (total)	**25**	**17**	**5**	**20,0**	**20**	**8**	**32,0**	**12**	**48,0**
Calamitaceae	6	5	0	0,0	6	1	16,7	5	83,3
Sphenophyllales	5	5	1	20,0	4	0	0,0	4	80,0
Sphenopsida (total)	**11**	**10**	**1**	**9,1**	**10**	**1**	**9,1**	**9**	**81,8**
Marattiales	4	1	0	0,0	4	3	75,0	1	25,0
Zygopteridales	4	3	1	25,0	3	1	25,0	2	50,0
Filicales	10	7	4	40,0	6	3	30,0	3	30,0
Pteridopsida (total)	**18**	**11**	**5**	**27,8**	**13**	**7**	**38,9**	**6**	**33,3**
Medullosales	9	2	0	0,0	9	7	77,8	2	22,2
Callistophytales	2	0	0	0,0	2	2	100,0	0	0,0
Lyginopteridales	5	1	0	0,0	5	4	80,0	1	20,0
Pteridosperms Incertae sedis	6	6	1	16,7	5	0	0,0	5	83,3
Pteridospermopsida (total)	**22**	**9**	**1**	**4,5**	**21**	**13**	**59,1**	**8**	**36,4**
Noeggerathiales	**7**	**6**	**5**	**71,4**	**2**	**1**	**14,3**	**1**	**14,3**
Cordaitales	**5**	**5**	**4**	**80,0**	**1**	**0**	**0,0**	**1**	**20,0**
Dicranophyllales	**1**	**1**	**1**	**100,0**	**0**	**0**	**0,0**	**0**	**0,0**
Species in total	**89**	**59**	**22**	**24,7**	**67**	**30**	**33,7**	**37**	**41,6**

Figure 7. Diversity of the Velká opuka and Mydlák floras with regard to systematic groups.

layer like the Sternberg´s specimen. From this point of view both species represent the same taxon and must be synonimized. Nevertheless, later many authors described under the names *Corynepteris angustissima* or *C. sternbergii* different zygopterid species (e.g., Zeiller, 1899; Galtier & Scott, 1979). Galtier & Scott (1979, p. 12) revised *C. sternbergii* and incorrectly compared Ettingshausen´s specimen with well preserved Kidston´s specimens, which represents a different species. The main difference between both species is in type of reproductive organs where Sternberg´s *C. angustissima* has "*Biscalitheca*" type of sporangia (unpublished observation), while *C. sternbergii sensu* Galtier & Scott (1979) has typical "*Corynepteris*" type of sporangia. The problem is that species similar to *C. sternbergii sensu* Galtier & Scott (1979) were described as *C. angustissima* or *C. sternbergii* in many palaeobotanical papers. Specimens from the Velká opuka and Mydlák lack the *Biscalitheca* type of sporangia and for that reason we use the name *C. sternbergii sensu* Galtier & Scott (1979).

Zygopterids formed lush underbrush and also were able to climb on trees (Opluštil et al., 2009a, b). Their morphological and inferred physiological attributes suggest their adaptation to relatively drier and sunny environments (Phillips & Galtier, 2005). Dennis (1974) and Phillips & Galtier (2005) inferred from rhizome apices and frond primordia that zygopterids had a capacity for arrested growth responses or dormancy. Evidence of dormancy, in particular, suggests that these ferns were adapted to some limiting factors of habitat regarding water stress (Phillips & Galtier, 2005). Higher species diversity and frequency of occurrence correspond to the peat-forming assemblage in the Velka opuka. Similar observations were made in the Bělka tuff bed in the roof of the Lower Radnice Coal, which also carries *in situ* preserved peat-swamp plant taphocoenoses, with an understory characterized by zygopterid ferns (Opluštil et al., 2009a, b). Presence of these plants in the peat substrate may indicate instability of water table.

Leptosporangiate ferns are represented by several taxa of the following filicalean families: Tedeleaceae: *Senftenbergia plumosa* (Artis) Stur and *S. pennaeformis* (Brongniart) Stur; Sermayaceae: *Oligocarpia gutbieri*

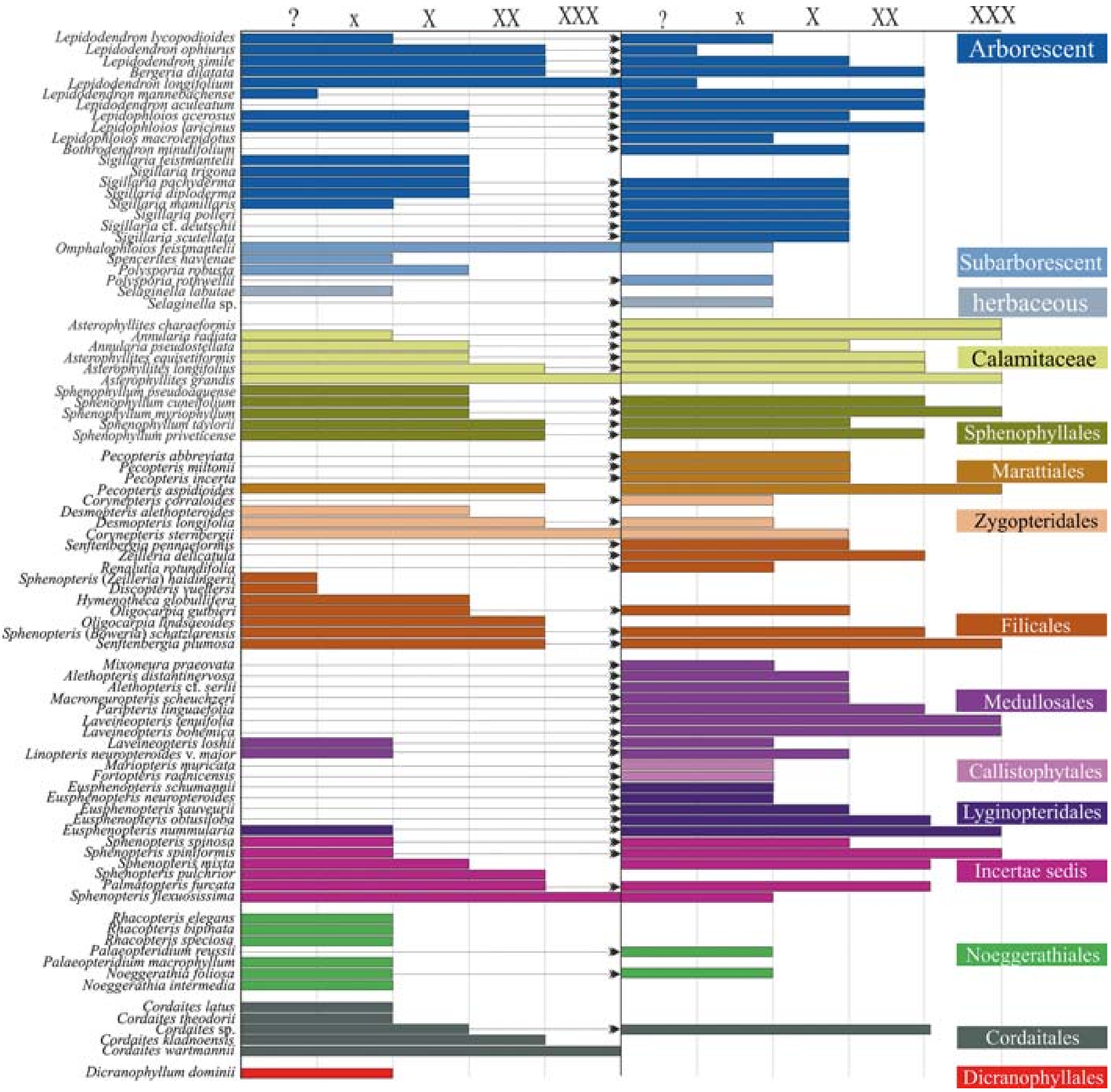


Figure 8. Semiquantitative distribution of species identified from the Velká opuka and Mydlák in the Kladno Coalfield.

Goeppert and *O. lindsaeoides* (Ettingshausen) Stur; and others, the systematic classification of which remains still unclear: *Hymenotheca globulifera* Němejc, *Renaultia rotundifolia* (Andrae) Zeiller, *Discopteris vuellersii* Stur, *Sphenopteris* (*Boweria*) *schatzlarensis* (Kidston) Jongmans, *Sphenopteris* (*Zeilleria*) *delicatula* Sternberg and *Sphenopteris* (*Zeilleria*) *haidingerii* Ettingshausen. Pennsylvanian leptosporangiate ferns acquired a variety of growth habits and occupied a wide range of ecological habitats (DiMichele & Phillips, 2002).

Tedeleaceae ferns having *Ankyropteris*-type of anatomy (Phillips & Galtier, 2011) in the studied horizons are represented by the compression genus *Senftenbergia* (Jennings & Eggert, 1977), which had a vine/climbing habit (Rössler, 2000; Phillips & Galtier, 2011). Remains of this genus are often found in association with zygopterid ferns as observed not only in the horizons studied but also in some coals of the Illinois Basin (Phillips & Galtier, 2005) and in the Union Seam (England) (Holmes & Fairon-Demaret, 1984). All these observations are consistent with the presumed ecological preferences of Zygopterid

