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Vegetation patterns of Westphalian and Lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic

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Abstract

Several volcanoclastic beds in coal-bearing strata of the Late Palaeozoic continental basins in the Czech Republic contain *in situ* buried peat-forming plant ecosystems the study of which provides a unique insight into their structural pattern and species composition. Middle Pennsylvanian peat-forming plant assemblages at 14 localities in basins of central and western Bohemia and from the Intra-Sudetic Basin (NE Bohemia) were characterised based on collections of plants preserved in five successive tuff beds: the tuff of the 3rd Žďárky Coal (Duckmantian), the Whetstone Horizon in the roof of the Lower Radnice Coal (Bolsovian), the Velká opuka intercalated in the Upper Radnice Coal (Bolsovian), the Z-tuff capping the Lower Lubná Coal (Bolsovian), and the tuff of the Chotíkov Coal (Westphalian D/Cantabrian). Analysis of plant remains preserved in these beds reveals the co-existence of several ecologically controlled plant assemblages ranging from structurally simple, low-diversity to high-diversity phytocoenoses, with complex structural patterns and synecological relationships. Most of these assemblages represent variations of the basic lepidodendrid-dominating forest with co-dominance or sub-dominance of other basic plant groups. This pattern is comparable to the forests of the paralic basins located in coastal settings. An assemblage dominated by the sub-arborescent lycopsid *Omphalophloios feistmantelii* (Feistmantel) comb. nov. was recognised in the Upper Radnice Coal. Only a few assemblages are poor in lycopsids. These are mostly mixed fern–calamites or pteridosperm-dominated phytocoenoses.

The assemblages described represent various stages of hydroseral succession. The initial stage consists of a low-diversity fern–calamites-dominated assemblage of 5 species, not higher then 1–1.5 m which re-colonised the previously drowned mire. The climax stage of the succession is represented by high-diversity lepidodendrid forests with well-developed ground-cover and shrubs. The number of taxa of such assemblages varies between 20 and 30 species within an area of about 100 m^2.

A comparison of the peat-forming flora with the clastic substrate floras preserved in mudstones or roof shales revealed substrate preference of individual species. Most of them grew in both types of substrates; only a few were adapted to only one type of substrate.

Keywords: Palaeoecology; plant assemblages; Pennsylvanian; fossiliferous tuffs

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1. Introduction

The Pennsylvanian Euramerican equatorial floristic province was characterised by a predominance of spore-producing vegetation accompanied by early seed plants which preferred mostly wetland habitats of coastal and intermontane lowlands. However, the unique character of this extinct flora precludes its comparison with any modern equivalent and thus makes it difficult to fully understand its ecosystems, despite the significant progress achieved in last few decades (e.g. Havlena, 1970; Scott, 1977, 1978, 1979, 1990; DiMichele and Aroson, 1992; DiMichele and Phillips, 1994; Phillips and DiMichele, 1998; Falcon-Lang and Scott, 2000; DiMichele et al., 2001, 2002; Gastaldo et al., 2004 etc.). The Pennsylvanian flora is generally divided into wetland and upland (extrabasinal) flora (e.g. Havlena, 1970; Wagner, 2001). There is low potential for preservation of any organic remains from the upland flora because of its location mostly in areas of erosion or only occasional local sedimentation. Consequently, the flora of this biome is only poorly known from small drifted plant fragments or charcoal (Falcon-Lang, 2000; Wagner, 2001; Falcon-Lang, 2003). In contrast, the wetland environment provided a high potential for the preservation of its flora in the sedimentary record and is therefore well known. It is usually subdivided into (i) the mire flora of peat or organic-rich substrates and (ii) the flood basin flora of clastic substrate wetlands (Gastaldo et al., 1995; DiMichele et al., 2001). Both floras are characterised by the same basic plant groups, however, relative dominance–diversity patterns and species composition were distinct (DiMichele et al., 2002). The flood basin flora of clastic substrates was far more environmentally heterogeneous than the flora of the peat swamps (Gastaldo et al., 1995). It is well known from compressions preserved in fine-grained siliciclastic sediments, but data on the anatomy of the plants and the spatial distribution of individual plants are scarce. Preservation of such details requires special conditions related to fast burial, e.g. during catastrophic floods. Such events, however, are often accompanied by at least some transportation of the plant remains, especially of plant litter and of the small herbaceous plants forming the understorey. Associations of clastic sediments, for example of roof shales, therefore represent mostly allochtonnous to para-autochthonous remains. Only rarely do they represent *in situ* buried original phytocoenosis (e.g. Scott, 1978; Bateman and Scott, 1990; Gastaldo et al., 1995; Calder et al., 1996; Gastaldo et al., 2004).

The coal-forming flora cannot normally be studied directly from coal due to the intensive de-compositional and diagenetic processes which have transformed the original plant tissues into coal matter. It is possible only where early diagenetic permineralised peat known as coal-balls occurs, i.e. in seams of paralic basins directly related to marine influence (e.g. Scott et al., 1996). Coal-balls provide the best direct insight into the species composition of peat and their volumetric contribution (Phillips et al., 1976, 1985; Lyons et al., 1997). Since the peat accumulates in low dynamic environments, coal-balls consist mostly of *in situ* preserved plant assemblages with only a minimal taphonomic bias. However, studies of plant organs indicate that much of the aerial parts of plants were lost to decay. Extensive decay may have led to the enrichment of the peat in lepidodendrid bark (DiMichele and Phillips, 1994). Where the coal-balls are not available, other methods are used to obtain valuable data on vegetation history of fossil mires. Among them, palynology (both microspores and megaspores) is the most common being applicable to coals of low to medium ranks (e.g. Bartram, 1987; Mahaffy, 1988; Eble et al., 1994). This method is based on the identification of dispersed spore assemblages from coals and their correlation with parent plants. However, it is subject to several biases critical in translating dispersed miospore spectra into vegetational patterns: (1) interpretations of dispersed spore assemblages are based on an assumption that spores were produced by local population of parent plants, i.e. are of (para) autochthonous origin; (2) qualitative correlation of palynological data depends on knowledge of the parent plants of the dispersed miospore species. This is quite well known at the generic level, whereas correlation to species remains still problematic. Similarly, interpretation of quantitative composition of plant assemblage based on the palynological record is impossible due to an uneven production of spores by the parent plants.

Important data on the composition and structure of coal-forming plant assemblages provide some fossiliferous tuff beds intercalated in coal seams or in their roof (Wagner, 1989; Rössler and Barthel, 1998). In comparison to coal-balls, plant fossils in tuff beds are preserved mostly as compressions providing thus morphological characteristics although anatomically preserved coalified compressions also occur (Pšenička et al., 2003). Unfortunately, tuff beds which are thick enough to bury plants are restricted mostly to continental basins located closer to volcanic centres than the paralic basins (e.g. Lyons et al., 1994). Depending on type of eruption, surrounding topography and distance of volcanic centre from vegetation, various scenarios of entombing plants by volcanic ash can occur concerning the intensity of taphonomical bias (Walker, 1981; Clarkson et al., 1988; Jashemski, 1990; Burnham, 1994). Those volcanoclastic beds generated by simple volcanic ash fall may contain plants buried *in situ* with only minimum taphonomic biases. Thus the taphocenosis

preserved in such fossiliferous tuffs are very similar to former coal swamp phytocoenosis and provide unique data not only on species composition of plant assemblages but also on their structure and the spatial distribution of individual plants, including the density of the understorey. Findings of large, nearly complete specimens allow the correlation of isolated organs to their parent plants, or improvement of whole plant reconstructions.

Revision of plant collections derived from these volcanoclastic horizons have revealed various plant taphocoenoses, not only between stratigraphically different horizons but also within particular tuff beds. This indicates co-existence of ecologically controlled assemblages in Pennsylvanian mires. The flora of these mires is similar to that of clastic substrates to generic level, but differ often in species composition and vegetation patterns. Comparison of peat-forming plant assemblages with flora of clastic substrates preserved either in roof shales or floodplain mudstones allows us to recognise the substrate preference of most Westphalian to early Stephanian species in the continental basins of the Czech Republic.

2. Geological and stratigraphical characteristics of the Late Palaeozoic continental basins of the Czech Republic

Pennsylvanian continental basins of the Czech Republic (Fig. 1) are typical post-orogenic, extension-dominated basins formed in the final phases of the Variscan orogeny. They are subdivided into four groups of basins in the following areas, which differ in their tectono-sedimentary histories: (1) Central and Western Bohemia, (2) Lusatian area, (3) Krušné hory (Erzgebirge) Mountains and (4) grabens. Deposition in most of the basins was accompanied by volcanic activity and is responsible for the frequent occurrence of volcanoclastics and locally for magmatic extrusions.

3. Material and methods

The beginning of systematic collecting and study of the Late Carboniferous flora in the territory of the Czech Republic dates back to the first half of the 19th century, having been closely related to the rapid development of coal mining industry. Since that time, a large number of plant fossils has been collected including those preserved in pyroclastic rocks. However, the volcanic origin of these rocks was only recognised much later, in the second half of the 20th century (e.g. Mašek, 1973). Even then, the importance of these beds for palaeoecological studies was only fully appreciated following the systematic excavation of the *in situ* buried flora and a revision of the specimens from major collections (Opluštil, 2003).

Pyroclastic rocks are quite common in the Late Palaeozoic continental basins of central and western Bohemia and in the Sudetic area; however only the thicker layers were able to bury herbaceous and shrubby vegetation, and to break off the tree branches. Volcanoclastic beds less than 10 cm thick usually lack any aerial plant remains. Instead, they are heavily rooted by post-eruption vegetation. In the Central and Western Bohemia, fossiliferous tuffs occur only in the Kladno Formation (Fig. 1B), the oldest lithostratigraphic unit in this area (Bolsovian–Cantabrian). They are especially common in the lower part of the formation in the most important coal-bearing unit called the Radnice Member. In the Intra-Sudetic Basin only one fossiliferous tuff bed was found in the Prkenný Důl–Žďárky Member of late Duckmantian age (Fig. 1B).

All these fossiliferous volcanoclastic beds consist of well-sorted rhyolitic tuffs composed dominantly of angular to subangular fragments/crystalls of sanidin, quartz and vermicular kaolinite dispersed in kaolinitic matrix (e.g. Mašek, 1973; Opluštil, 1991). Studied plant remains are derived from tuff layers that are always sharp- but non-erosional-based, massive, 10 to 70 cm thick beds either intercalated in coal seams or capping them. They are laterally very persistent, usually over tens of kilometres (some of them have basin-wide distribution) with only gradual thickness changes. They display no sedimentary structures. These tuffs bear non-chared plant fragments of various sizes concentrated mostly at the base of beds. Upright stems of various plant species are common ranging from large lycophyte trunks more than 1 m in diameter to fern and calamite axis less than 1 cm in diameter (Fig. 2). All these characteristics indicate that the studied fossiliferous tuff beds were formed by deposition of volcanic ash from eruption cloud dispersed downwind. The same origin of these beds was interpreted also by Mašek (1973). The mode of occurrence of plant fossils indicates only minimal taphonomical biases. Small herbaceous plants forming understorey were more or less completely buried *in situ* whereas shrubby and arborescent plants were only partly damaged by volcanic ash the load of which broke off only branches and fronds and buried them around the trunk. Plant taphocoenoses of these tuff beds thus provide excellent opportunity to study composition and structure of peat-forming ecosystems. Here, only the composition of coal-forming plant assemblages is reconstructed based on extensive collections of plant fossils preserved in these tuffs.

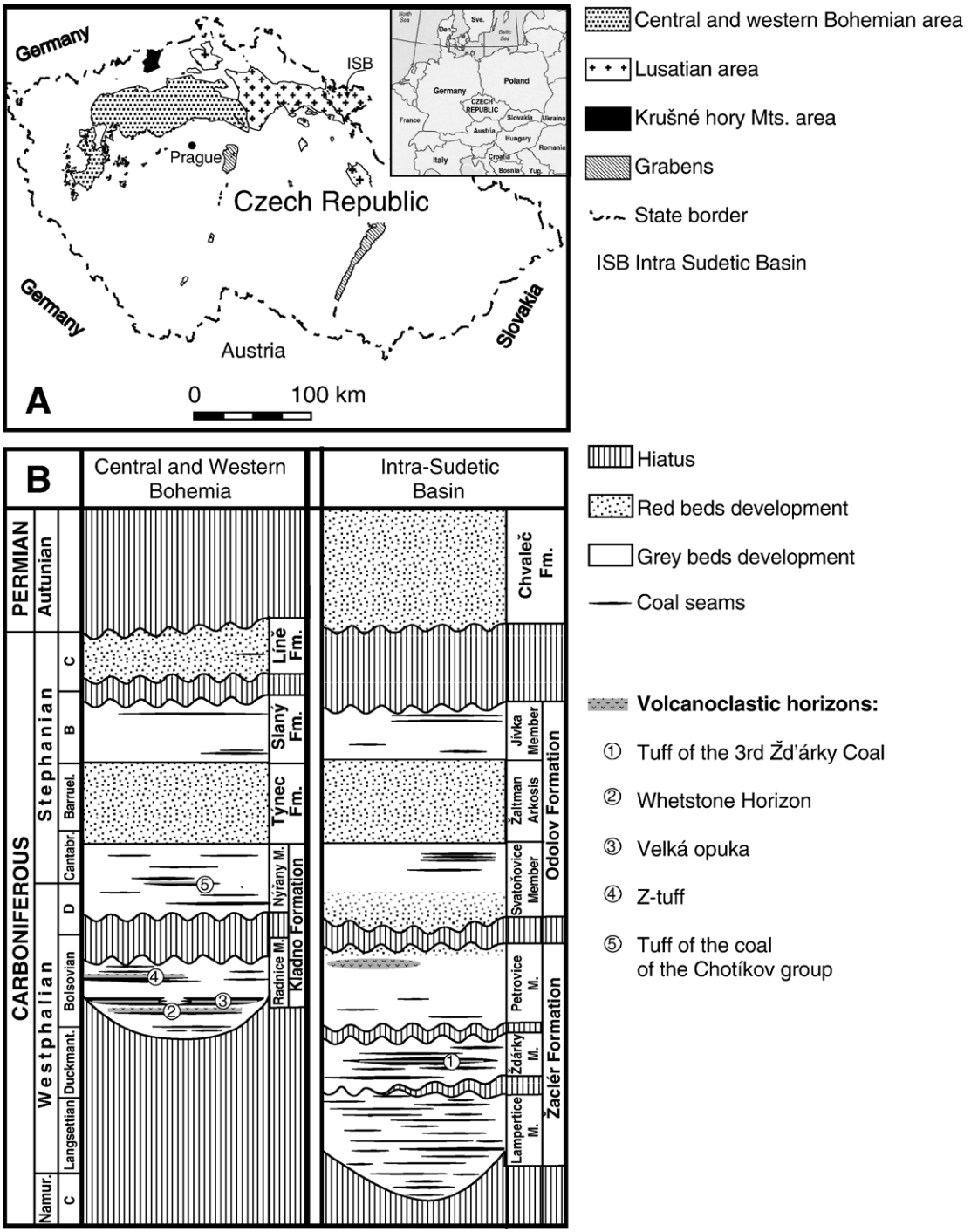


Fig. 1. (A) Late Palaeozoic continental basins of the Czech Republic and their subdivision. (B) Stratigraphical subdivision of the basins in central and western Bohemia and of the Intra-Sudetic Basin with indicated position of studied tuff beds.

The reconstruction of coal-forming plant assemblages performed here is based upon a revision of extensive collections of plant fossils preserved in volcanoclastic horizons and recent excavations of plant fossils-bearing tuff beds. Revised collections are held in several institutions including the National Museum in Prague, Czech Geological Survey in Prague, Faculty of Science of the Charles University

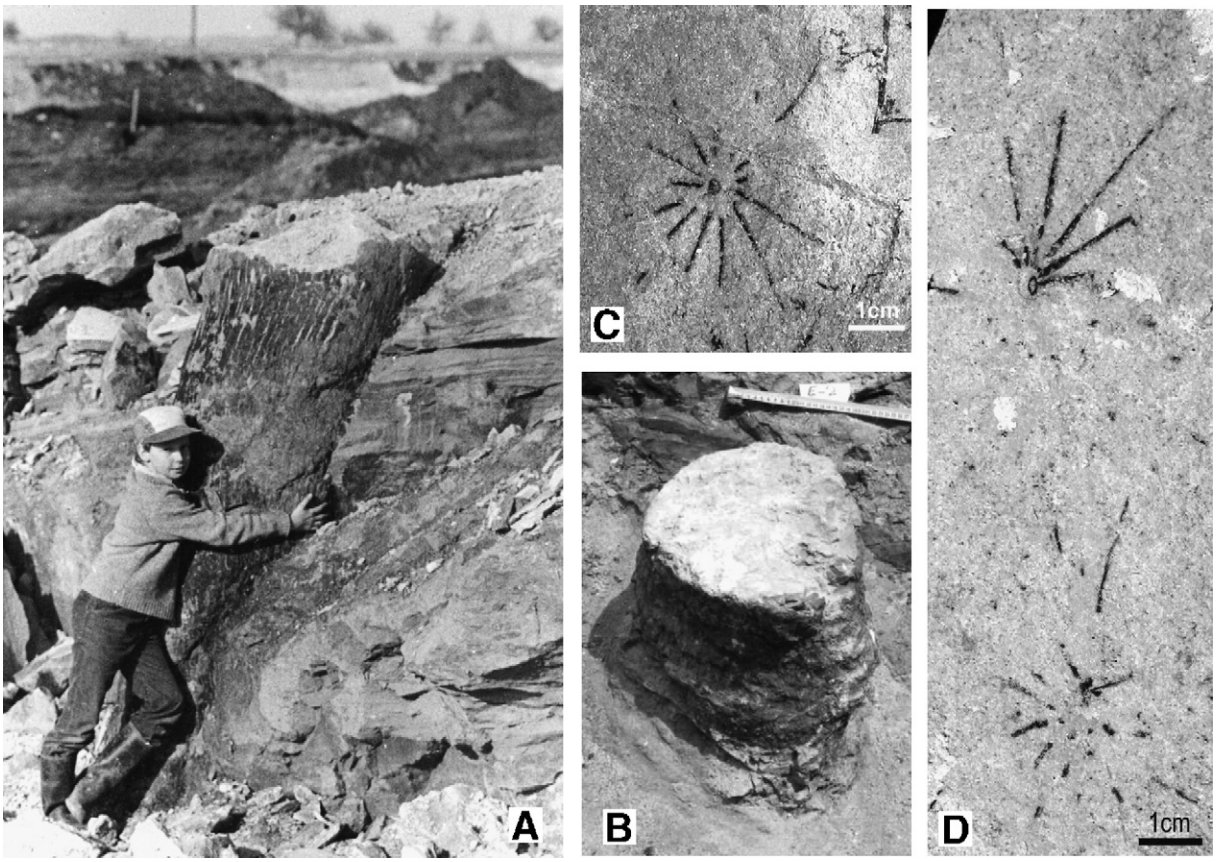


Fig. 2. Upright stems preserved in the Whetstone Horizon: A — Large lycophyte stem filled with tuffitic mudstone of the upper part of the Whetstone Horizon (Ovčín opencast mine). The stem is rooted in the roof of the Lower Radnice Coal (photo: K. Drábek); B — base of decorticated lepidodendron trunk rooted in the Lower Radnice Coal; C, D — upright stems with leaves of small calamites preserved in the bělka tuff bed at the Štilec locality. All these calamites are rooted in the roof of coal below.

in Prague and West Bohemian Museum in Pilsen. Several tens of other specimens were studied in the collections of the Natural History Museum in Vienna, the Geological Survey of Austria in Vienna, and the Museum für Naturkunde in Berlin. Only those specimens where the locality and stratigraphic position were recorded were taken into account. In all, over 2000 specimens were examined, of which some were parts and counterparts, and others represented fragments which evidently belonged to one specimen. Finally, about 1000 specimens were recorded in a computer database. Each database record contains information on one slab: catalogue number of the specimen, volcanoclastic horizon, locality (mine, part of coalfield or coalfield), the list of species preserved in the slab, and their basic characteristics concerning whether they are preserved as leafy shoots or stem (including diameter), last order pinna or isolated pinnules, etc. The association preserved in each slab represents species that grew in close proximity. Consequently, these data were arranged according to individual stratigraphic horizons and within each horizon according to particular localities. As a result, the list of specimens from each locality served as a basis for the list of species of these localities. This database set of specimens does not involve fossils excavated by the current authors at localities Ovčín and Štilec, where other thousands of specimens have been found. However, only the list of flora from these localities was made for the purpose of this paper. Another step was an estimation of an area from which the material was derived. Since most of the material was collected over many decades, it was impossible to localise them to a certain part of the mining field of any coal mine. More precise estimation was possible only when the authors of the current paper collected the material, either at coal tip or in small excavations.

The ecological evaluation of the flora preserved in these tuffs is based on an assumptions that (1) plants were buried *in situ* and did not undergo any

taphonomic bias due to transport and that (2) association of species occurring together in any tuff slab had to grow in close proximity and must therefore represent part of a natural assemblage. Critical for further ecological considerations is the first assumption of minimal taphonomical bias. This is based on published data (e.g. Mašek, 1973; Drábková, 1986) as well as on our own field observations in excavations exposing the Whetstone Horizon at localities Štilec and Ovčín. As already mentioned earlier, all these data indicate simple taphonomical history of plant remains preserved in the bělka volcanic ash bed.

Based on these assumptions, the database of species preserved in each slab was recorded and further processed. The resulting data provided information on the species diversity of the main plant groups, as well as on the composition of the whole coal-swamp plant assemblages at various localities. Comparison of plant assemblages from localities of the same volcanoclastic horizon thus revealed the co-existence of various plant assemblages.

Plant habit is interpreted for adults and follows our personal observations and experience, as well as published data (e.g. Scott, 1978; Pšenička et al., 2003; Drábková et al., 2004). Plants not taller than 1–1.5 m maximum are assigned to understorey, whereas vines involve all the climbing species. Plants reaching between 1.5 and 7–8 m in growth are considered as shrubs or small trees. Taller plants are ascribed to trees.

4. Results

The coal-forming floras of the following fossiliferous tuffs from various localities were studied (Figs. 3 and 4): (1) Whetstone Horizon, (2) Velká opuka tonstein, (3) Z-tuff, (4) tonstein of the coal of the Chotíkov Group and (5) tonstein of the 3rd Žďárky Coal. The first four of them occur in the Late Palaeozoic continental basins of the central and western Bohemia, the remaining one is from the Intra-Sudetic Basin.

4.1. Floristic assemblage of the 3rd Žďárky Coal tonstein (Upper Duckmantian)

– *Characteristics of the horizon*: The 3rd Žďárky Coal is the most important seam of the Prkenný Důl–Žďárky Member, Žacléř (Schatzlar) Formation. An about 10–20 cm thick volcanoclastic parting in its middle part (Fig. 3) consists of pale green-grey fine-grained (0.02–0.1 mm) crystallo-vitric tuff followed by grey laminated tuffite and locally to mudstone at top. The tuff yielded a rich plant association enriched in the tuffite by several para-autochthonous elements (e.g. *Senftenbergia plumosa* (Artis) Bek and Pšenička, 2001). Therefore, only specimens from the basal tuff bed were used to characterise the plant assemblage.
– *Origin and characteristics of the material*: The plant collection consists of about 200 specimens stored in the Czech Geological Survey in Prague. All the available material comes from the Zdeněk Nejedlý Mine (formerly Ida) in Malé Svatoňovice, the Intra-Sudetic Basin. It was collected at the coal mine spoil tip in two consecutive field seasons. The area from which the samples come is estimated to be up to several tens of thousand square metres.
– *Local palaeogeography*: The mire of the 3rd Žďárky Coal was formed on an extensive alluvial plain (Tásler et al., 1979). Sampling site was located most probably in the interior part of former mire where thickness of peat was highest and the coal is thick enough to be mined.
– *Taphocoenoses* consist of about 16 biological species (Table 1) and are characterised by a high diversity of pteridosperms (6 species) and ferns (6 species). Sphenopsids are represented by three species and lycopsids are absent. The most abundant plant remains belong to *Alethopteris idae* Šimůnek, *Mariopteris muricata* (Schlotheim) Zeiller and *Cordaites* sp. accompanied by several ferns with sphenopterid type of pinnules (Plate 1). Common were also *Calamites cf. suckowii* Brongniart and *Calamites cf. cistii* Brongniart.
– *Interpretation*: The presence of species with different life-strategies indicates the existence of a single, mixed pteridosperm–cordaites–calamites–fern assemblage. Small trees to shrubby storeys were dominated by *Alethopteris idae* Šimůnek, *Cordaites* sp., *Calamites cistii* Brongniart and *C. suckowii* Brongniart. The understorey consisted probably of small well-diversified sphenopterid ferns and *Sphenophyllum cuneifolium* (Sternberg) Zeiller. Lianas were represented especially by lyginodendrid pteridosperms, especially by *Mariopteris muricata* (Schlotheim) Zeiller (Fig. 5).

4.2. Floristic assemblages of the Whetstone Horizon (Lower Bolsovian)

This up to several metres thick horizon forms the roof of the Lower Radnice Coal (Fig. 3). In its typical development, it consists of about 50 to 60 cm of massive pale yellow fine sand-grained vitrocrystallic tuff at the base followed by a several metres thick bed of laminated

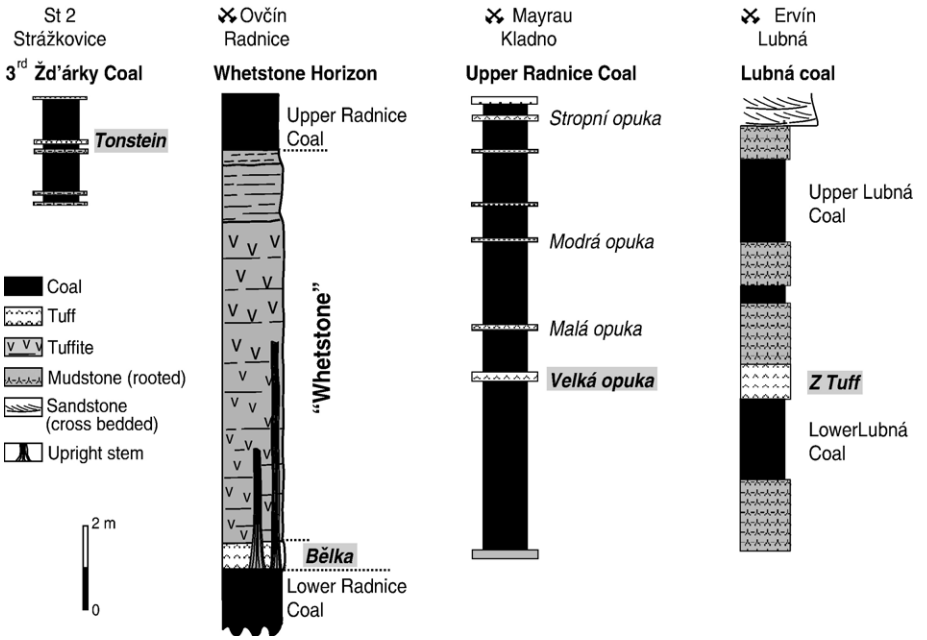


Fig. 3. Sections of coals with the studied volcanoclastic beds.

grey tuffite called "brousek" or "whetstone" (Mašek, 1973). The tuff bed at the base of the Whetstone Horizon, called "bělka" by miners, consists dominantly of kaolinite matrix with scattered clasts of sanidine and quartz crystals or their angular to subangular fragments the size of which usually varies between 0.01and 0.2 mm (Fig. 6). Common are also vermicular kaolinite crystalls.