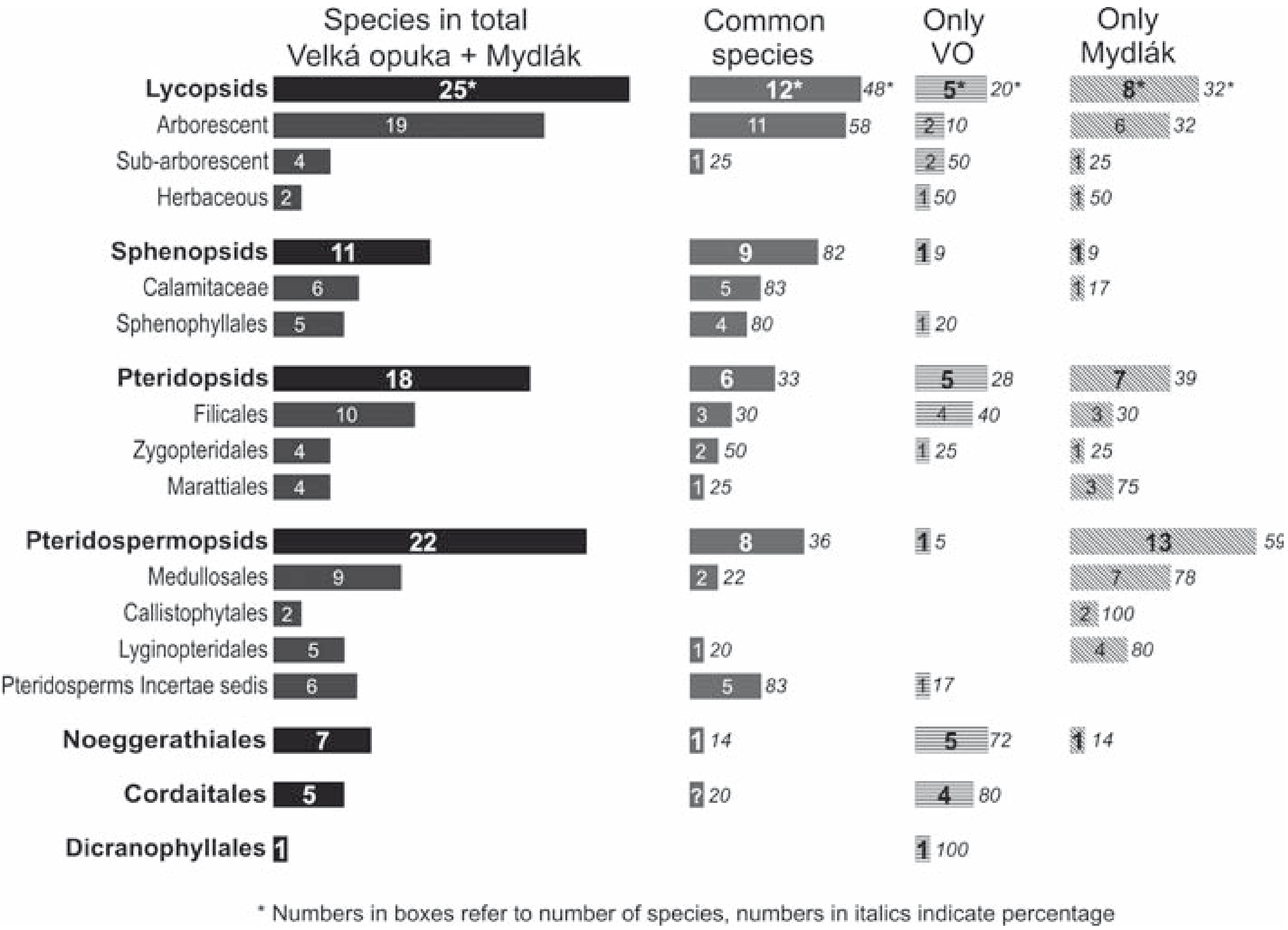


Figure 9. Fossil plant diversity of the Velká opuka and Mydlák according to their systematic position. Species common to both horizons are indicated, as are those unique to only one of them.

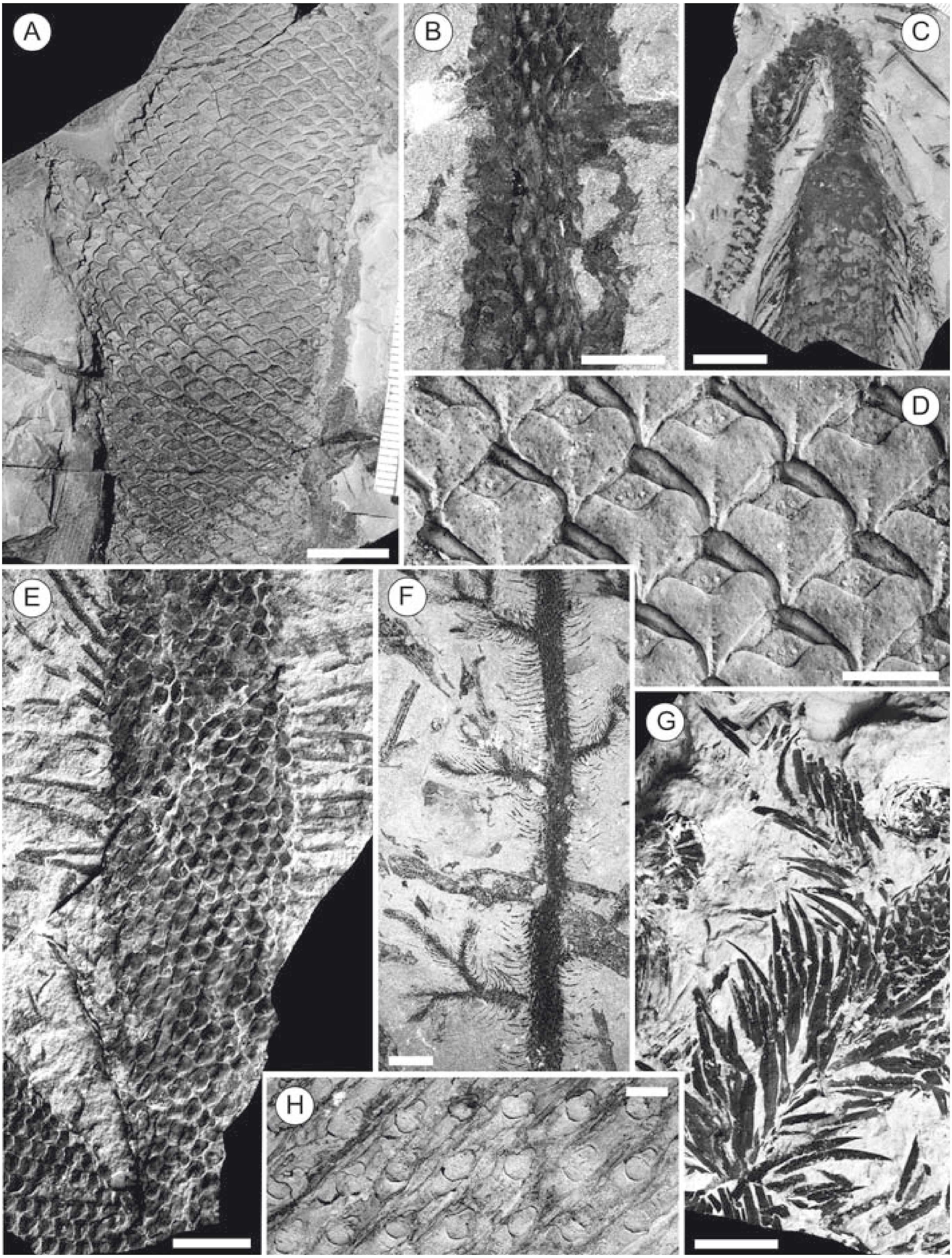
ferns in disturbed, water-stressed environments with (?) fluctuating water table and/or exposed substrates (Phillips & Galtier, 2005). *Senftenbergia* is also a common part of plant associations in the Mydlák as derived from marginal areas, where exposed substrates do not occur.

Ferns of Sermayaceae have an *Anachoropteris*-type anatomy and *Oligocarpia*-type reproductive organs (Eggert & Delevoryas, 1967). Most species with *Anachoropteris*-type of anatomy come from non-coal swamp environments (Galtier & Phillips, 2014), except for some species preserved in a tuff bed in the roof of the Lower Radnice Coal (Corda, 1845), which colonized peat-forming habitats. Generally *Anachoropteris* foliar remains were borne on *Tubicaulis*-type stems (Phillips, 1974; Galtier & Phillips, 2014) having semi-erect to erect habitus. DiMichele & Phillips (2002) suggested that they are "walking ferns", which produced stem buds on scrambling frond rachides enabling them to spread rapidly across the substrate. Another type with *Anachoropteris* anatomy shows a scrambling or climbing adaptation (Corsin, 1937; Galtier, 2008). This adaptation can be seen in *Oligocarpia lindsaeoides* with recurved penultimate pinna rachides arching over the adaxial side of the main rachis. This species is more or less common in the Velká opuka.

Our knowledge of the last group of filicaleaen ferns placed into *Incertae sedis* (Fig. 6) is very limited because only reproductive organs are known. They suggest affinities to *Anachoropteris*, *Psalixochlaena*, *Tubicaulis*, *Ankyropteris* or *Sermaya*. Nevertheless, without relevant data on anatomy of the rachides, it is impossible to determine their ecological role in the assemblage.

5.4. Pteridospermopsida

Medullosan pteridosperms are uncommon in the Velká opuka and common in the Mydlák in the Kladno Coalfield (Figs 6, 16, 17). The most common medullosalean species are those assigned formerly to *Neuropteris* (Brongniart) Sternberg. However, cuticular studies have allowed their classification into several genera (Cleal & Shute, 1995; Šimůnek & Cleal, 2011). *Laveineopteris loshii*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(Brongniart) Cleal, Shute & Zodrow is abundant in the “Bělka”, a volcanic band in roof of the Lower Radnice Coal, but only occurs sporadically in the Velká opuka and Mydlák. *Laveineopteris tenuifolia* (Sternberg) Cleal, Shute & Zodrow and *L. bohemica* (formerly identified as *Neuropteris attenuata* by Havlena, 1953), are relatively abundant in the Mydlák. This is also the case of isolated pinnules of *Paripteris linguaefolia* (Bertrand) Laveine. In contrast, *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zodrow is less common in the Mydlák. Linopterids are represented by a single species, *Linopteris neuropteroides* Gutbier forma *major* Potonié. Its detached pinnules occur in places in the Mydlák and sporadically also in the Velká opuka.