Bělka contains the *in situ* buried coal-forming assemblage of the Lower Radnice Coal. Large fragments or nearly complete aerial parts of plants and up to 6 m high upright trunks (mostly decorticated lycophyte) always rooted in the roof of the Lower Radnice Coal (Fig. 2) are common. Species determination of these decorticated upright stems is mostly based on leafy shoots and branches surrounding the stems and preserved in bělka. There is no indication of rooted plants at any higher level of the tuff bed (bělka) which provides an evidence that all the plant remains preserved in this bed represent plants which grew in the roof of the Lower Radnice Coal. Occurrence of plant remains is generally structured depending on plant habit. Small herbaceous plants are usually concentrated at or near the base of the tuff bed being often accompanied by deciduous organs of larger plants, especially by lycophyte cones or their leafy shoots. Thick branches are most often found in middle and upper parts of the tuff bed associated locally with some ferns or pteridosperms (*Oligocarpia*, *Eusphenopteris*, *Mariopteris* etc.), probably of vine habit. Large trunks, except those in upright position, occur either at the base of the bělka (at its contact with coal seam) or penetrate this bed diagonally the base of trunk starting in the roof of coal from where it continues into various levels of the tuff bed, often up to its top.

Two widespread raindrop imprint horizons in the upper part of the tuff bed indicate three consecutive volcanic ash falls the first of them having been the strongest one. Whetstone part of the horizon consists of laminated mudstones with volcanic admixture the amount of which generally decreases upward. Fossils in the whetstone are quite rare and fragmentary being either scattered or concentrated into particular bedding planes which together with the absence of roots indicate an allochtonous origin of the flora. The location of the volcanic centre of the Whetstone Horizon has been interpreted from the increasing thickness of the basal tuff layer to the north which indicates its position in the northern Bohemia (Mašek, 1973), approximately 60 to 100 km far from the studied localities.

Plant assemblages of the basal tuff (bělka) of the Whetstone Horizon represent a coal swamp flora of a planar, mineral-rich eutrophic mire. Revised specimens were collected at eight different localities in the Pilsen, Radnice and Kladno–Rakovník basins and in small relics of Carboniferous strata in their surroundings (Fig. 4). Assemblages of these localities differ in species diversity of basic plant groups, related to ecological controls but partly also as a consequence of unequal sampling area and sample set.

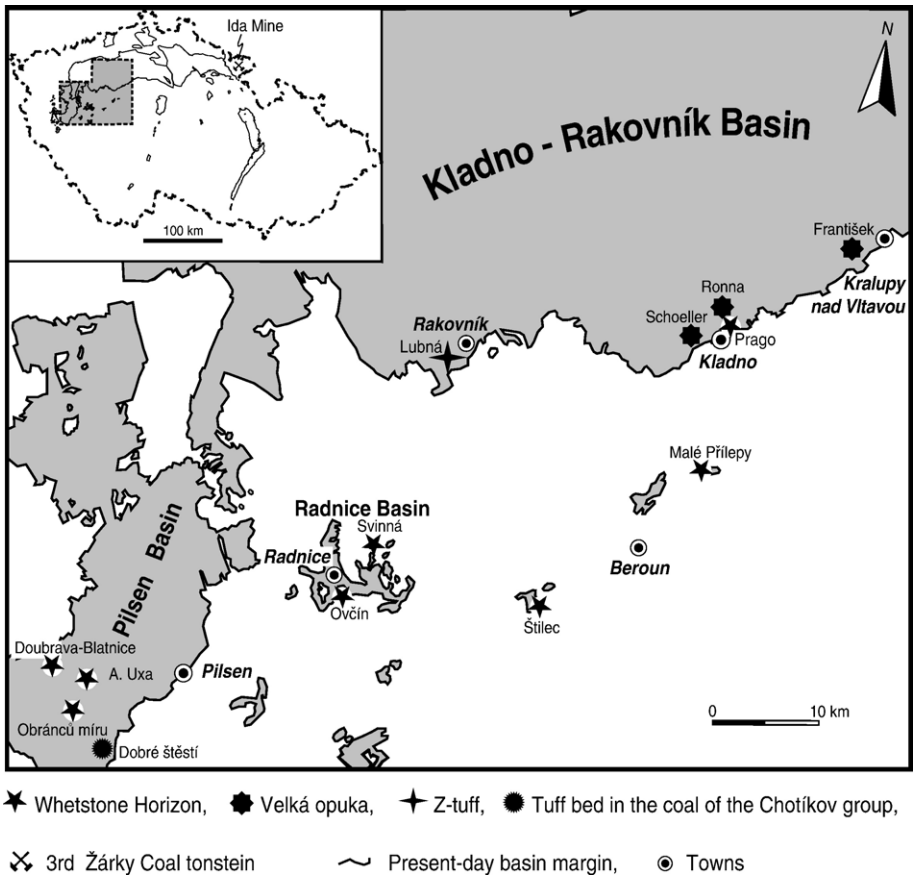


Fig. 4. Map of the studied localities in basins of central and western Bohemia.

4.2.1. A. Uxa Mine (formerly Krimich II) in Tlučná SW of Pilsen, Pilsen Basin

– *Origin and characteristics of the material*: The studied set of about 50 specimens was collected at the coal mine spoil tip during the field season of 1986 and is stored in the Czech Geological Survey in Prague. According to the mine geologist, all the tuff material was extracted in a gallery from a very small area of several tens of square metres. Here, the bělka tuff bed forms the roof of the Lower Radnice Coal. Since the material was collected at the coal mine spoil tip it is impossible to provide more information about the local taphonomical conditions, but these are believed to be similar to those at localities where it was possible to do field observations in excavations.
– *Local palaeogeography*: The Lower Radnice Coal exploited by the A. Uxa Mine formed from an extensive mire developed between palaeohighs in about 1–2 km wide and several kilometres long river valley entering the central depression of the Pilsen Basin dominated by fluvial deposits (Fig. 7).
– *Taphocoenoses* collected at the A. Uxa Mine consists of about 13 biological species (Table 2) with well-diversified sphenopsids and zygopterid ferns, whereas lycopsids, pteridosperms, progymnosperms and cordaites were quite rare or completely absent in the studied material. Sphenopsids are the commonest group represented by five species. Three of them are calamites as indicated by three types of leafy shoots (*Annularia* sp., *Asterophyllithes equisetiformis* (Sternberg) Brongniart and *A. grandis* (Sternberg) Geinitz) and by the same number of stem species (*Calamites suckowii* Brongniart, *C. cistii* Brongniart and *C.* sp.). The remaining two species belong to *S. cuneifolium* (Sternberg) Zeiller and *S. myriophyllum* Crépin. Ferns are also abundant, represented by two zygopterid species *Corynepteris angustissima* (Sternberg) Němejc and *Desmopteris longifolia* Presl in Sternberg as well as by the marattialean fern *Pecopteris aspidioides* Sternberg. Lycopsids are represented by only a single specimen of *Lepidophloios laricinum* Sternberg bark impression. Similarly,

Table 1
Species composition and estimated number of biological species of taphocoenoses from the 3rd Žď'árky Coal
Tuff of the 3rd Žď'árky Coal — Locality: Ida Mine

	Plant groups			Species / habits	
1	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes equisetiformis*	
2				*Asterophyllithes longifolius*	
3			Stems	*Calamites suckowii*	S
4				*Calamites cistii*	S
5		Sphenophylls		*Sphenophyllum cuneifolium*	U
6	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
7		Other ferns		*Sphenopteris schatzlarensis*	V/U
8				*Sphenopteris cf. damesii*	V/U
9				*Sphenopteris cf. charaeophylloides*	V/U
10				*Sphenopteris cf. delicatula*	V/U
11				*Sphenopteris* sp.	V/U
12	Pteridospermopsida	Medullosalean Pteridosperms		*Alethopteris idea*	S
13				*Alethopteris pillosa*	S
14				*Paripteris linguaefolia*	S
15		Lyginodendrid Pteridosperms		*Mariopteris muricata*	V
16				*Eusphenopteris nummularia*	V
17				*Palmatopteris furcata*	V
18	Cordaitopsida	Cordaites		*Cordaites* sp.	T
Number of morphospecies				18	
Estimated number of biological species				16	
Area of sampling				< 50 000 m^2	

Plant habits: T — trees, S — sub-trees and shrubs, V — vines, U — understorey, V/U — vines or understorey elements (precise habit unknown).

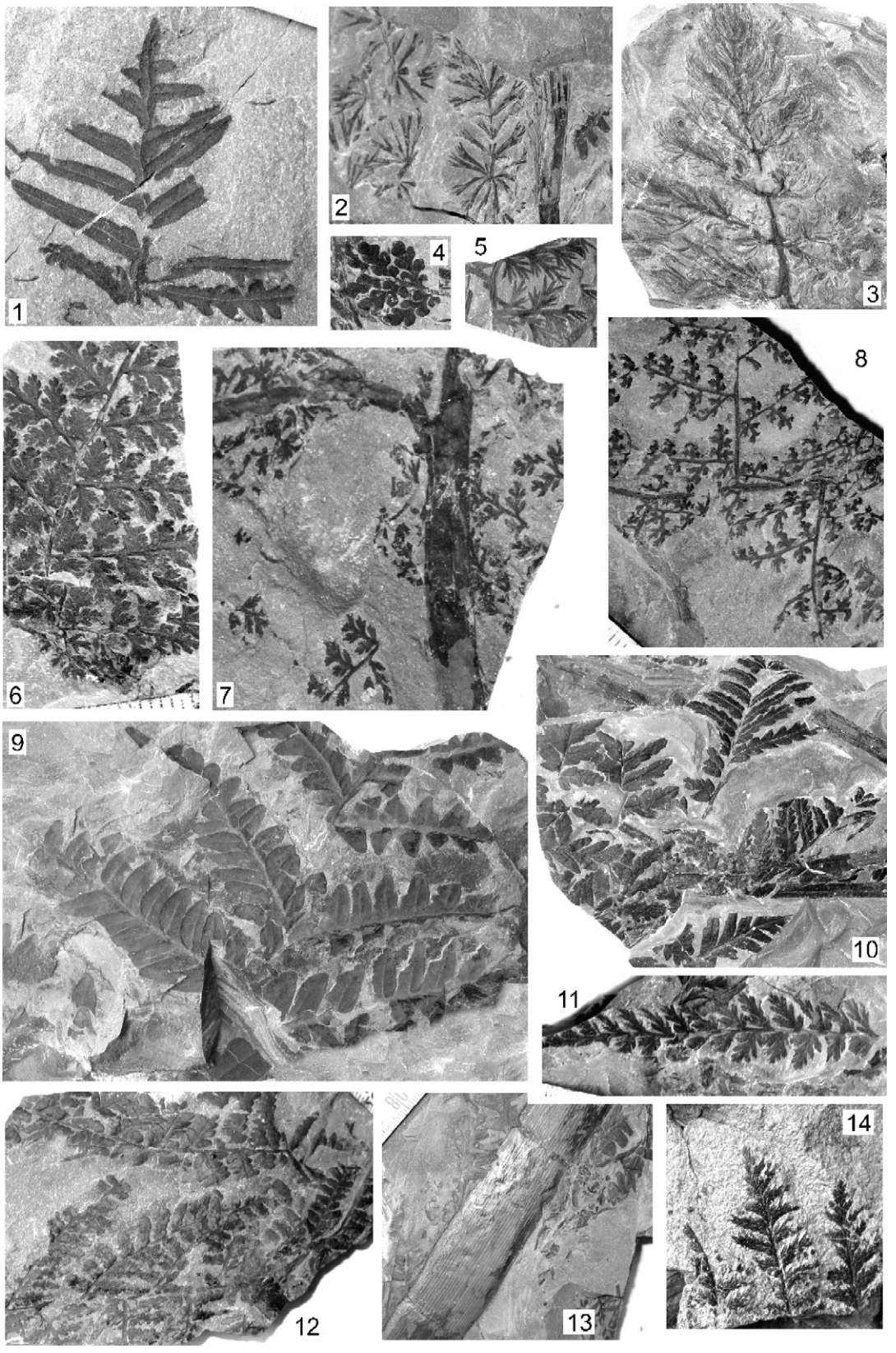
pteridosperms and progymnosperms are only poorly represented whereas cordaites are absent.

– *Interpretation*: The plant association described above represents most probably only part of the plant assemblage which colonised the mire of the Lower Radnice Coal. Small area of sampling is probably responsible for the lower species diversity. The assemblage of the A. Uxa Mine could be characterised as a calamites–fern dominant, low tree forest (Figs. 8 and 9).

4.2.2. Mines between Doubrava and Blatnice, SW of Pilsen, Pilsen Basin

– *Origin and characteristics of the material*: This locality covers an area of about 3–4 km^2 located in the western part of the Nýřany Coalfield. Specimens were collected at spoil tips of several coal mines which operated in this area during the 19th and the first half of the 20th century. Revised material represents about 200 specimens stored in the collections of the West Bohemian Museum in Pilsen, National Museum in Prague and the Charles University in Prague. No details on how plants occurred in tuff are available. Nevertheless rocks in which plant remains are preserved display no roots or sedimentary structures and resemble strongly this tuff from other localities.
– *Local palaeogeography*: The Lower Radnice Coal is developed in a W–E striking palaeo-valley, several kilometres long and 1 or 2 km wide filled by sediments of the Radnice Member (Fig. 7).
– *Taphocoenoses*: In all, about 45 biological species were identified (Table 3). Ferns are the most diversified plant group being represented by 19 species. Thirteen of them are small ferns with mostly sphenopteris type of pinnules, five belong to zygopterid ferns whereas only *Pecopteris aspidioides* Sternberg represents marattialean tree ferns. This locality is also typified by the occurrence of several species (e.g. *Sonapteris barthelii* Pšenička *et al.*, *Rhodeites subpetiolata* Němejc, *Rhodeites gutbieri* (Ettingshausen) Němejc, *Discopteris doubravensis* Pšenička *et al.*, *Discopteris kettneri* Pšenička *et al.*, *Urnatopteris* sp., etc.) that are absent or very rare at the other localities.