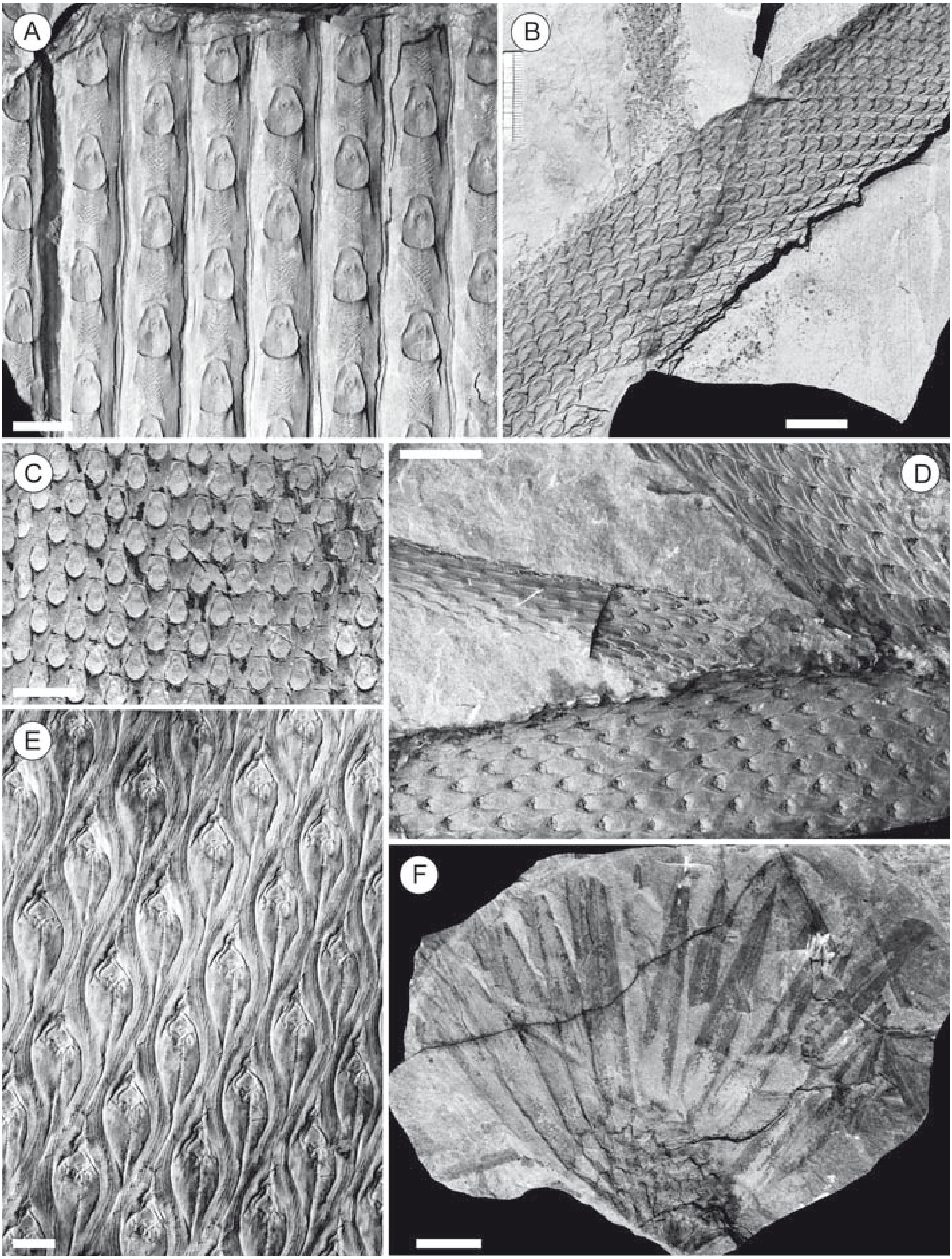
Alethopterids are represented only by *Alethopteris distantinervosa* Wagner and *A.* cf. *serlii* (Brongniart) Goeppert, which both occur in the Mydlák. *A. distantinervosa*, originally described as *Alethopteris grandini* (Brongniart) by Němejc (1936), is more common, whereas *Alethopteris* cf. *serlii* is represented by only a few specimens (Fig. 17G). Wagner (1968) distinguished two quite similar species *Alethopteris distantinervosa* and *Alethopteris grandinioides* Kessler in Central Bohemia. However, Šimůnek (1989) considered these species as varieties of *Alethopteris grandinioides* Kessler because of the strong similarity of their cuticles. Since *Alethopteris grandinioides* is typical for late Bolsovian and Asturian in western Europe, Šimůnek & Cleal (2002) again revised specimens of these two species and came to the conclusion that there is only one species with wide pinnule variability and that the correct name is *Alethopteris distantinervosa.* The species *Alethopteris* cf. *serlii* has been described by Němejc (1936) and by Wagner (1968) as *Alethopteris serlii.* However, Cleal (pers. com.) claims that true *Alethopteris serlii* is known only from Great Britain and North America, so we describe it here as *Alethopteris* cf. *serlii* because of its strong similarity.

“Mariopterids” are represented by *Mariopteris muricata* (Schlotheim) Zeiller and *Fortopteris radnicensis* (Němejc) Boersma. Both species are relatively rare in the Radnice coal group and occur only in Mydlák. Much more common are representatives of the order Lyginopteridales, particularly the genus *Eusphenopteris* Simson-Sharold. The following species occur in the Radnice group of coals: *Eusphenopteris nummularia* (Gutbier) Novik, *E. obtusiloba* (Brongniart) Novik, *E. neuropteroides* (Boulay) Novik, *E. sauveurii* (Crépin) Simson-Sharold and *E. schumannii* (Stur) van Amerom. Nearly all these species have been found only in the Mydlák, except for *E. nummularia*, which also occurs rarely in the Velká opuka. *E. nummularia* and *E. obtusiloba* belong to the most common species in the Mydlák. The species *E. sauveurii* is also relatively common but *E. neuropteroides* and *E. schumannii* are very rare.

There are several species of uncertain affinity assigned mostly to the genus *Sphenopteris* (Brongniart) Sternberg except *Palmatopteris furcata* (Brongniart) Potonié. Pinnules of these species are of sphenopterid type and fructifications are usually unknown. *Palmatopteris furcata* is common in the Mydlák and Velká opuka. Fairly abundant in the Mydlák are *Sphenopteris* (*Palmatopteris*) *spiniformis* Kidston and *S. mixta* Schimper whereas *S. spinosa* Goeppert is quite rare here. Most common in the Velká opuka are *S. pulchrior* Gothan & Jongmans (also *Eusphenopteris* – van Amerom, 1975) and especially *S. flexuosissima* Stur, the latter originally identified as the fern *Sphenopteris* cf. *crepinii* (Opluštil *et al*., 2007). In this study we re-interpreted this species as *Sphenopteris flexuosissima* and assigned it within pteridosperms. The reason is the presence of Lyginopterid-type of pollen organs (Fig. 16D) similar to those of *Crossotheca kentuckiensis* (Stubblefield *et al*., 1982). *In situ* miospores (unpublished data) are monolete, showing an affinity to pollens rather than to spores.

The most “exotic”, very sporadic species is *Havlenaea praeovata* (Němejc) Šimůnek & Cleal, found in the Kladno Coalfield only by a few fragments in the Mydlák and probably representing a species drifted in from habitats situated higher elevations, possibly from basement palaeohighs in the surroundings of the valley.

Figure 10. Examples of lycopsids identified from the Velká opuka. **A)** *Lepidodendron longifolium* Presl *in* Sternberg. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **B)** *Spencerites chalonerii* Drábková *et al*. Holotype. Prago Mine, National Museum collection, Prague (E 3684); scale bar 10 mm. **C)** *Lepidostrobus cernuus* (Sternberg) Němejc. A *Cappasporites*-bearing cone attached to the shoot of *Lepidodendron longifolium*. Ronna Mine, National Museum in Prague; scale bar 20 mm. **D)** *Lepidodendron longifolium* Presl *in* Sternberg. Detail of leaf cushions of a branch. Mayrau Mine, S. Opluštil collection; scale bar 5 mm. **E)** *Omphalophloios feistmantelii* (Feistmantel) Bek *et al.* Ronna Mine, National Museum in Prague (E973); scale bar 20 mm. Previously figured in Opluštil *et al*. (2007, pl. VII, fig. 6) **F)** *Lepidodendron ophiurus sensu* Němejc (non Brongniart). Leafy shoot from the Ronna Mine. Same as Opluštil *et al*. (2007, pl. VII, fig. 1). West Bohemian Museum in Pilsen; scale bar 10 mm. **G)** *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner. Leafy shoot. Kladno, National Museum in Prague; scale bar 20 mm. **H)** *Sigillaria pachyderma* Brongniart. Schoeller Mine, S. Opluštil collection; scale bar 20 mm.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5.5. Noeggerathiales

The members of this group of plants are relatively rare at both horizons (Figs 6, 18). They are represented by two families: Noeggerathiaceae and Discinitaceae. Noeggerathiaceae comprise two species *Noeggerathia foliosa* Sternberg and *N. intermedia* Feistmantel (Šimůnek & Bek, 2003). *N. foliosa* occurs rarely in both fossil-bearing horizons (but seems to be more common in the "Velká opuka"), whereas *N. intermedia* has been found so far only in the "Velká opuka". According to Šimůnek & Bek (2003) these plants were about 1-1.5 m tall "trees", which may be considered as an adaption to habitats with unstable soft substrate, e.g., peat.

The family Discinitaceae is represented by two genera, *Rhacopteris* Schimper and *Palaeopteridium* Kidston (Fig. 6). Their common character is that they produced *Discinites* Feistmantel cones (Bek & Šimůnek, 2005). *Rhacopteris* (*Rhacopteris elegans* (Ettingshausen) Schimper, *R. bipinnata* Němejc and *R. speciosa* Ettingshausen) was found only in the Velká opuka. *Palaeopteridium* is represented by *P. macrophyllum* Němejc in the Velká opuka, and by *P. reussii* Ettingshausen in the Mydlák (Fig. 6). That *Rhacopteris* belonged to the family Discinitaceae was demonstrated by Němejc (1941), who found a fragment of discinite-type cone attached to *Rhacopteris bipinnata* rachis.

Absence of information on the anatomy of these plants limits speculation on their ecological role in phytocoenoses.

5.6. Cordaitanthales

During the 19th and the 20th century only few cordaitalean species were identified in the Kladno-Rakovník Basin including the Kladno Coalfield (Figs 6, 18). Their specific determination was based solely on venation pattern (e.g., Feistmantel, 1874). However, the modern cuticular studies by Šimůnek (2007) and Šimůnek & Haldovský (2015), revealed the higher diversity of this plant group than previously suspected. Four Cordaitalean species were distinguished in the Velká opuka; unfortunately, no sample from Mydlák was macerated (Fig. 6). All species possess lanceolate leaves, except the very rare *Cordaites latus* Šimůnek, which has clavate leaves. The species *C. kladnoensis* Šimůnek and *C. wartmannii* Šimůnek are relatively common. *Cordaites theodorii* Šimůnek & Haldovský, on the other hand, occurs only sporadically and is the only cordaitalean species with a dentate leaf margin; it is further characteristic by densely papillated epidermal cells, a morphological feature typical of peat-forming cordaitaleans (Šimůnek & Florjan, 2013).

5.7. Dicranophyllales

When listing plant species found in the Velká opuka, we must not forget to *Dicranophyllum dominii* Němejc, 1929, which was described originally from this bed (Fig. 6). This short-leaved form is relatively rare in the Velká opuka. The systematic position of dicranophylls remains problematic, but most authors prefer to place them with the conifers (Barthel & Noll, 1999; Taylor *et al.*, 2009).

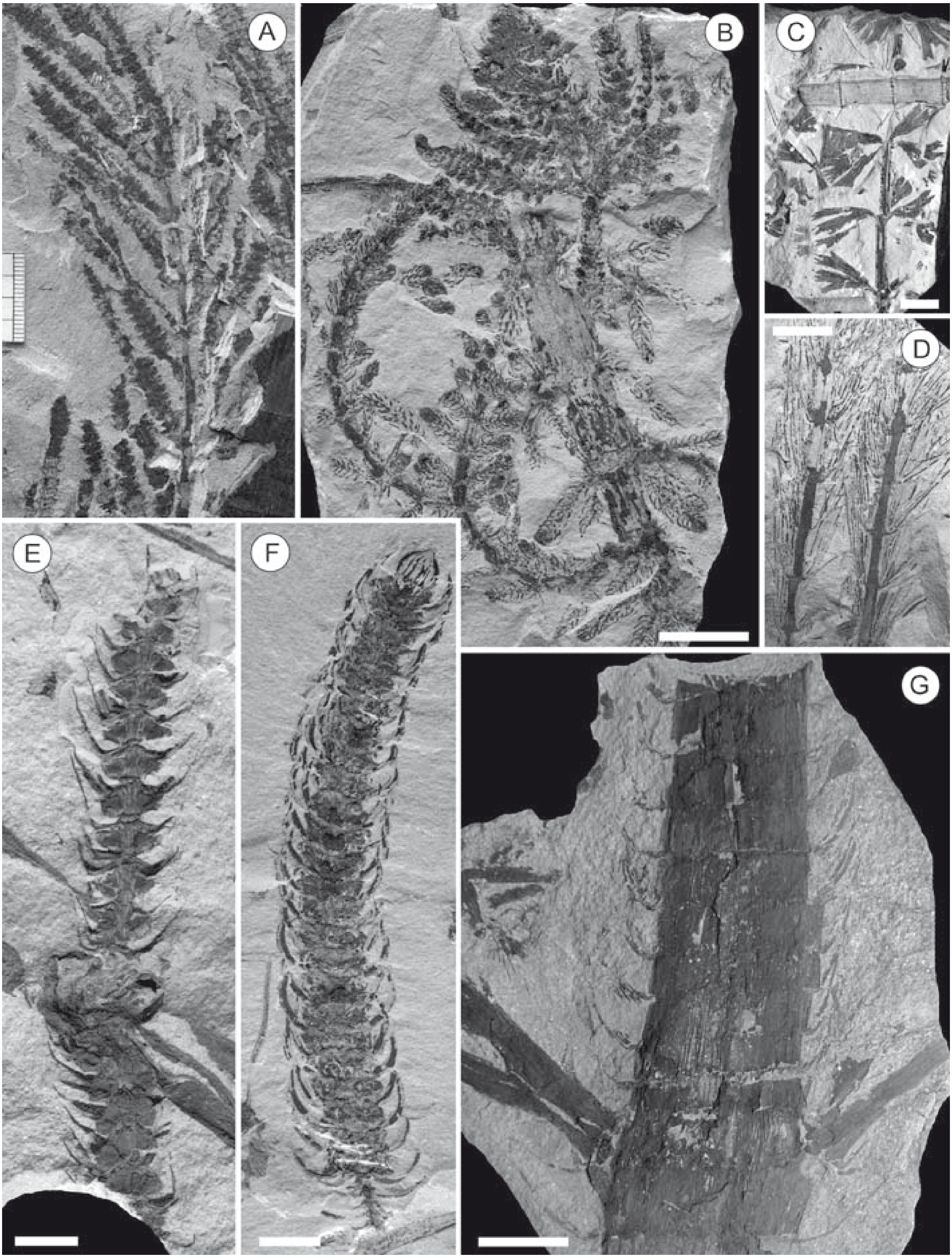
6. ASSEMBLAGES OF THE VELKÁ OPUKA AND MYDLÁK

Analyses performed on the data presented in Figures 6 and 7 and further expressed in Figures 8, 9 and 19 suggest differences in composition and diversity of vegetation that colonized the Kladno coalfield during the deposition of the Velká opuka and the Mydlák. In addition, differences also were observed in the frequency of occurrence of taxa common to the two horizons.

6.1. Velká opuka

A simple reading of the data in Figure 6 suggests that the flora of the Velká opuka (VO) is less diverse than that of the Mydlák, and is dominated by lycopsids, calamitaleans and some ferns; pteridosperms occupy a subordinate position. Although this is generally true, a more detailed analysis shows that two contrasting plant assemblages may be recognised in the Velká opuka based on detailed studies of the macroflora (Opluštil *et al.*, 2007) and palynoflora (Opluštil *et al.*, 1999). The first assemblage is dominated by sub-arborescent lycopsid *Omphalophloios feistmantelii* which is very typical of the Velká opuka (Bek *et al.*, 2015). In the second

Figure 11. Lycopsids from the Mydlák. **A)** *Sigillaria pachyderma* Brongniart. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **B)** *Lepidodendron mannebachense* Presl *in* Sternberg. Theodor Mine, J. Haldovský collection; scale bar 20 mm. **C)** *Sigillaria trigona* Sternberg. Ronna Mine, Faculty of Sciences collection, Charles University in Prague; scale bar 10 mm. **D)** *Bergeria dilatata* (Lindley & Hutton) Álvarez-Vázquez & Wagner. Kladno Coalfield, precise mine unknown. National Museum in Prague (E1914), scale bar 20 mm. **E)** *Lepidodendron aculeatum* Sternberg. Kladno Coalfield, precise mine unknown. National Museum in Prague; scale bar 10 mm. **F)** *Lepidostrobophyllum majus* (Brongniart) Hirmer. Part of a cone. Theodor Mine, J. Haldovský collection; scale bar 20 mm.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assemblage lepidodendrid lycopsids bearing lycospores and *Cappasporites* are predominant. Common to abundant are *Lepidodendron longifolium* and *L. ophiurus*, both typical of the Velká opuka. Fairly common in the Velká opuka are also *Lepidodendron simile* and *Lepidophloios laricinus*. Both assemblages in the Velká opuka are accompanied by abundant calamitaleans; especially common are the foliage *Asterophyllites grandis* and *A. longifolius* foliage, and the strobili *Palaeostachya ettingshausenii*, *P. gracillima*, *P. distachya*, *P. elongata* and *Calamostachys grandis*. Common are also sphenophylls including *Sphenophyllum pseudoaquense,* typical of the Velká opuka, *S. priveticense*, *S. taylorii* and *S. cuneifolium*. Ferns of the Upper Radnice Coal preserved in the Velká opuka mostly belong to *Corynepteris sternbergii* (zygopterid) with subdominant *Desmopteris longifolia* (zygopterid)*, Senftenbergia plumosa* (ankyropterid anatomy), *Oligocarpia lindsaeoides* and the marattialean fern *Lobatopteris aspidioides*. The autochtonous co-occurrence of ankyropterids and zygopterids highlights a water-stressed environment (Phillips & Galtier, 2005). Pteridosperms are generally rare, except *Sphenopteris flexuossisima* (= *S. crépinii*?) and *S. pulchrior*, which are fairly abundant.

6.2. Mydlák

Plant associations found in the Mydlák vary from place to place but are generally dominated by *Calamites*. Most common are pit casts of *Calamites undulatus* and *C. suckowii* with subordinate *C. goeppertii*. These are associated with the strobili *Palaeostachya ettingshausenii*, *P. pedunculata* and *Calamostachys grandis*.

Calamitalean foliage typical for the Mydlák includes *Annularia radiata* and *Asterophyllites grandis* (also abundant in the VO), *A. equisetiformis*, *A. longifolius*; typical only for the Mydlák is *A. charaeformis*. Sphenophylls are also abundant; the most common is *Sphenophyllum myriophyllum*, characteristic of the Mydlák, also with *S. priveticense* and *S. cuneifolium* (common also in the VO).

Pteridosperm are among the most common remains found in the Mydlák. Of about 21 species of this group identified at this horizon, *Laveineopteris bohemica* and/or *L. tenuifolia* are most abundant. *Paripteris linguaefolia* has a subordinate presence. Elsewhere, similarly abundant is the association of *Eusphenopteris nummularia* together with *Sphenopteris spiniformis*, whereas *Palmatopteris furcata* and *E. obtusiloba* are less common.

Lycopsids are locally frequent, typically represented by *Lepidodendron aculeatum* and *L. mannebachense* (*L. obovatum*), which are rare or absent in the VO. Also common are *Bergeria dilatata* and *Lepidophloios laricinus* but these also occur in the VO.

Ferns are relatively less common in the Mydlák than in the Velká opuka, except for abundant *Senftenbergia plumosa* and *Lobatopteris aspidioides*. Locally common are also *Sphenopteris schatzlarensis* and *S. delicatula*, both belonging to the Filicales.

Locally common are also cordaitaleans, however, their diversity is based only on the venation pattern, and thus is not comparable with cuticular study-based diversity of this group in the VO.