Well-diversified sphenopsids are represented by two calamite and five sphenophyll species. Similarly, pteridosperms occur also in seven species; three of them being of medullosalean type including *Laveineopteris*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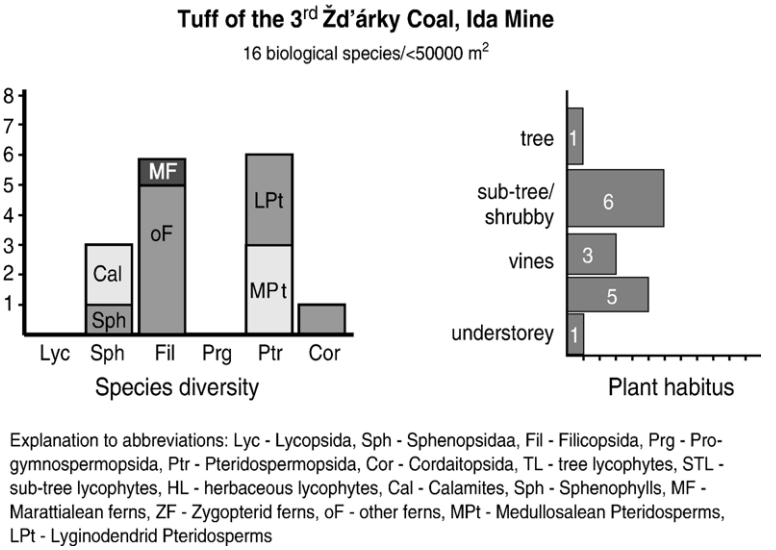


Fig. 5. Species and plant groups diversity and habitus of the assemblage preserved in tonstein of the 3rd Žďárky Coal in the Intra-Sudetic Basin.

loshii (Brongniart) Cleal, Shute and Zodrow which is a characteristic species of the Whetstone Horizon. There are also six lycopsid species mostly of a tree habit. *Lepidodendron simile sensu* Němejc (1947) and *Lepidodendron lycopodioides* Sternberg seem to be the most characteristic lycopsids for this locality (Plate 2).

– *Interpretation*: Since the area of sampling is very large, it is assumed that the studied specimens are derived from several plant assemblages as indicated also by the high number of species. Variety of plant habits and living strategies suggest the existence of well-diversified and structured forest ecosystems dominated by *Lepidodendron simile sensu* Němejc (1947) and *L. lycopodioides* Sternberg (Tables 4 and 5). Understorey was occupied by several species of zygopterid ferns, sphenophylls and also herbaceous lycopsids (*Selaginella bayerii n.* sp.).

4.2.3. Opencast Mine Ovčín near Radnice in the Radnice Basin

– *Origin and characteristics of the material*: The locality is situated in the southern part of the Radnice Basin (Fig. 4). Several thousand specimens were obtained recently by present authors from three large and two small excavations, covering a continuous area of about 150 m^2. This material is, however, of special importance and detailed analysis of gathered data will be performed separately. Here only basic data and general characteristics are provided. All the material is stored in the collection of the West Bohemian Museum in Pilsen. All the upright stems

Plate I. Characteristic plants of the 3rd Žďárky Coal, Prkenný důl Žďárky Member (Duckmantian), Intra-Sudetic Basin.

1. *Alethopteris idae*, apical part of pinnae of the penultimate order, (0.5×)
2. *Sphenophyllum cuneifolium*, (0.8×)
3. *Asterophyllithes cf. equisetiformis*, (0.7×)
4. *Sphenopteris nummularia*, (0.7×)
5. *Sphenopteris damesii*, (0.7×)
6. *Sphenopteris cf. charaeophylloides*, (1×)
7. *Sphenopteris cf. delicatula*, (1×)
8. *Sphenopteris cf. delicatula*, (0.8×)
9. *Alethopteris idae*, pinnae of the penultimate order, (0.5×)
10. *Mariopteris muricata*, (0.5×)
11. *Sphenopteris schatzlarensis*, (0.8×)
12. *Pecopteris aspidioides*, (0.5×)
13. *Calamites cf. cistii* associated with fragments of *Alethopteris idae*, (0.7×)
14. *Sphenopteris* sp., (1×).

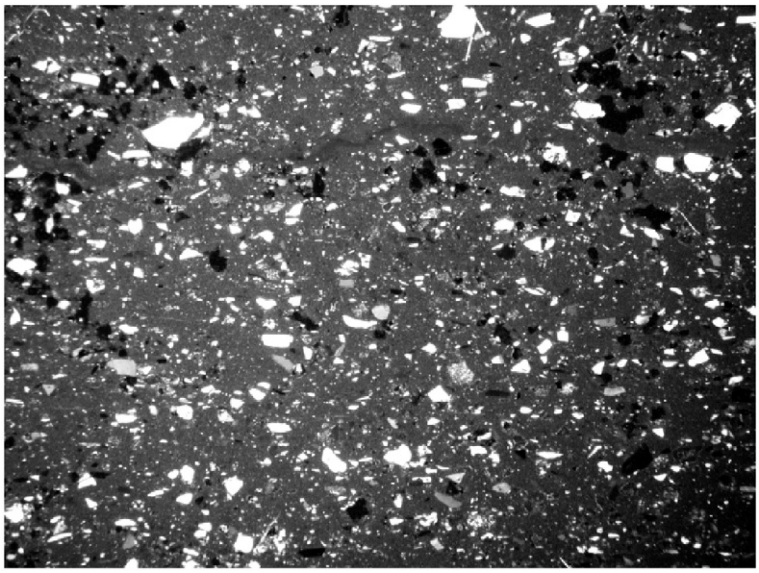


Fig. 6. Thin-section of the bělka tuff bed showing fragments/crystalls of quartz and sanidine scattered in kaolinite matrix. Crossed Polaroids.

found were rooted in the roof of coal seam immediately below it. No roots were found in the tuff bed. Plant fossils are not chared.

– *Local palaeogeography*: The Radnice Basin consists of several isolated relics of Carboniferous strata formerly connected with the Kladno–Rakovník and

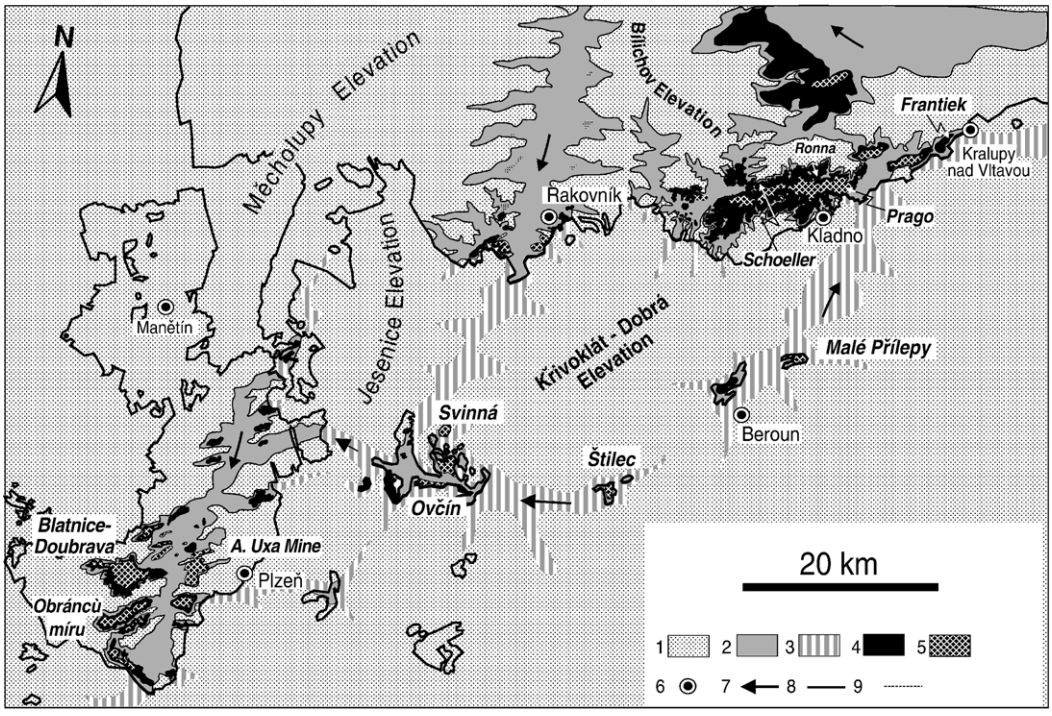


Fig. 7. Palaeogeographic map of the Radnice Member during the formation of the Radnice group of coals (=Lower and Upper Radnice coals) with distribution of mires of both coal seams. 1. Area of erosion, 2. preserved extent of the Radnice Member, 3. Assumed extent of the Radnice Member outside the present-day basin limit, 4. Proved extent of the Upper Radnice Coal, 5. Proved extent of the Lower Radnice Coal, 6. Towns, 7. Direction of clastic transport, 8. Present-day basin limit. According to Opluštil (2003).

Table 2
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from the A. Uxa Mine

Whetstone horizon — Locality: A. Uxa Mine, Tlučná

	Plant groups			Species/habits	
1	Lycopsida	Arborescent form	Stem	*Lepidophloios laricinum*	T
2	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes equisetiformis*	
3				*Asterophyllithes grandis*	
4				*Annularia* sp.	
5			Stems	*Calamites suckowi*	S
6				*Calamites cf. cisti*	S
7				*Calamites* sp.	S
8		Sphenophylls		*Sphenophyllum cuneifolium*	U
9				*Sphenophyllum myriophyllum*	U
10	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
11		Zygopterid ferns		*Corynepteris angustissima*	U
12				*Desmopteris longifolia*	U
13		Other ferns		*Sphenopteris cf. crepinii*	U/V
14				*Pecopteris pennaeformis*	V
15	Progymnospermopsida			*Rhacopteris bipinnata*	S
16	Pteridospermopsida	Lyginodendrid Pteridosperms		*Eusphenopteris nummularia*	V
Number of morphospecies				16	
Estimated number of biological species				13	
Area of sampling				< 100 m^2	

Pilsen basins (Fig. 7). Boreholes and opencast mine data revealed a transition of coals to mudstone and fine-grained sandstone, and subsequently to arkosic sandstones with pebbles and conglomerate intercalations, corroborating the existence of a fluvial channel only a few hundred metres north of the opencast mine. The mire of the Lower Radnice Coal at the Ovčín locality was formed on a floodplain not far from the active river channel. Occasional flooding is evidenced by the high ash content and thin siliciclastic partings in the coal seam which indicate existence of planar (ground-water supplied) eutrophic mire at this locality.

– *Taphocoenoses*: An association of 30 biological species was identified in the excavations (Table 4, Plate 3) within an area of about 150 m^2. All the basic spore-producing plant groups are well-diversified (Figs. 8 and 9), especially lycopsids (nine species), ferns (six species) and sphenophylls (six species). Calamites are represented by two and pteridosperms by three species. *Corynepteris angustissima* (Sternberg) Němejc, *Sphenophyllum majus* (Bronn) Bronn, the pteridosperm *Sphenopteris cf. mixta* Schimper and the lycopsids *Lepidodendron lycopodioides* Sternberg and *Lepidophloios acerosus* Lindley and Hutton are among the most abundant species. Up to 1.4 m long lycopsid branches and leafy shoots irregularly covered most of the excavations, being located especially in the basal 10 cm thick layer of the tuff bed. Their highest concentration was found around upright decorticated lycopsid stems with a swollen base. The diameter of these stems about 70 cm above the roof of the coal seam varied usually between 15 and 30 cm, but increased towards the base up to 50 cm. *C. angustissima* (Sternberg) Němejc and *S. majus* (Bronn) Bronn covered densely all the excavated area except sites occupied by *Cordaites borassifolius* (Sternberg) Unger. Locally abundant were also *Pecopteris aspidioides*, *Laveineopteris loshii* (Brongniart) Cleal *et al.*, *C. borassifolius* (Sternberg) Unger and both *Calamites* species. Characteristic species of this locality are *Spencerites havlenae* Drábková et al. (2004), *Selaginella n.* sp. 1 and *Selaginella n.* sp. 2. Only minor changes in species composition were observed between particular excavations. Each of them provided the same basic species pattern.

– *Interpretation*: The assemblage exposed at this locality consists of plants, which follow several different life-strategies, and as a whole represented a highly-diversified and structured coal-forming forest with well-developed individual storeys (Fig. 9). The

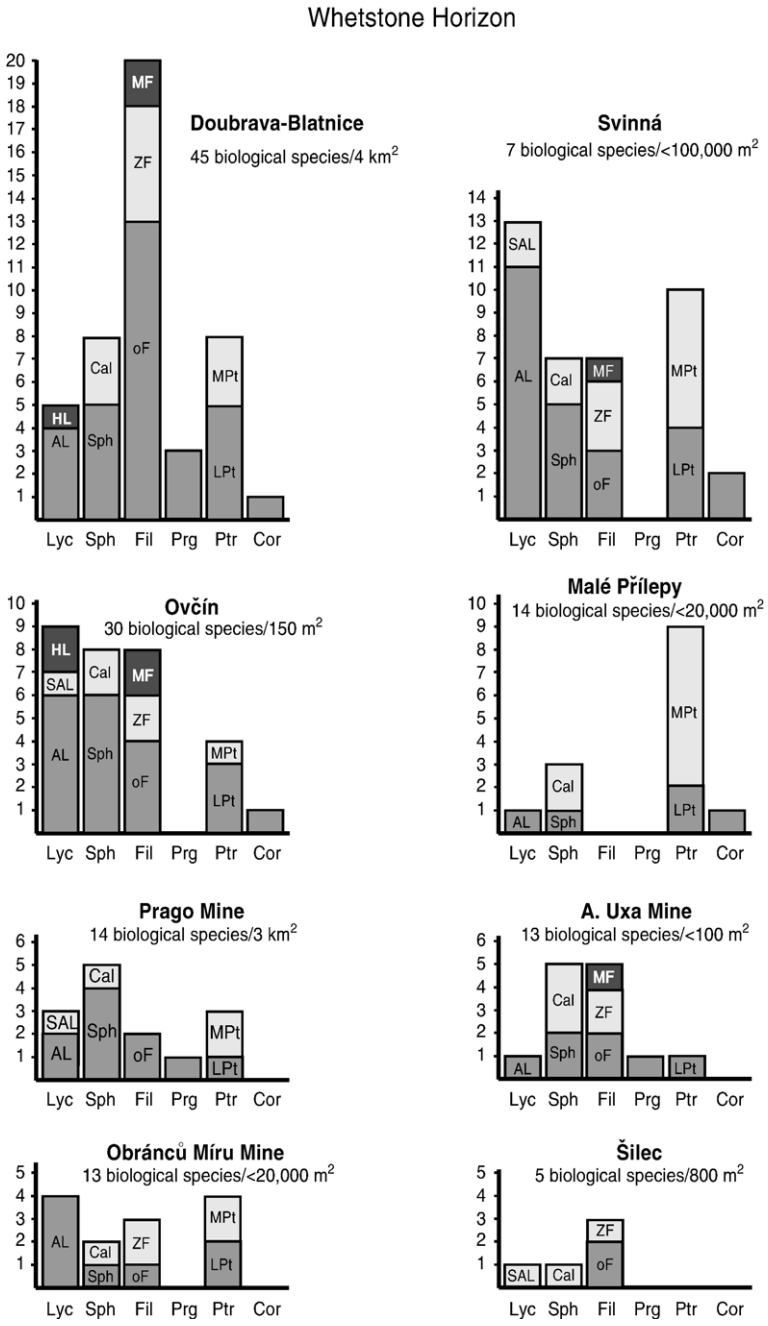


Fig. 8. Species and plant groups diversity of the assemblages preserved in the bělka–tuff bed at the base of the Whetstone Horizon at the studied localities in basins of central and western Bohemia. For explanation see Fig. 5.

arborescent storey consisted of *Lepidodendron lycopodioides* Sternberg, *Lepidophloios acerosus* and *Lepidodendron simile sensu* Němejc (1947). The growth of the storey is estimated to vary between 10 and 15 m, however, it is impossible to define exactly the height of these species since only the lower part of upright trunks or several metres long parts of fallen trunks were found. Spatial distribution of the trees varies usually between 2 and 5 m. They formed relatively dense forest with rich canopy. Low-trees and shrubs were represented by *Psaronius* (*Pecopteris aspidioides*), *Spencerites havlenae*, two calamite species and the pteridosperms *Laveineopteris loshii* and *Sphenopteris cf. mixta* Schimper.

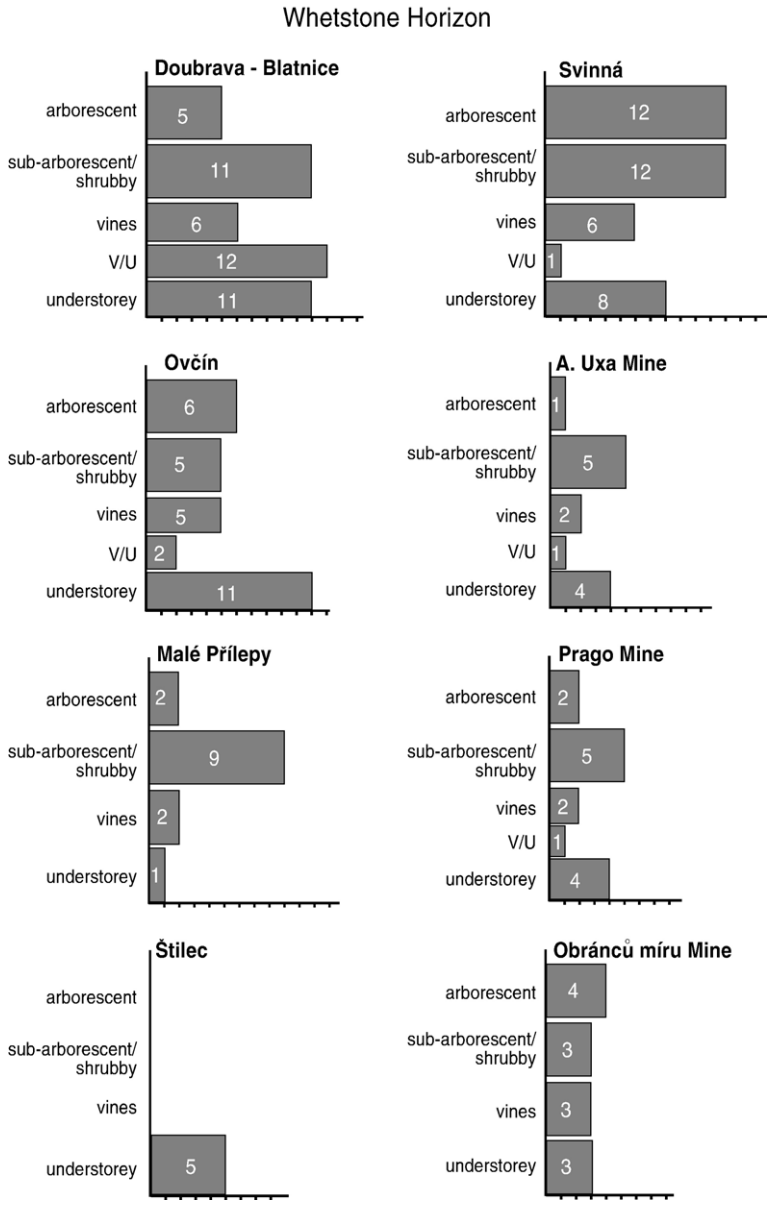


Fig. 9. Habitus of plants preserved in the bělka bed of the Whetstone Horizon at the studied localities.

The understorey consisted of a mixture of small ferns and sphenophylls among which *Corynepteris angustissima* and *Sphenophyllum majus* prevail. Vines were dominated by pteridosperms *Eusphenopteris nummularia* (Gutbier) Novik and *Palmatopteris furcata* (Brongniart) Potonie and by ferns *Senftenbergia plumosa*, and *Oligocarpia lindsaeoides* (Ettingshausen) Stur.

This rich assemblage of plants of different life-strategies probably represent a pre-climax or climax stadium of a hydroseral succession.

4.2.4. Opencast mine Štilec west of Beroun

– *Origin and characteristics of the material*: The flora was collected in six small excavations of about 2 to 5 m^2 scattered randomly on the floor of an abandoned opencast mine, over an area of about 800 m^2. Each of them provided the same plant association. About one thousand specimens are stored in the collections of the West Bohemian Museum in Pilsen and in the National Museum in Prague.
– *Local palaeogeographic and ecologic conditions*: Štilec opencast mine is located in a small relic of the

Table 3
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from Doubrava–Blatnice district

Whetstone Horizon				Locality: Doubrava–Blatnice	
	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidostrobus sternbergii*	
2			Stems, leafy shoots	*Lepidodendron mannabachense*	T
3				*Lepidodendron simile*	T
4				*Lepidodendron ophiurus*	T
5				*Lepidodendron lycopodioides*	T
6		Herbaceous forms		*Selaginella bayeri n.* sp.	U
7	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes equisetiformis*	
8				*Asterophyllithes longifolius*	
9			Cones	*Palaeostachya cf. distachya*	S
10				*Palaeostachya germanica*	S
11				*Cingularia* sp.	S
12			Stems	*Calamites cistii*	
13				*Calamites* sp.	
14		Sphenophylls		*Sphenophyllum myriophyllum*	U
15				*Sphenophyllum majus*	U
16				*Sphenophyllum trichomatosum*	U
17				*Sphenophyllum cuneifolium*	U
18				*Sphenophyllum chaloneri*	U
19	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
20				*Pecopteris tuffitica*	S
21		Zygopterid ferns		*Corynepteris angustissima*	U
22				*Corynepteris winslowii*	U
23				*Corynepteris similis*	U
24				*Corynepteris corraloides*	U
25				*Desmopteris longifolia*	U
26		Other ferns		*Crossotheca nyranensis*	V/U
27				*Zeilleria zodrowii*	V/U
28				*Zeilleria avoldensis*	V/U
29				*Zeilleria frenzlii*	V/U
30				*Sonapteris barthelii*	V
31				*Hymenotheca* sp.	V/U
32				*Sphenopteris schatzlarensis*	V/U
33				*Sphenopteris cf. crepinii*	V/U
34				*Urnatopteris* sp.	V/U
35				*Rhodeites gutbieri*	V/U
36				*Rhodeites subpetiolata*	V/U
37				*Discopteris kettneri*	V/U
38				*Discopteris doubravensis*	V/U
39	Progymnospermopsida			*Palaeopteridium macrophyllum*	S
40				*Rhacopteris speciosa*	S
41				*Saaropteris guthorlii*	S
42	Pteridospermopsida	Medullosalean Pteridosperms		*Laveineopteris loshii*	S
43				*Linopteris neuropteroides f. major*	S
44				*Macroneuropteris scheuchzeri*	S
45		Lyginodendrid Pteridosperms		*Eusphenopteris obtusiloba*	V
46				*Eusphenopteris nummularia*	V
47				*Dicksonites irregularis*	V
48				*Fortopteris radnicensis*	V
49				*Mariopteris muricata*	V
50	Cordaitopsida	Cordaites		*Cordaites borassifolius*	T
Number of morphospecies				50	
Estimated number of biological species				45	
Area of sampling				$<4\ km^2$	

Radnice Member sediments situated east of the Radnice Basin (Figs. 4 and 7). It represents the fill of a W–E-striking river palaeo-valley. High ash content in the Lower Radnice Coal and abundant thin sedimentary partings indicate permanently increased input of mud suspension into the planar eutrophic mire and its frequent inundation.

– *Taphocoenoses*: The association exposed in all the excavations consists only of five mostly endemic species of small growth, not more than one or two metres of maximum height (Table 5, Figs. 8 and 9 and Plate 4). The most diversified plant group is the ferns represented by three species (Fig. 8). Sphenopsids and lycopsids occur with one species in each group, whereas cordaites and pteridosperms are completely absent. The most abundant are *Calamites n.* sp., and the ferns *Dendraena pinnatilobata* Němejc and *Kidstonia heracleensis* Zeiller. Calamites stems grew in clusters. They are about 1 cm in diameter and bear fully mature *Palaeostachya feistmantelii* strobili. Small and dichotomously branching lycopsids *Spencerites n.* sp. (Plate 4) with mature sporangia arranged into fertile zones/apices were subdominant elements of the phytocoenoses. Except for *Desmopteris alethopteroides* Ettingshausen, all the remaining species have been found only at this locality (Table 15).

  Plants are not chared and all the upright stems are rooted in the coal below. No roots have been found in the tuff.

– *Interpretation*: The phytocoenosis of the Štilec locality is interpreted as a pioneer calamites–fern dominated assemblage re-colonising a previously drowned mire. This is indicated by the presence of about 10 cm of thick sapropelic coal in the roof of the Lower Radnice Coal, indicating a lacustrine phase of mire development. As the lake shallowed it started to be colonised by pioneer plants. This explains the apparently poor species diversity, which is typical only for this locality. Similar observations where calamites were pioneer colonisers are mentioned also by other authors (e.g. Pfefferkorn et al., 2001).

4.2.5. Malé Přílepy north of Beroun

– *Origin and characteristics of the material*: Approximately 80 specimens are stored in the collection of the National Museum in Prague. They were probably collected at coal mine tips during a period of a few decades in the first half of the 20th century. The area of sampling is estimated to be smaller than 20 000 m^2.

– *Local palaeogeography*: The Malé Přílepy Coalfield is about 1 km^2 large relic of the Radnice Member sediments, located 15 km south of the present-day southern margin of the Kladno–Rakovník Basin. It is assumed to be connected to this basin via a NNE–SSW striking river palaeo-valley (Fig. 7).

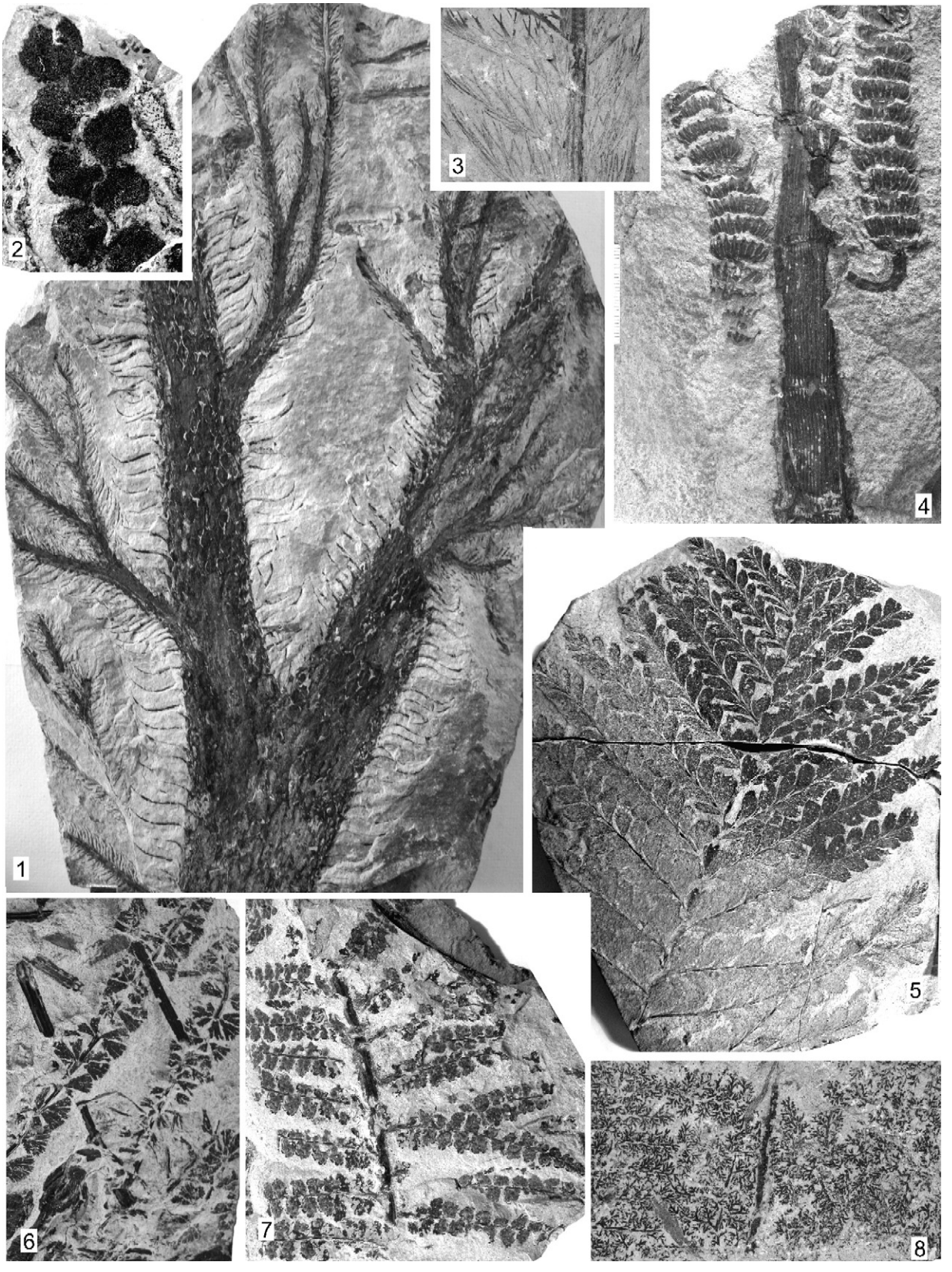
– *Taphocoenosis* consists of 14 biological species dominated by 7 medullosalean pteridosperm taxa (Fig. 8, Table 6). Sphenopsids are the second most diversified group being represented by two calamites species with *Asterophyllithes grandis* and *A. longifolius* (Sternberg) Brongniart type of leafy shoots, and by *Sphenophyllum wingfieldense*. Ferns and lycopsids are only very poorly represented in the studied collection. However, abundant long and narrow lycopsid leaves accompanying most of the revised specimens indicate that representatives of this plant group may be quite common at this locality. The presence of arborescent lycopsids is also indicated by the presence of lepidodendrid cones *Lepidostrobus sternbergii* (Corda) Bek *et al*. Most abundant species in the collection are *Alethopteris distantinervosa* Wagner, *A. lonchitica* and *Laveineopteris loshii*. Local species typical for this locality are *Laveineopteris bohemica* (Ettingshausen) comb. nov., *Palaeoweischelia defrancei* (Brongniart) Potonié and Gothan and *Praecallipteridium n.* sp. Common also are remains of calamites and cordaites leaves.