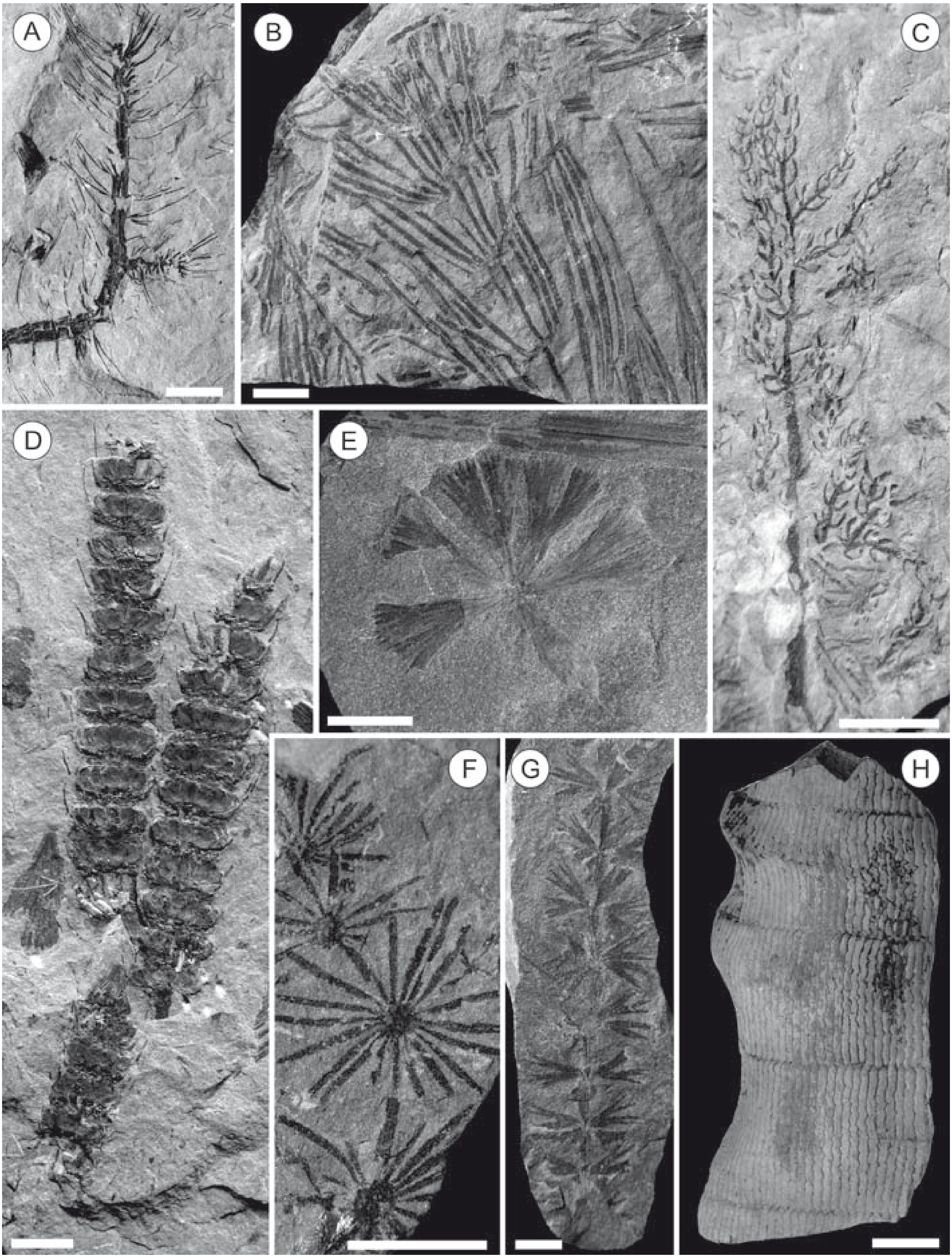
7. COMPARISONS

The list of taxa provided in Figure 6 and its graphic expression (Figs 8, 9) show differences between floras of the VO and the Mydlák. These differences do not only refer to species composition but also the abundance of some taxa. The Mydlák flora is also characterized by twice the higher diversity, and also a greater abundance of pteridosperms compared to the VO. A higher diversity, although less striking, also exists with regard to the arborescent lycopsids and pteropsids. On the other hand, only minor differences in the number of species were found for the sphenopsids.

Field collecting of fossils in the VO and Mydlák during several last decades shows that both horizons are very rich in remains of sphenopsids and arborescent lycopsids. However, differences may exist in the abundance of common species and the presence/absence of species unique for only one of the horizons. Striking examples are the abundance of *Lepidodendron aculeatum* and *L. mannebachense* in the Mydlák, whereas these are absent or very rare in the VO. On the other hand, *L. ophiurus* and *L. longifolium* are abundant in the VO but nearly absent in the Mydlák.

Although diversity of pteridosperms in the Mydlák is high, only 8 species are really abundant. The most

Figure 12. Sphenopsids from the Velká opuka. **A)** *Palaeostachya gracillima* Weiss. Kladno Coalfield, precise mine unknown. National Museum in Prague. **B)** *Asterophyllites grandis* (Sternberg) Geinitz. Kladno Coalfield, precise mine unknown. National Museum in Prague; scale bar 20 mm. **C)** *Sphenophyllum priveticense* Libertín *et al*. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **D)** *Asterophyllites longifolius* (Sternberg) Brongniart. Ronna Mine, Sládeček Museum in Kladno; scale bar 20 mm. **E)** *Palaeostachya ettingshausenii* Kidston. Kladno Coalfield. National Museum in Prague; scale bar 5 mm. **F)** *Calamostachys grandis* (Zeiller) Jongmans. Kladno Coalfield. National Museum in Prague; scale bar 5 mm. **G)** *Calamites* (*Calamitina*) *goeppertii* (Ettingshausen) Weiss. Kladno Coalfield, Sládeček Museum in Kladno; scale bar 20 mm.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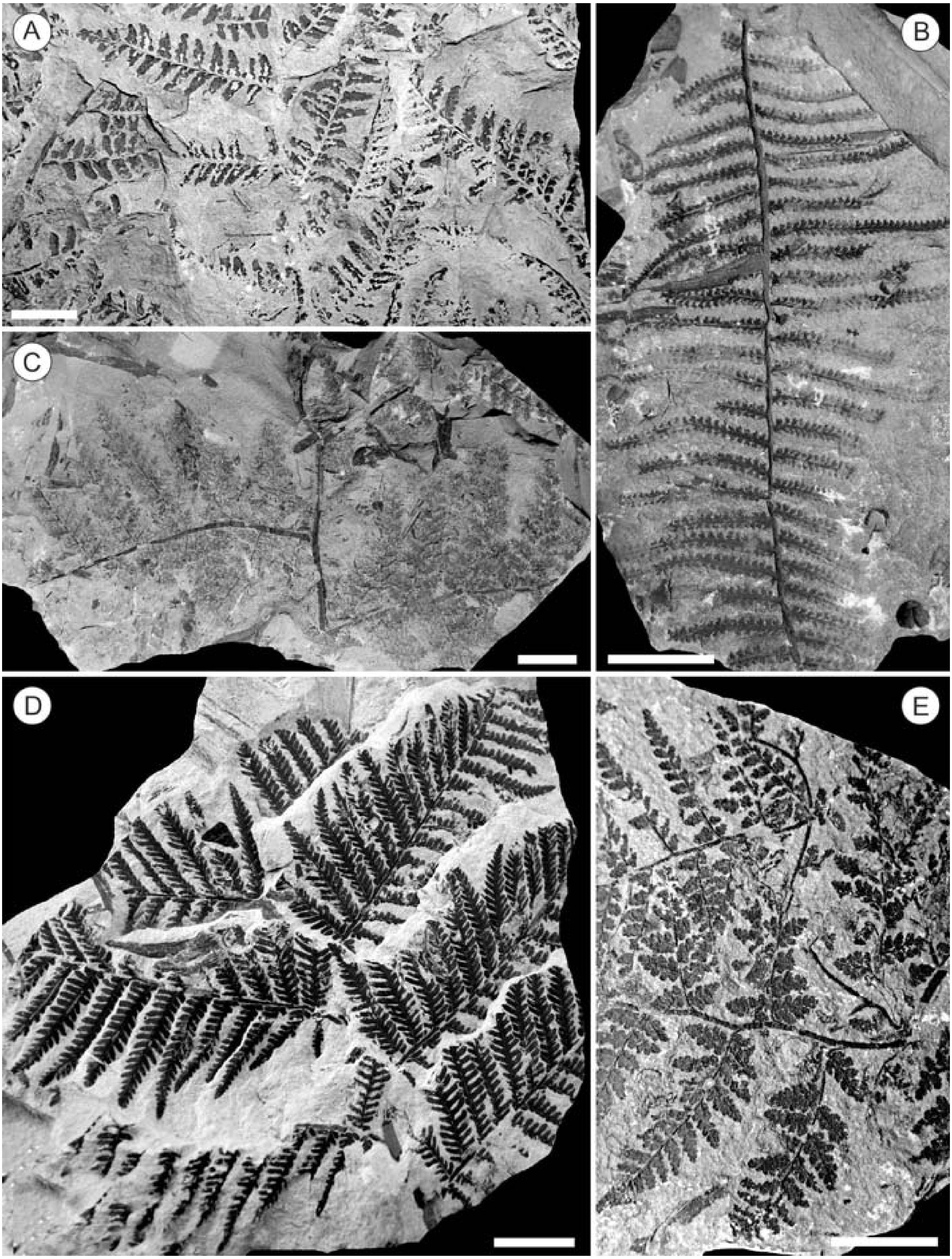
important ones are: *Laveineopteris bohemica*, *L. tenuifolia*, *Eusphenopteris nummularia*, *Sphenopteris spiniformis* and *Palmatopteris furcata*. Other taxa are subordinate or rare, as in the case of the genus *Alethopteris*. Other species which are very abundant in only one of the horizons, and thus characterize it, include *Sphenophyllum myriophyllum* for the Mydlák, whereas *Corynepteris sternbergii* and *Omphalophloios feistmantelii* are characteristic of the VO. These are the most salient examples, but, of course, there are additional species that characterize one or the other horizon. However, these are not abundant (e.g., *Spencerites chalonerii*, *Dicranophyllum dominii* in the VO).