– *Interpretation*: The studied collection is characterised by an apparent diversity and abundance of medullosalean pteridosperms (Fig. 8). Consequently, the phytocoenosis of the locality was probably also dominated by pteridosperms, whereas arborescent lycopsids and sphenopsids were probably subdominant. However, lack of any information on how the material was collected, makes this conclusion rather speculative.

4.2.6. Prago Mine in Kladno

– *Origin and characteristics of the material*: This mine, located in the eastern part of the Kladno Coalfield (Figs. 4 and 7), exploited the Lower Radnice Coal between 1950 and 1990 from an area of about 3 km^2. Specimens were collected at coal mine spoil tip through several decades, however, only little attention was paid to this locality. Consequently, only about 70 specimens are stored in the collection of the National Museum in Prague. Part of the material was collected coal mine spoil tip by the current authors.

– *Local palaeogeography*: The locality occupies the eastern part of the Kladno Coalfield, located in the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W–E striking palaeo-valley of the same name (Opluštil, 2003). The mire of the Lower Radnice Coal covered most of the approximately 15 km long valley, however, it is best developed just in the mining field of the Prago Mine (Fig. 7). Here, the coal seam is between 1 and 1.5 m thick with abundant sedimentary partings and a generally high ash content of about 40%.

– *Taphocoenoses*: 14 biological species were identified in the studied set of specimens (Table 7). The most diversified plant groups are pteridosperms (four species) and Sphenopsids represented especially by four species of sphenophylls (Fig. 8). Lycopsids are represented by *Lepidodendron mannabachense* Sternberg (formerly *L. obovatum*), some species of the genus *Lepidophloios* (bearing *Lepidostrobus sternbergii* Bek and Opluštil) and *Polysporia robusta* Drábek. However, the most abundant species in the plant collection and at coal mine tip are *Laveineopteris loshii, Alethopteris distantinervosa* and *Lepidodendron mannabachense*. *Polysporia robusta*, *Sphenophyllum cuneifolium* and *S. myriophyllum* are subdominant elements of the assemblage.
– *Interpretation*: The presence of only 14 species obtained from the large area does not allow us to assume the existence of only a single phytocoenoses, probably as a consequence of the small set of samples. However, the experience of the current authors who have collected the specimens in the last decade of the mine's operation suggests the existence of a pteridosperm–lycopsid dominated assemblage with sub-dominant calamites (Fig. 8). Characteristic elements are *Laveineopteris loshii*, *Lepidodendron mannabachense* and *Polysporia robusta*.

4.2.7. Mines of the Svinná Coalfield near Radnice

– *Origin and characteristics of the material*: The revised material involved about 150 specimens stored in the collection of the National Museum in Prague, the West Bohemian Museum in Pilsen, the Natural History Museum in Vienna, the Geological Survey of Austria in Vienna, and the Museum für Naturkunde in Berlin. The material was collected during the 19th century at coal mine tips by many palaeobotanists including Sternberg, Presl, Feistmantel and Ettingshausen. It is a type locality of many species described by these authors. Area of sampling is estimated to be approximately 100 000 m^2.
– *Local palaeogeography*: The Svinná Coalfield represents a small, less than 1 km^2 relic of the Radnice Member sediments, formerly connected with the Radnice Basin s.s., located a few kilometres to the south (Figs. 4 and 7).
– *Taphocoenoses*: This classical locality has provided one of the most-diversified plant associations. It consists of about 39 biological species, which represent all the basic plant groups (Fig. 8, Table 8). The most diversified lycopsids occur as 13 species represented by lepidodendrids and sigillarias including *Asolanus camptotaenia* Wood. Small sub-arborescent lycopsids *Polysporia robusta* and *Spencerites havlenae* also occur. Sphenopsids are represented by five species of sphenophylls and only two calamites species. Ferns are also common, especially *Pecopteris aspidioides*, *Corynepteris angustissima*, *Desmopteris longifolia* and *Senftenbergia plumosa*. Pteridosperms are represented by ten species, among which the most common are *Laveineopteris loshii*, *Alethopteris distantinervosa* and *Eusphenopteris nummularia*. Svinná is the type locality of *Cordaites borassifolius* (Plate 5).
– *Interpretation*: Since the sampling area is quite large and nothing is known about the methods of sampling and selection of the material for the collections, it is difficult to characterise the former phytocoenoses. The high number of species suggests the existence of several plant assemblages. Diversified lepidodendrid forest phytocoenoses similar to that of the Ovčín locality were probably common. Characteristic elements of this locality are sigillarias.

Plate II. Selected species of the plant association of the Lower Radnice Coal at the Doubrava locality, Whetstone Horizon, Radnice Member (Bolsovian).

1. *Lepidodendron* (? *Paralycopodites*) *simile* (*sensu* Němejc 1947), (0.5×)
2. *Sonapteris barthelii*, (0.5×)
3. *Rhacopteris speciosa,* (0.7×)
4. *Palaeostachya cf. distachya*, (0.5×)
5. *Palaeopteridium macrophyllum*, (0.4×)
6. *Sphenophyllum majus*, (0.4×)
7. *Discopteris doubravensis*, (0.5×)
8. *Crossotheca nyranensis*, (0.5×).

Table 4
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from the Ovčín opencast mine near Radnice

Whetstone Horizon — Locality: Ovčín near Radnice

	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidocarpon majus*	
2			Stems	*Lepidodendron mannabachense*	T
3				*Lepidodendron simile*	T
4				*Lepidodendron lycopodioides*	T
5				*Lepidophloios acerosus*	T
6				*Sigillaria* sp.	T
7		Sub-arborescent forms		*Spencerites havlenae*	S
8		Herbaceous forms		*Selaginella n.* sp. 1	U
9				*Selaginella n.* sp. 2	U
10	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes* sp.	
11			Cones	*Palaeostachya* sp. 1	
12				*Palaeostachya* sp. 2	
13			Stems	*Calamites* sp. 1	S
14				*Calamites* sp. 2	S
15		Sphenophylls		*Sphenophyllum myriophyllum*	U
16				*Sphenophyllum majus*	U
17				*Sphenophyllum pseudoaquense*	U
18				*Sphenophyllum brasense*	U
19				*Sphenophyllum cuneifolium*	U
20				*Sphenophyllum chaloneri*	U
21	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
22		Zygopterid ferns		*Corynepteris angustissima*	U
23				*Desmopteris longifolia*	U
24				*Etapteris* sp.	U
25		Other ferns		*Oligocarpia lindsaeoides*	V
26				*Sphenopteris cf. schatzlarensis*	V/U
27				*Senftenbergia plumosa*	V
28				*Sonapteris bekii n* sp.	V
29	Pteridospermopsida	Medullosalean pteridosperms		*Laveineopteris loshii*	S
30		Lyginodendrid Pteridosperms		*Sphenopteris cf. mixta*	V/U
31				*Palmatopteris furcata*	V
32				*Eusphenopteris nummularia*	V
33	Cordaitopsida	Cordaites		*Cordaites borassifolius*	T
Number of morphospecies				33	
Estimated number of biological species				30	
Area of sampling				150 m^2	

4.2.8. Obránců míru (formerly Masaryk Jubilejní) Mine in Zbůch, Pilsen Basin

– *Origin and characteristics of the material*: Plants were collected by Němejc (1932), who published the list of species which he found between 1928 and 1932. Plant specimens were probably derived from a rather small part of the mining field, from an area of about less than 20 000 m^2.
– *Local palaeogeography*: The Obránců míru Mine operated in the Zbůch Coalfield, located in a *c.* 10 km long coal-bearing part of a WSW–ENE-striking palaeo-valley in the western part of the

Table 5
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from Štilec

Whetstone Horizon				Lokality: Štilec Mine near Beroun	
	Plant groups			Species/habits	
1	Lycopsida	Shruby form		*Spencerites n.* sp.	U
2	Sphenopsida	Calamites	Stem	*Calamites n.* sp.	U
3			Cone	*Palaeostachya feistmantelii*	
4	Filicopsida	Zygopterid ferns		*Desmopteris alethopteroides*	U
5		Other ferns		*Dendraena pinnatilobata*	U
6				*Kidstonia heracleensis*	U
Number of morphospecies				6	
Estimated number of biological species				5	
Area of sampling				~ 800 m^2	

Pilsen Basin (Figs. 4 and 7). The mine was located in the central part of the coalfield.

– *Taphocoenoses*: Němejc (1932) reported 13 biological species, among which lycopsids and ferns are the most diversified groups (Fig. 8, Table 9). Nevertheless, other basic plant groups are also present. The most abundant are *Laveineopteris loshii* and *Sigillaria* aff. *rugosa* Brongniart. He reported also *Asolanus camptotaenia* Wood, which is very rare in the Radnice Member, whereas *Corynepteris angustissima* and *Desmopteris longifolia* belong to very common peat-forming species.
– *Interpretation*: The association of plants described by Němejc most probably represents part of a single phytocoenosis dominated by arborescent lycopsids and pteridosperms (Figs. 8 and 9). Tree storey was occupied by *Sigillaria* aff. *rugosa*, *Lepidodendron longifolium* (determined as *Lepidodendron dichotomum*), *Lepidodendron laricinum* and *Asolanus camptotaenia*. Low tree to shrubby storeys were dominated by medullosalean pteridosperms, and calamites with *Asterophyllithes equisetiformis* type of leafy shoots. *Sphenophyllum cuneifolium* and zygopterid ferns including *Corynepteris angustissima* formed the understorey.

4.3. Floristic assemblages of the velká opuka tonstein (Lower Bolsovian)

Velká opuka is the thickest volcanoclastic parting intercalated in the Upper Radnice Coal, Radnice Member (Figs. 1B and 3) and was interpreted by Mašek and Pešek (1979) as an acid tuff. Its average thickness varies between 13 and 18 cm, however locally can exceed 1 m being here composed of a whitish tuff bed at the base overlain by horizon of grey, laminated mudstone with volcanic admixture interpreted as re-deposited volcanic ash. This parting has been recognised only in the Kladno–Rakovník Basin in central Bohemia and in the Radnice Basin in western Bohemia.

Plant remains of this tuff bed consist of pre-eruption and post-eruption flora. The former is preserved as fragments of aerial part of plants broken during the volcanic ash fall. Common are upright stems (only their basal parts) rooted in the coal below. Post-eruption flora is preserved as roots penetrating horizontally to subhorizontally the tuff bed, however, only where it is immediately overlain by coal, not by laminated mudstone (Fig. 10).