Comparison can be made with taphonomically similar floras elsewhere. The peat-forming flora of the VO can be best compared with that of the Bělka tuff bed (Opluštil *et al*. 2009a, b, 2014) and from coal balls (Phillips *et al*., 1985). The Bělka is an about half a metre thick volcanic ash bed in the roof of the Lower Radnice Coal and situated just below the Upper Radnice Coal, being of comparable age and palaeogeographic position. Excavations made in the Radnice Basin 60 km SW of the Kladno Coalfield exposed an *in situ* preserved lepidodendrid – cordaitalean-dominated forest association with abundant calamitaleans in the understory and a dense herbaceous groundcover. Although the lepidodendrid species are partly different from those in the VO, a common feature of both volcaniclastic beds is the absence of *Lepidodendron aculeatum* and only rare occurrences of *L. mannebachense*, as well as a dominant presence of certain taxa (e.g., *L. lycopodioides*), which are found sporadically in clastic sediments accompanying the Lower Radnice Coal. Similarly for the Bělka and VO the filicalean fern *Senftenbergia plumosa* and of zygopterid fern *Corynepteris* (*C. angustissima* in the Bělka) occur abundantly. Apart of the VO, however, the Bělka forest shows a higher abundance of medullosalean pteridosperms as represented by *Laveineopteris loshii* which is nearly absent in the VO. Fairly abundant pteridosperms include also *Eusphenopteris nummularia*, *Mariopteris muricata* and *Palmatopteris furcata*, which are characteristic of the Mydlák. Only the remains of *Sphenopteris mixta* are common in both beds; this is a species very similar to *S. flexuosissima*, which is very abundant in the VO. A relative abundance of pteridosperms in the Bělka thus matches the flora of the Mydlák more than that of the VO.

Besides the peat-forming vegetation preserved in tuff beds, the VO flora may also be compared with coal ball floras as studied by Phillips *et al*. (1985). These authors show that late Duckmantian peats were composed of nearly 70 vol. % of lycopsids, mostly of the arborescent type, whereas the other plant groups only represent ≤ 10 % of peat volume. Although these frequency values are not directly comparable with our data from the VO, which are only semi-quantitative, they both demonstrate the important role played by arborescent (mostly lepidodendrid) lycopsids in the peat-forming vegetation of those times. However, appart from the pteridosperms, the VO flora shows more important role of sphenopsids, with particular regard to the calamitaleans in the peat swamp of the Upper Radnice Coal. This difference may be, however, of taphonomic nature. Analysis of coal-ball peat showed that calamitaleans are often preferentially abundant in highly degraded peats, where they are often represented mainly by rhizomes and roots (the aerial debris having decayed). Thus they may be "under-represented" in many coal ball floras, if they were growing in areas where peat decay was common (W.A. DiMichele, pers. comm.).

The Mydlák can be compared with roof shale floras of similar age elsewhere. For instance, a Langsettian fossil forest preserved in the roof-shales of the Blue Creek Coal in the Mary Lee Coal zone of the Black Warrior Basin, Alabama (Gastaldo *et al*., 2004) is dominated by arborescent lycopsids of the genera *Lepidodendron*, *Lepidophloios* and *Sigillaria* with abundant undergrowth consisting of calamitaleans, pteridosperms (*Lyginopteris*, *Alethopteris*, *Neuralethopteris*) and a ground cover or lianas as represented by *Eusphenopteris* and *Palmatopteris*. Despite the stratigraphically older position of this flora, the abundance of pteridosperms and calamitaleans within a lepidodendrid forest of varying density is similar to that of the Mydlák. In contrast, an early Asturian plant assemblage from roof shale of Secor Coal in Oklahoma (DiMichele *et al*., 1991) is dominated by medullosan pteridosperms, with subdominant marattialen ferns and calamiteans, whereas arborescent lycopsids are quite rare and represented by sigillarians. Although this forest differs from that of the deposits described herein, in the subordinate role of arborescent lycopsids, a dominant presence of pteridosperms (together with calamitaleans and

Figure 13. Sphenopsids from the Mydlák. **A)** *Sphenophyllum myriophyllum* Crépin. Tuchlovice Mine, S. Opluštil collection; scale bar 20 mm. **B)** *Asterophyllites* cf. *longifolius* (Sternberg) Brongniart. Theodor Mine, collection of S. Opluštil; scale bar 10 mm. **C)** *Asterophyllites charaeformis* (Sternberg) Goeppert. Barré Mine, S. Opluštil collection; scale bar 10 mm. **D)** *Palaeostachya ettingshausenii* Kidston. Tuchlovice Mine, S. Opluštil collection; scale bar 5 mm. Figured by Bek & Opluštil (1998, pl. 3, fig. 12). **E)** *Sphenophyllum priveticense* Libertín *et al*. Tuchlovice Mine, S. Opluštil collection; scale bar 10 mm. **F)** *Annularia radiata* (Brongniart) Sternberg. Schoeller Mine, S. Opluštil collection; scale bar 10 mm. **G)** *Sphenophyllum taylorii*. Tuchlovice Mine, S. Opluštil collection; scale bar 5 mm. **H)** *Calamites* (*Stylocalamites*) *undulatus* Sternberg. Max Mine, S. Opluštil collection; scale bar 20 mm.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tree ferns) is similar to that of the Mydlák and seems to be a typical feature of mineral-rich wetlands (Gastaldo, 1987). Our data thus confirms that pteridosperms had a stronger preference for mineral-enriched wetlands that immediately followed upon the development of peat swamps.

8. SUMMARY AND CONCLUSIONS

1) The Upper Radnice Coal (late Duckmantian) is the principal seam of the Kladno Coalfield in the southern sector of the Kladno-Rakovník Basin. Its formation was controlled by palaeotopographic features. The peat swamp which developed into the coal covered nearly the entire width of a palaeovalley and was surrounded by basement palaeohighs.

2) Intercalated in the lower part of the coal is a ~ 10 cm thick volcaniclastic bed called Velká opuka, which contains a flora buried *in situ* by volcanic ash. The coal is capped by laminated roof shales (Mydlák), carrying parautochthonous to mostly allochthonous coalified plant compressions transported over short distances, less than 2 km.

3) Floras of both these fossiliferous horizons comprise the same families and genera, but differ in their proportions (abundance) and, largely, in species composition.

4) Differences in the composition of both floras with respect to their taphonomy suggest that the plant fossils in the Velká opuka represent the peat-forming vegetation growing on an organic substrate, whereas plant remains in the Mydlák are mostly derived from the vegetation occupying mineral-rich coastal wetlands, which were established after the peat swamp withdrew.

5) About 59 biological plant species have been identified from the Velká opuka and 67 species from the Mydlák. In all, 89 biological taxa have been identified in both fossiliferous horizons. This number includes 37 species which they have in common; 22 species are found only in the VO and 30 species have been identified so far only from the Mydlák.

6) The flora of the VO is dominated by lycopsids, either by arborescent lepidodendrids with subordinate sigillarians or by the subarborescent genus *Omphalophloios*. Co-dominant are the sphenopsids, calamitaleans as well as sphenophylls, whereas ferns and cordaitaleans are locally common. Pteridosperms, especially medullosaleans, are rare and less diverse in VO as compared with the Mydlák.

7) The Mydlák flora is more diverse and differs from that of the Velká opuka by a significantly higher diversity and the abundance of pteridosperms, including medullosaleans. Lycopsids are less abundant, especially the lepidodenderids.

8) The VO and Mydlák floras are further characterized by some taxa, which are only dominant in one of these fossiliferous beds. Characteristic of the Velká opuka are the abundant remains of *Omphalophloios feistmantelii*, *Lepidodendron longifolium* and *L. ophiurus* (*sensu* Němejc, 1947). Dominant in the Mydlák are remains of *Laveineopteris tenuifolia*, *L. bohemica*, *Sphenopteris spiniformis*, *Eusphenopteris nummularia*, *Lepidodendron aculeatum* and *L. mannebachense*.

9) Our data thus support earlier observations suggesting that the clastic wetlands floras tend to be dominated by pteridosperms, sphenopsids and ferns, with subdominant lycopsids.

ACKNOWLEDGEMENTS

We are very pleased to have the opportunity to contribute to the volume in honour of Robert H. Wagner, an excellent palaeobotanist and our friend, who dedicated his life to the Carboniferous palaeobotany. The authors are very grateful to William DiMichele and John Knight for their careful revision of the manuscript and useful suggestions, which improved the paper significantly. These authors are also thanked for language revision of the text. Our thanks belong also to Carmen Álvarez-Vázquez for her effort, when handling the submitted manuscript during revision process. The authors greatly appreciate the cooperation with Jan Haldovský, an amateur collector from Pchery near Kladno, who made his extensive collection of plant fossils from the Kladno Coalfield available for examination. Thanks are given to the National Museum in Prague and to the Sládeček Museum in Kladno for access to their plant fossil collections. This paper benefited from a support via the project P210-12-2053 of the Grant Agency of the Czech Republic. Mr. Josef Seifert is thanked for providing a photo in the Figure 4B.

Figure 14. Ferns from the Velká opuka. **A)** *Senftenbergia* cf. *pennaeformis* (Brongniart) Stur. Kladno Coalfield, Sládeček Museum in Kladno; scale bar 20 mm. **B)** *Corynepteris sternbergii*. Kladno Coalfield, Sládeček Museum in Kladno; scale bar 20 mm. **C)** *Oligocarpia gutbieri* Goeppert. Kladno Coalfield, Sládeček Museum in Kladno; scale bar 20 mm. **D)** *Senftenbergia plumosa* (Artis) Stur. Same as Opluštil *et al*. (2007, pl. VII, fig. 3). Kladno Coalfield. National Museum in Prague; scale bar 20 mm. **E)** *Oligocarpia* sp. Kladno, Sládeček Museum in Kladno; scale bar 20 mm.

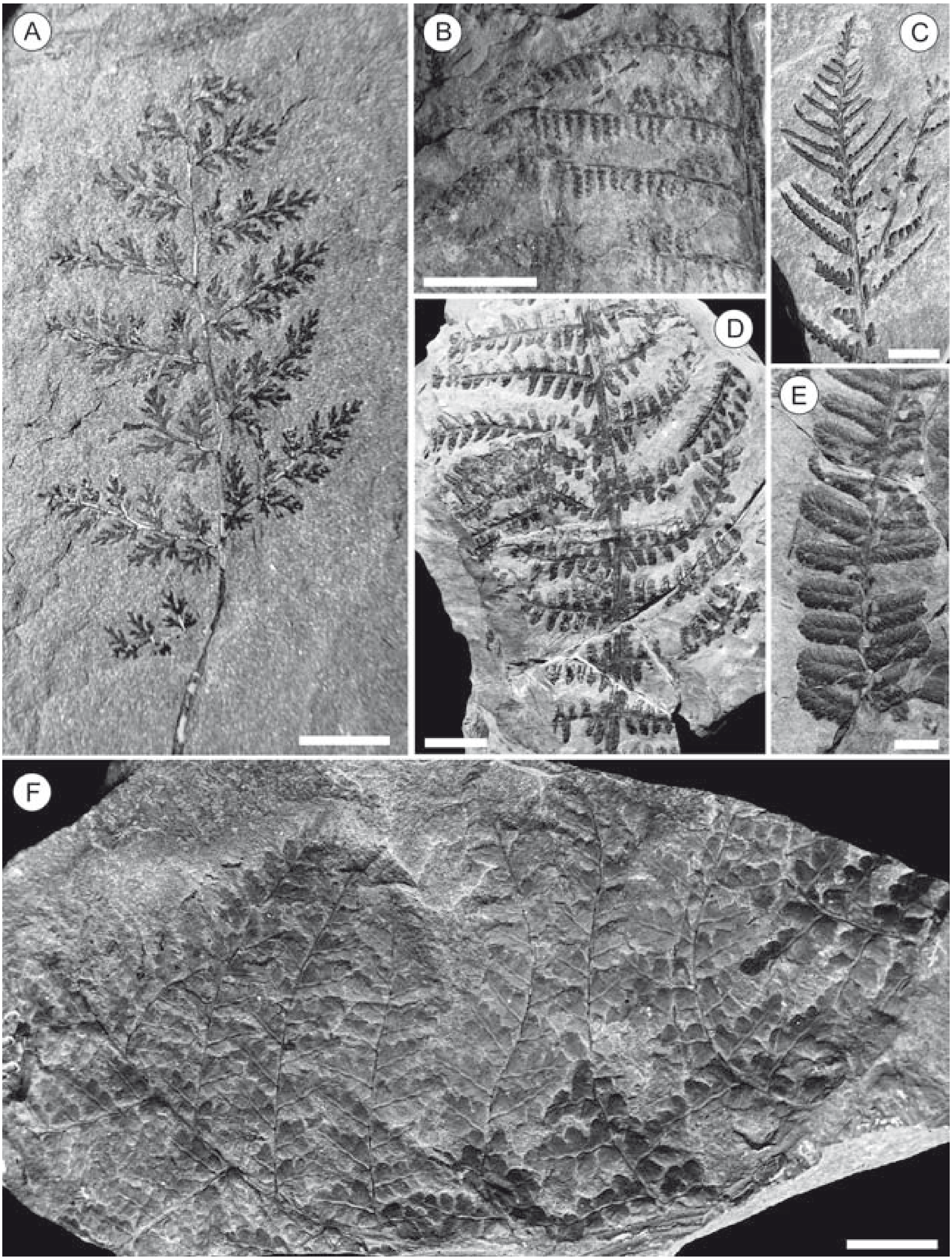

Figure 15. Ferns from the Mydlák. **A)** *Zeilleria delicatula* Kidston. Kladno Coalfield, Sládeček Museum in Kladno (Pa 918); scale bar 10 mm. **B)** *Corynepteris coralloides* (Gutbier) Zeiller. Schoeller Mine, S. Opluštil collection; scale bar 20 mm. **C)** *Senftenbergia plumosa* (Artis) Stur. Tuchlovice Mine, S. Opluštil collection; scale bar 10 mm. **D)** *Senftenbergia pennaeformis* (Brongniart) Stur. Tuchlovice Mine, S. Opluštil collection; scale bar 10 mm. **E)** *Pecopteris abbreviata* Brongniart. Max Mine, S. Opluštil collection; scale bar 5 mm. **F)** *Renaultia rotundifolia*. Theodor Mine, J. Haldovský collection, scale bar 10 mm.

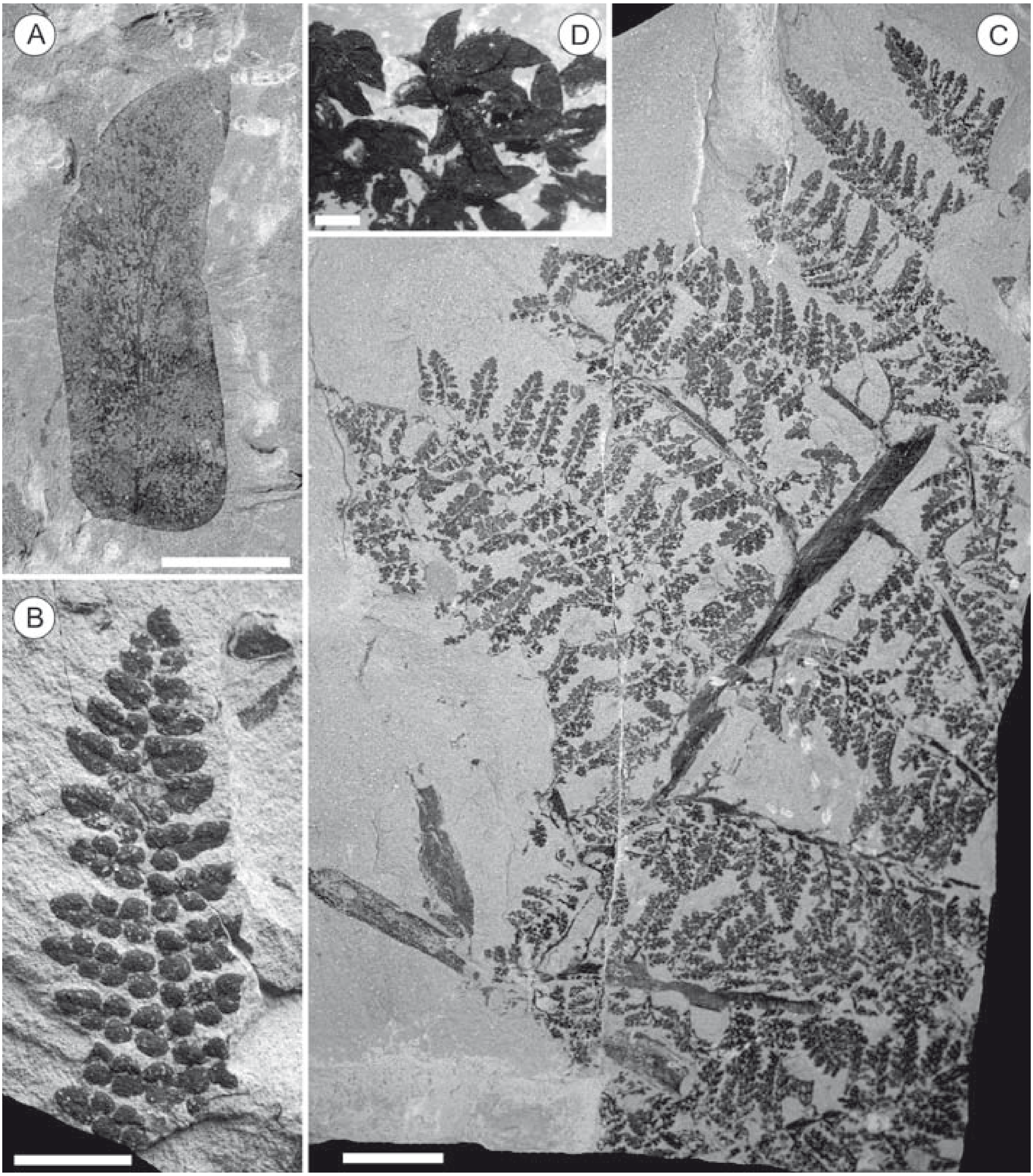

Figure 16. Pteridosperms from the Velká opuka. **A)** *Linopteris neuropteroides* Gutbier forma *major* Potonie. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **B)** *Eusphenopteris* cf. *nummularia* (Gutbier) Novik. Same as Opluštil *et al*. (2007, pl. VII, fig. 11). Kladno Coalfield. National Museum in Prague (E 6240); scale bar 10 mm. **C)** *Sphenopteris flexuosissima* (Stur). Figured as *Sphenopteris* cf. *crepinii* in Opluštil *et al*. (2007, pl. VII, fig. 10). Kladno Coalfield. National Museum in Prague; scale bar 20 mm. **D)** Details of pollen organs attached to *Sphenopteris flexuosissima*. Ronna Mine, S. Opluštil collection; scale bar 1 mm.