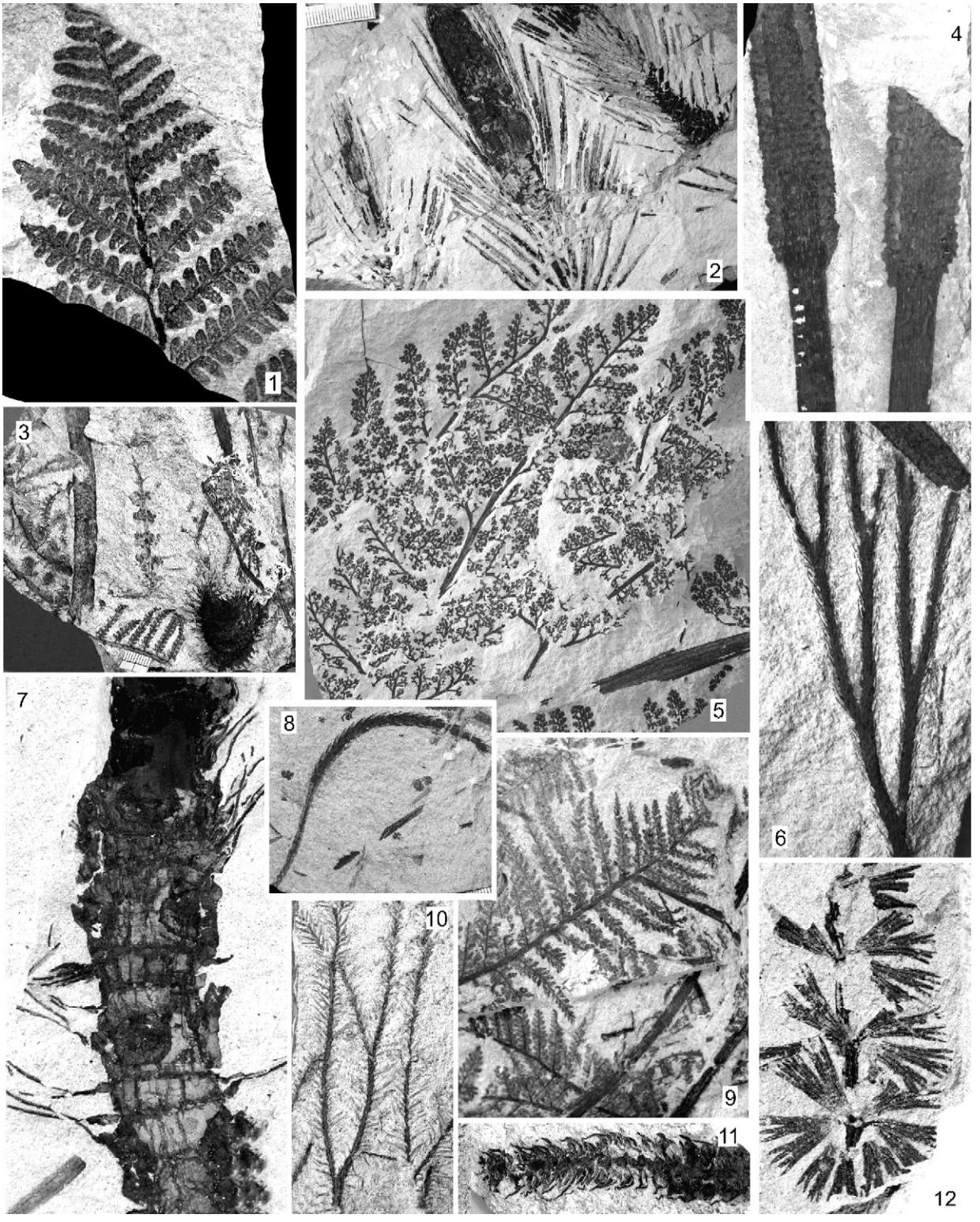
A rich and diversified flora was found especially in the Kladno and Otvovice coalfields in the SE part of the Kladno–Rakovník Basin (Figs. 4 and 7). It preserved the coal-forming flora of the Upper Radnice Coal which differs from flora preserved in roof shale of this coal seam in absence/presence of some species (e.g. absence of *Lepidodendron aculeatum* in the velká opuka and its common occurrence in the Upper Radnice Coal roof shale). Collections from three localities provided sufficient samples to be examined in detail: Schoeller and Ronna Mines in Kladno and František Mine in Otvovice, which are several kilometres apart (Fig. 4).

4.3.1. František Mine, Otvovice near Kralupy nad Vltavou

– *Origin and characteristics of the material*: All the specimens were collected in a small excavation about 5 m^2 located at an outcrop of the Upper Radnice Coal near the former František de Paula Mine in Otvovice. The collection consists of about

300 samples partly deposited at the Charles University in Prague, Faculty of Science and partly in a private collection.

– *Local palaeogeography*: The Otvovice coalfield represents the northern margin of a W–E-striking river palaeo-valley filled by coal-bearing strata of the



Radnice Member (Fig. 7). The proximity of the mire-margin is indicated by the reduced thickness of the seam, which wedges-out gradually on a palaeohigh located to the north. Velká opuka tonstein at this locality is about 13 cm thick and was represented by massive sharp-based whitish tuff bed.

– *Taphocoenoses* obtained from the excavation consist of 12 biological species representing most of the basic plant groups (Table 10, Plate 6). The most diversified are lycopsids and ferns (Fig. 11), represented by 4 and 5 species respectively, whereas only one cordaites and two sphenopsids species occurred. No pteridosperms have been found. The most common species is *Lepidodendron simile* (*sensu* Němejc, 1947), represented by leafy shoots and large fragments of branches up to 6 cm in diameter. They densely covered the whole excavation, being concentrated mostly in the basal 2 or 3 cm of the tuff. Upright stem have not been found. Among other species, the most common are *Sigillaria diploderma* Corda, *Omphalophloios feistmantelii, Pecopteris aspidioides* and *Desmopteris longifolia*. *S. diploderma* was represented by 6 cm broad stems, whereas for *O. feistmantelii* both fertile (*O. feistmantelii*) and sterile stems have been found. Fragments of ultimate to penultimate pinnae of *P. aspidioides* and *D. longifolia* were the most common non-lycopsid plant remains. The remaining species were found only rarely in a few isolated specimens (*Lepidocarpon majus* (Brongniart) Hemingway, *Calamites* sp.).
– *Interpretation*: The very small area of sampling is insufficient to fully characterise the whole former plant assemblage of this locality, but indicates the existence of a diversified peat-forming lycopsid forest with well-developed individual storeys (Fig. 11). The assemblage found in the excavation was dominated by *Lepidodendron simile*. Its height is estimated to have reached about 10 to 15 m, based on findings from several other localities. The absence of upright stems indicates that the plant grew outside the excavated area, and only branches and leafy shoots were found, some perhaps broken-off partly before the eruption but mostly broken by falling volcanic ash. The proximity of another arborescent lycopsid species (*Lepidophloios* sp.) is indicates by rare findings of *Lepidocarpon majus*.
The low-tree storey was represented by *Sigillaria diploderma* and *Omphalophloios feistmantelii* the height of which is estimated to be between 4 and 7 m. The absence of a swollen base indicates that these plants grew close to the excavated area but not in it. The shrubby storey was dominated by *Cordaites* sp. and the fern *Pecopteris aspidioides*. The understorey was colonised by the zygopterid ferns *Corynepteris angustissima* and *Desmopteris longifolia*, together with *Sphenophyllum majus* and small *Calamites* species, the stem of which attained a diameter of about 1 cm. We interpret *Senftenberg plumosa* and *Sphenopteris cf. crepinii* to have been vines.

4.3.2. Ronna Mine, Kladno

– *Origin and characteristics of the material*: About 200 specimens are stored in the collections of all the institutions mentioned earlier were studied. The specimens were collected at the coal mine tip during several decades when the mine operated on an area of about 1 km^2.
– *Local palaeogeography*: The Ronna Mine is located in the NE part of the Kladno Coalfield, in the SE part of the Kladno–Rakovník Basin (Figs. 4 and 7). The Upper Radnice Coal is developed here in a river palaeo-valley about 15 km long and 2 to 5 km wide (Fig. 7).
– *Taphocoenoses* consist of about 26 biological taxa (Table 11, Plate 7). Lycopsids occur as 11 species, most of them being arborescent (Fig. 11). *Lepidodendron longifolius* Presl in Sternberg and

Plate III. Characteristic species of the Lower Radnice Coal at the Ovčín opencast mine, Whetstone Horizon, Radnice Member, (Bolsovian).

1. *Pecopteris aspidioides*, (0.9×)
2. Leafy shoots of *Lepidodendron mannabachense* with cone *Lepidostrobus obovatus*, (0.5×)
3. *Corynepteris angustissima* associated with fructification and strobilus of *Sphenophyllum majus*, (0.4×)
4. *Spencerites havlenae*, (0.5×)
5. *Sphenopteris cf. mixta*, (0.4×)
6. *Lepidodendron lycopodioides*,
7. *Calamites* sp. 1, (0.7×)
8. *Selaginella n.* sp. 1, (0.5×)
9. *Senftenbergia plumosa*, (0.7×)
10. Leafy shoots of *Lepidodendron simile*, (0.5×)
11. *Calamostachys* sp. (related to *Calamites* sp. 2), (0.5×)
12. *Sphenophyllum majus*, (1×).

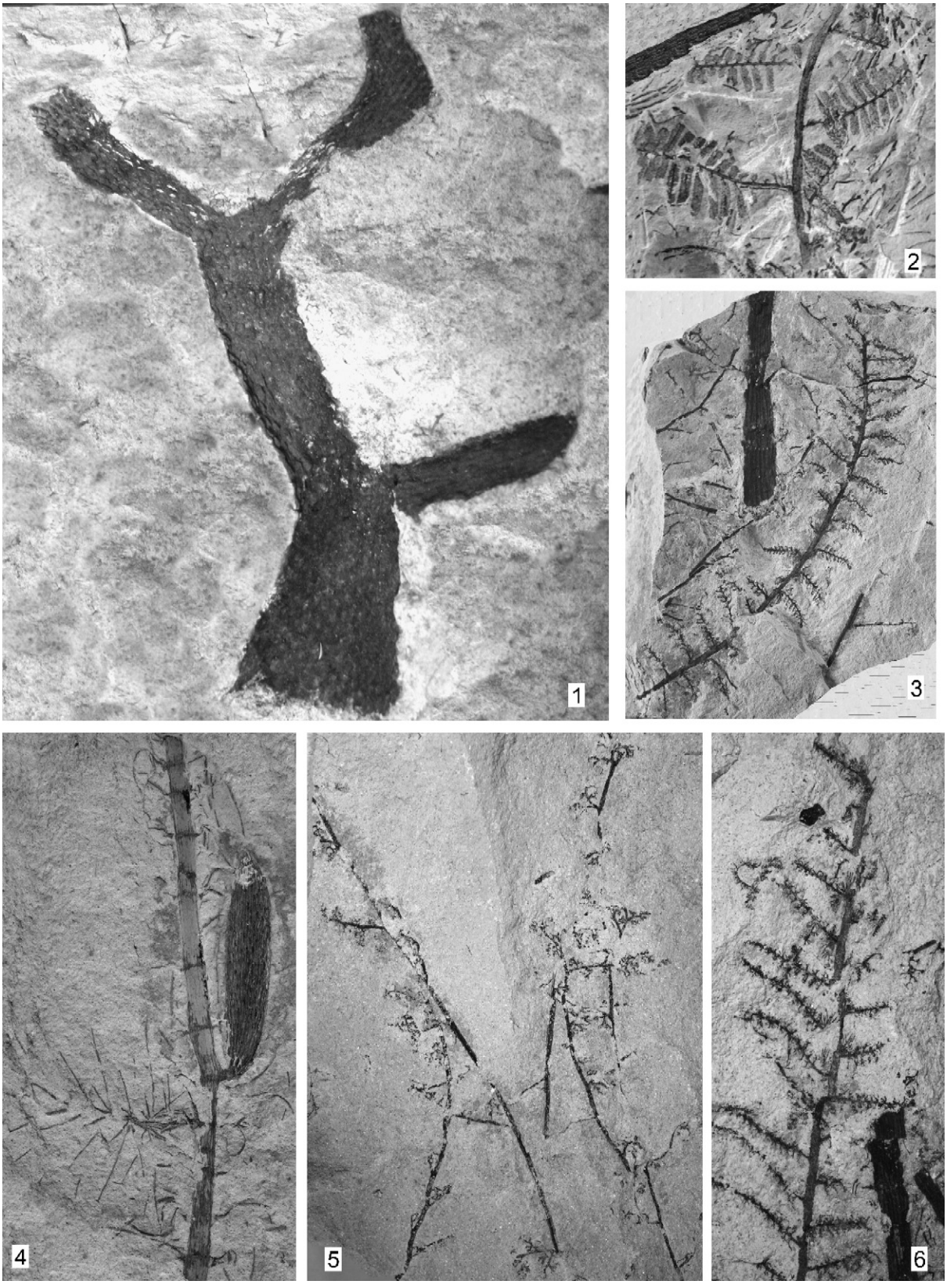

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Table 6
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from the Malé Přílepy Coalfield

Whetstone Horizon				Locality: Malé Přílepy near Beroun	
	Plant groups			Species/habits	
1	Lycopsida	Arborescent form (cone)		*Lepidostrobus sternbergii*	T
2	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes longifolius*	S
3				*Asterophyllithes grandis*	S
4		Sphenophylls		*Sphenophyllum wingfieldense*	U
5	Pteridospermopsida	Medullosalean pteridosperms		*Alethopteris distantinervosa*	S
6				*Alethopteris lonchitica*	S
7				*Laveineopteris loshii*	S
8				*Laveineopteris bohemica*	S
9				*Paripteris linguaefolia*	S
10				*Palaeoweischelia defrancei*	S
11				*Praecallipteridium n.* sp.	S
12		Lyginodendrid pteridosperms		*Sphenopteris spinosa*	V
13				*Dicksonites irregularis*	V
14	Cordaitopsida	Cordaites		*Cordaites borassifolius*	T
Number of morphospecies				14	
Estimated number of biological species				14	
Area of sampling				< 20 000 m^2	

Lepidodendron ophiurus are the most common species. *Lepidodendron simile*, *Lepidodendron acutum* Presl in Sternberg and *Omphalophloios feistmantelii* were sub-dominant elements whereas sigillarias are rare. Ferns and sphenopsids are each represented by 6 species. The most common are *Corynepteris angustissima*, *Sphenopteris cf. crepinii* and *Pecopteris aspidioides.* Present are two species of cordaites (not *Cordaites borassifolius*) and *Dicranophyllum dominii* Němejc. Pteridosperms are surprisingly absent in the revised set of samples.

– *Interpretation*: The potentially large area of sampling does not favour the interpretation of the studied plant association as a single plant assemblage. Instead, probably several, partly well-diversified and structured arborescent lycopsid-dominated plant communities are thought to have colonised this area.

4.3.3. Schoeller Mine, Libušín near Kladno

– *Origin and characteristics of the material*: The revised plant remains are preserved in loose blocks of the velká opuka tonstein collected at the coal mine tip during a single visit in 2003, a year after the closing of the mine. About 330 specimens were identified in the material, which was produced approximately during the last year of the mine's operation, when it worked in two long walls located about 1.5 km apart, and each representing an area of between 20 000 and 30 000 m^2. All the specimens are housed in a collection of the National Museum in Prague.
– *Local palaeogeography*: The Schoeller (Kladno) Mine is situated in the NW part of the Kladno Coalfield (Fig. 7) along southern margin of the Smečno Elevation. Before its closure this mine worked on marginal parts of coal seam located only tens to a

Plate IV. Complete assemblage of the Lower Radnice Coal from the Štilec opencast mine. Whetstone Horizon, Radnice Member, (Bolsovian).