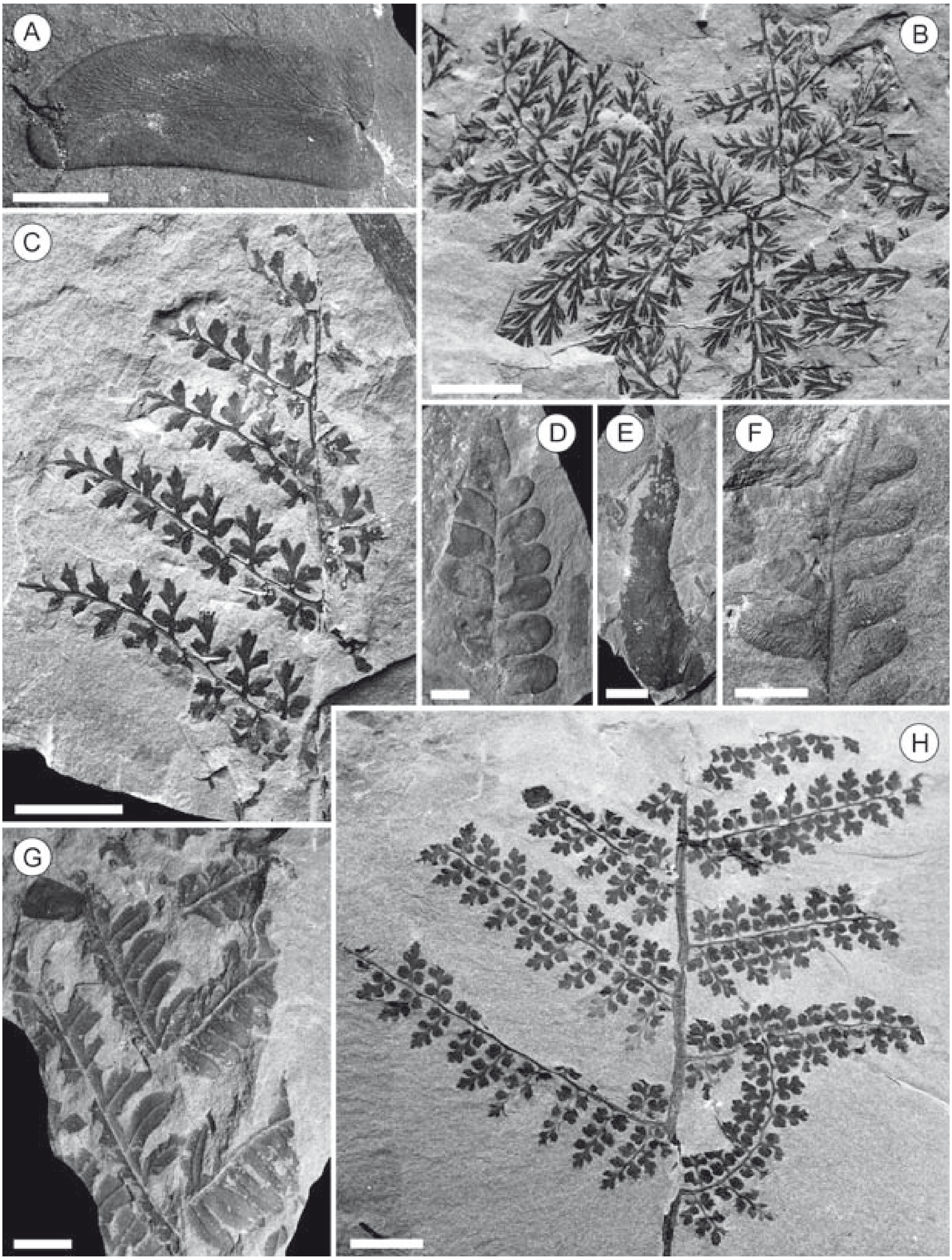

Figure 17. Pteridosperms from the Mydlák. **A)** *Linopteris neuropteroides* Gutbier forma *major* Potonié. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **B)** *Palmatopteris furcata* (Brongniart) Potonié. Tuchlovice Mine, S. Opluštil collection; scale bar 20 mm. **C)** *Eusphenopteris sauveurii* (Crépin) Simson-Scharold. Kladno Coalfield. National Museum in Prague (E 6242); scale bar 20 mm. **D)** *Mixoneura praeovata* Němejc. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **E)** *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zodrow. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **F)** *Alethopteris distantinervosa* Wagner. Theodor Mine, J. Haldovský collection; scale bar 10 mm. **G)** *Alethopteris* cf. *serlii* Brongniart. Tuchlovice Mine, S. Opluštil collection; scale bar 10 mm. **H)** *Eusphenopteris nummularia* (Gutbier) Novik. Mayrau Mine, S. Opluštil collection; scale bar 20 mm.

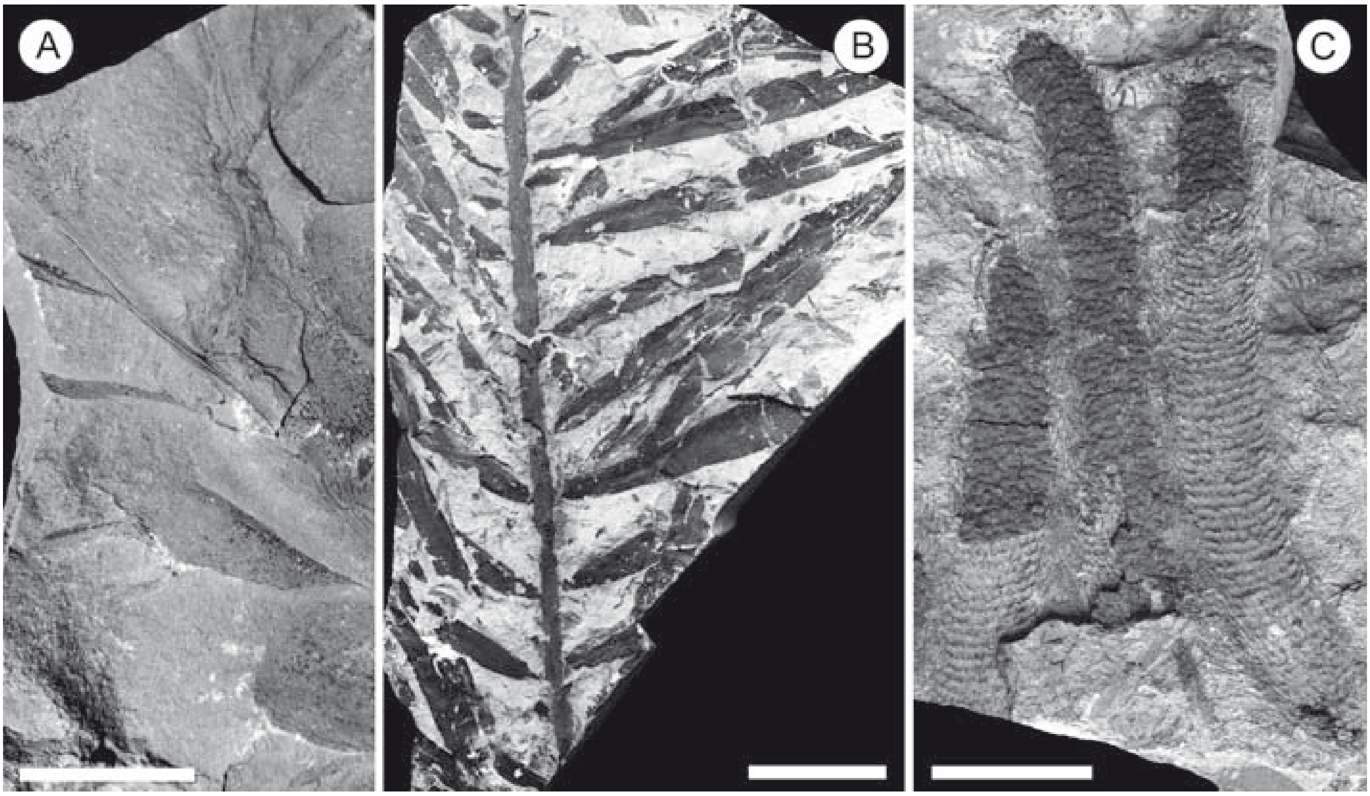

Figure 18. Additional Velká opuka species. **A)** *Noeggerathia foliosa* Sternberg. Kladno Coalfield, Sládeček Museum in Kladno; scale bar 30 mm. **B)** *Cordaites* sp. Kladno Coalfield. National Museum in Prague; scale bar 50 mm. **C)** *Bowmanites* sp. Schoeller Mine. National Museum in Prague; scale bar 20 mm.

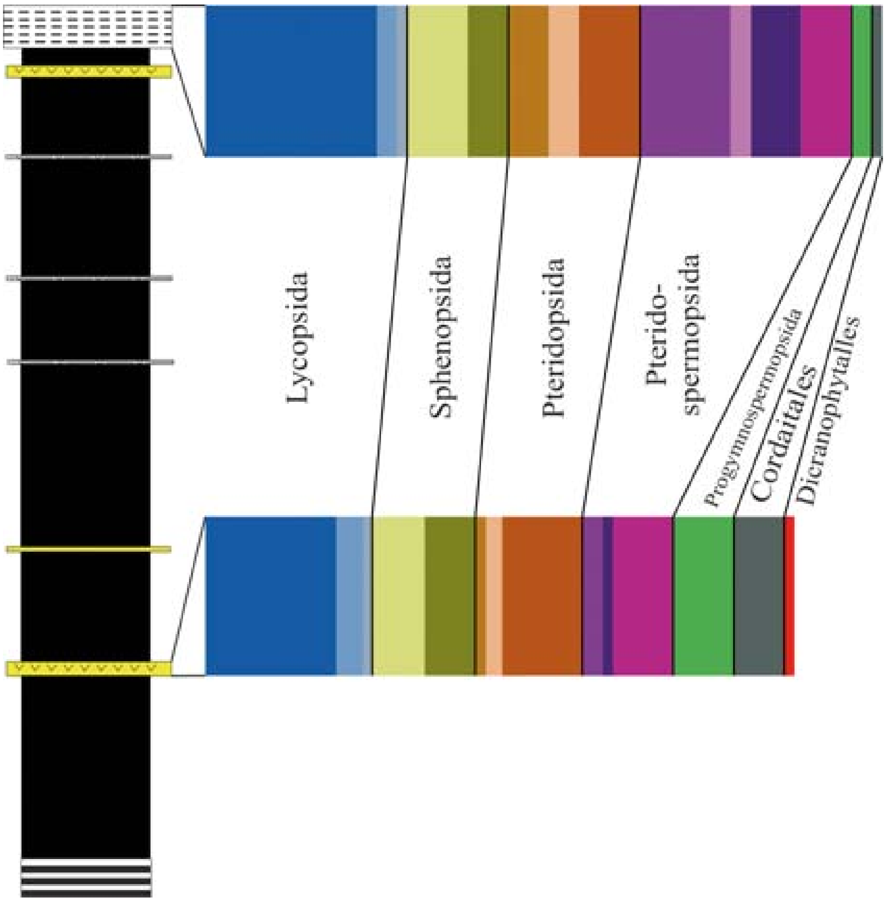

Figure 19. Vegetation patterns of the Velká opuka and Mydlák in the Kladno Coalfield.

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