1. *Spencerites n.* sp., (0.5×)
2. *Desmopteris alethopteroides*, (0.5×)
3. *Kidstonia heracleensis*, (0.7×)
4. *Calamites n.* sp. — part of the main axis with strobilus, (0.6×)
5. *Dendraena pinnatilobata*, (1×)
6. *Kidstonia heracleensis*, (1.2×).

Table 7
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from the Prago Mine in Kladno

Whetstone Horizon				Locality: Prago Mine, Kladno	
	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidostrobus sternbergii*	T
2			Stem	*Lepidodendron mannabachense*	T
3		Sub-arborescent form		*Polysporia robusta*	S
4	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes* sp.	
5			Stem	*Calamites cf. goeppertii*	S
6		Sphenophylls		*Sphenophyllum myriophyllum*	U
7				*Sphenophyllum cuneifolium*	U
8				*Sphenophyllum pseudoaquense*	U
9				*Sphenophyllum chaloneri*	U
10	Filicopsida			*Sphenopteris* sp.	V/L
11				*Senfenbergia plumosa*	V
12	Progymnospermopsida			*Rhacopteris bipinnata*	S
13	Pteridospermopsida	Medullosalean pteridosperms		*Alethopteris distantinervosa*	S
14				*Laveineopteris loshii*	S
15		Lygynodendrid pteridosperms		*Eusphenopteris nummularia*	V
Number of morphospecies				15	
Estimated number of biological species				14	
Area of sampling				~ 3 km^2	

few hundred metres away from palaeohigh on the slope of which the Upper Radnice Coal gradually wedges out. The present-day margin of the coal thus represents original margin of the former mire.

– *Taphocoenoses*: About 21 biological species have been identified (Table 12). The highest species diversity is exhibited by lycopsids and sphenopsids (Fig. 11). Ferns are less diversified being represented by 4 species, whereas there are only two species of seed plants, *Eusphenopteris nummularia* and *Cordaites* sp. The most common elements are *Sphenophyllum cuneifolium*, *S. chaloneri*, *S. pseudoaquense*, *Lepidodendron longifolius*, *Lepidodendron ophiurus sensu* Němejc (1947) and various calamite stems associated especially with *Asterophyllithes grandis* leafy shoots. Less common are *Lepidodendron acutum, O. feistmantelii* and fern *Sphenopteris cf. crepinii*. *C. angustissima*, abundant element at other localities, occurs only in two specimens.
– *Interpretation*: The estimated area of sampling indicates that this association may be derived from more than one plant assemblage. These included arborescent lycopsid forests, but abundant sphenophyte remains indicate also the possible existence of calamites-dominated assemblages (Fig. 11). Existence of another, drier peat substrate-preferring *Omphaloploios*-dominated assemblage, as an ecological counterpart of lepidodendrid forests, is corroborated by palynological study of the Upper Radnice Coal (Opluštil et al., 1999) as well as by rich findings of plant compressions in the velká opuka tuff bed. The understorey of former assemblages was represented especially by sphenophylls.

4.4. Floristic assemblages of the Z-tuff (Bolsovian)

– *Characteristics of the horizon*: This is the most important and widespread fossiliferous tuff bed (Mašek, 1973) of the Lubná group of coals, and is located in the roof of the Lower Lubná Coal or its clastic equivalent (Fig. 1). However, field observations indicate that plant fossils probably occur only where the tuff is underlain directly by coal. Ash content of this coal is often high attaining 30 to 60% of ash. This tuff is known only from the SW part of the Kladno–Rakovník Basin, from the surroundings of Rakovník (Fig. 4). The horizon consists of about 40 to 60 cm thick massive light grey vitrocrystallic tuff, with a kaolinitic matrix surrounding up to 2 mm large quartz and sanidine crystals. Despite the coarse grained character, this tuff bed yielded a quite well preserved *in situ* buried coal swamp and partly also clastic swamp flora. However, specimens stored in collections do not allow distinguishing between floras of these two habitats except observations in recently abandoned opencast mines. In the upper part of the

Table 8
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from the Svinná Coalfield

Whetstone Horizon				Lokality: Svinná near Radnice	
	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidostrobus sternbergii*	
2			Stems	*Lepidodendron mannabachense*	T
3				*Lepidodendron simile*	T
4				*Lepidodendron ophiurus*	T
5				*Lepidodendron longifolius*	T
6				*Lepidophloios acerosus*	T
7				*Asolanus* sp.	T
8				*Sigillaria pachyderma*	T
9				*Sigillaria rhytidolepis*	T
10				*Sigillaria rugosa*	T
11				*Sigillaria trigona*	T
12				*Sigillaria undulata*	T
13		Sub-arborescent/shruby forms		*Spencerites havlenae*	S
14				*Polysporia robusta*	S
15	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes grandis*	
16			Stems	*Calamites cistii*	S
17				*Calamites suckowii*	S
18		Sphenophylls		*Sphenophyllum myriophyllum*	U
19				*Sphenophyllum majus*	U
20				*Sphenophyllum brasense*	U
21				*Sphenophyllum cuneifolium*	U
22				*Sphenophyllum chaloneri*	U
23	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
24		Zygopterid ferns		*Corynepteris angustissima*	U
25				*Desmopteris longifolia*	U
26				*Desmopteris alethopteroides*	U
27		Other ferns		*Oligocarpia lindsaeoides*	V
28				*Zeilleria* sp.	V/U
29				*Senftenbergia plumosa*	V
30	Pteridospermopsida	Medullosalean pteridosperms		*Laveinopteris loshii*	S
31				*Alethopteris distantinervosa*	S
32				*Linopteris oblique*	S
33				*Macroneuropteris scheuchzeri*	S
34				*Neuropteris acutiloba*	S
35				*Lonchopteris* sp.	S
36		Lyginodendrid pteridosperms		*Mariopteris nervosa*	V
37				*Eusphenopteris obtusiloba*	V
38				*Eusphenopteris nummularia*	V
39				*Palmatopteris furcata*	V
40	Cordaitopsida	Dicranophytopsids		*Dicranophyllum* sp.	S
41		Cordaites		*Cordaites borassifolius*	T
Number of morphospecies				41	
Estimated number of biological species				39	
Area of sampling				~ 100 000 m^2	

horizon, a several centimetres thick layer of kaolinitic tuffite with drifted plant fragments occurs.

– *Origin and characteristics of the material*: Specimens were collected in the Rako Mine during the first half of the 20th century, and in the last three decades also in several small opencast mines extracting refractory claystones. All the mines operated in the Krčelák–Lubná Coalfield between Lubná and Rakovník. The estimated area of sampling reaches about 2 km^2. Material from the Rako Mine involved only several tens of specimens whereas that from opencast mines consists of more than one hundred specimens. Specimens are housed in the collection of the National Museum in Prague and the Czech Geological Survey in Prague respectively.
– *Local palaeogeography*: The Krčelák–Lubná Coalfield is located in the central part of the N–S striking central depression of the western part of the Kladno–Rakovník Basin (Pešek, 1994). The Lower Lubná Coal developed in planar mires, a few hundred metres

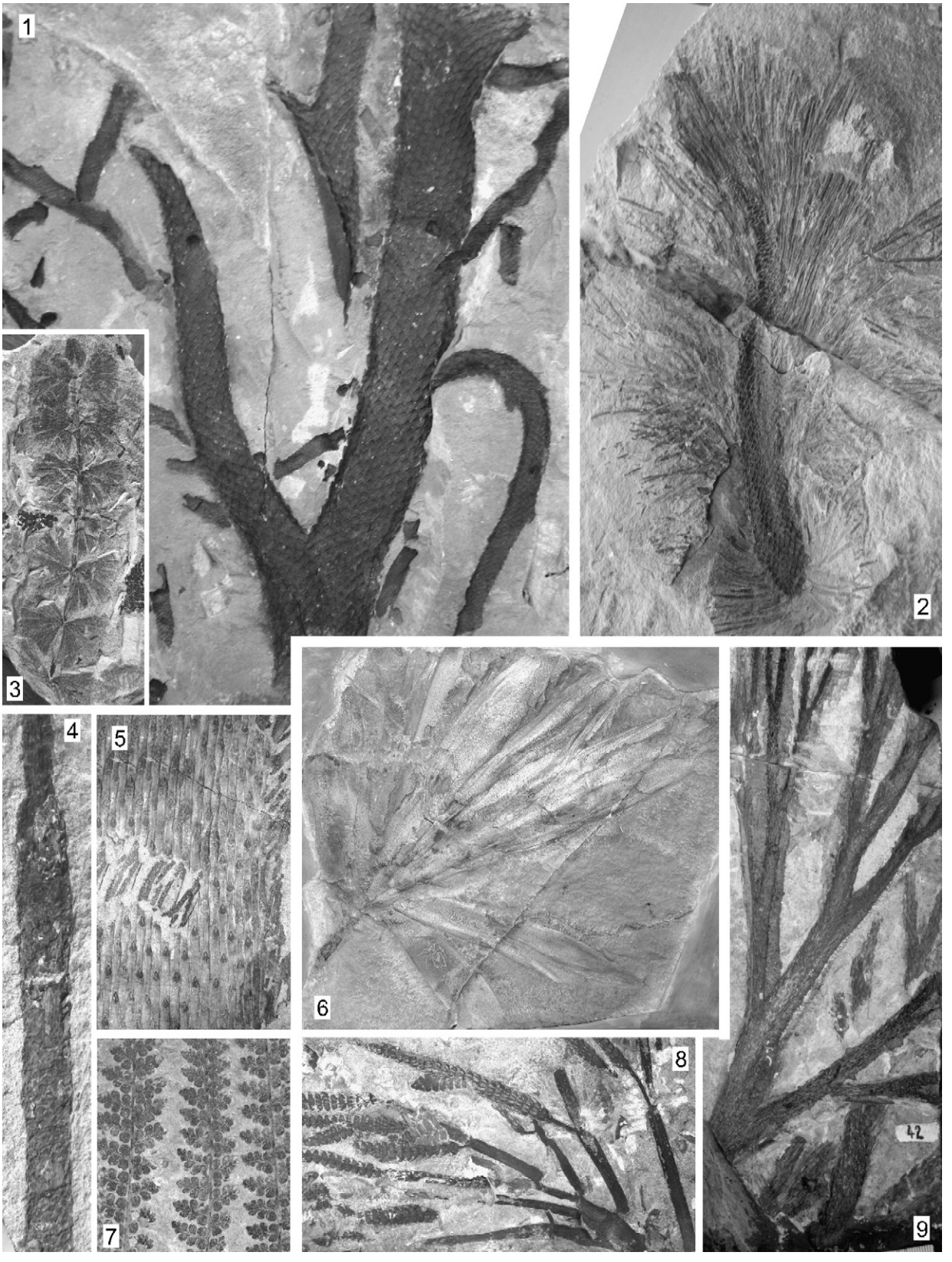
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Table 9
Species composition and estimated number of biological species of taphocoenoses of the Lower Radnice Coal preserved in the Whetstone Horizon from the Obrání míru Mine

Whetstone horizon				Locality: Obránců míru Mine, Zbůch	
	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Stems	*Asolanus camptotaenia*	T
2				*Lepidodendron dichotomum*	T
3				*Lepidophloios laricinum*	T
4				*Sigillaria aff. rugosa*	T
5	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes equisetiformis*	S
6		Sphenophylls		*Sphenophyllum cuneifolium*	U
7	Filicopsida	Zygopterid ferns		*Corynepteris angustissima*	U
8				*Desmopteris longifolia*	U
9		Other ferns		*Zeilleria schaumberg-lippeana (=? Sphenopteris cf. crepinii)*	V
10	Pteridospermopsida	Medullosalean Pteridosperms		*Alethopteris distantinervosa*	S
11				*Laveineopteris loshii*	S
12		Lyginodendrid Pteridosperms		*Sphenopteris spinosa*	V
13				*Diplotmema acutiloba*	V
Number of morphospecies				13	
Estimated number of biological species				13	
Area of sampling				< 100 m^2	

to more than 1 km large, scattered on a 3 or 4 km broad floodplain. The coal is characterised by a high ash and inertinite content and frequent thin sedimentary partings, indicating its formation in planar, occasionally flooded but relatively "dry" mires with fluctuating water table (Pešek, 1994; Opluštil et al., 1999).

– *Taphocoenoses*: About 18 biological species have been recognised among the revised specimens (Table 13, Plate 8). The highest species diversity occurs among sphenopsids, progymnosperms and pteridosperms, whereas experience from opencast mines indicates that the most abundant were *Omphalomphloios feistmantelii* with co-dominating calamites (Fig. 12). Typical elements of the locality are progymnosperms represented especially by *Palaeopteridium macrophyllum* Němejc, *Rhacopteris elegans* Ettingshausen and *Saaropteris guthorlii* Hirmer.
– *Interpretation*: The area that provided the samples was probably colonised by several plant assemblages now mixed in the revised set of samples. The presence of species absent or rare in other fossiliferous tuff horizons, e.g. the increased occurrence of progymnosperms and *Dicranophyllm* sp., may indicate the existence of special local ecological conditions. Observations in opencast mines indicates rather the existence of small groups dominated by one or two species, e.g. by *Omphalophloios feistmantelii*. In

Plate V. Some species of the Lower Radnice Coal from the Svinná in northern part of the Radnice Basin. Whetstone Horizon, Radnice Member, (Bolsovian).

1. *Lepidodendron mannabachense*, (0.25×)
2. *Lepidofloyos acerosus*, (0.3×)
3. *Sphenophyllum majus*, (0.7×)
4. *Polysporia robusta*, (0.25×)
5. *Sigillaria rhytidolepis*, (0.5×)
6. *Cordaites borassifolius*, (0.15×)
7. *Sphenopteris nummularia*, (0.5×)
8. *Palaeostachya elongata*, (0.3×)
9. *Lepidodendron lycopodioides*, (0.4×).

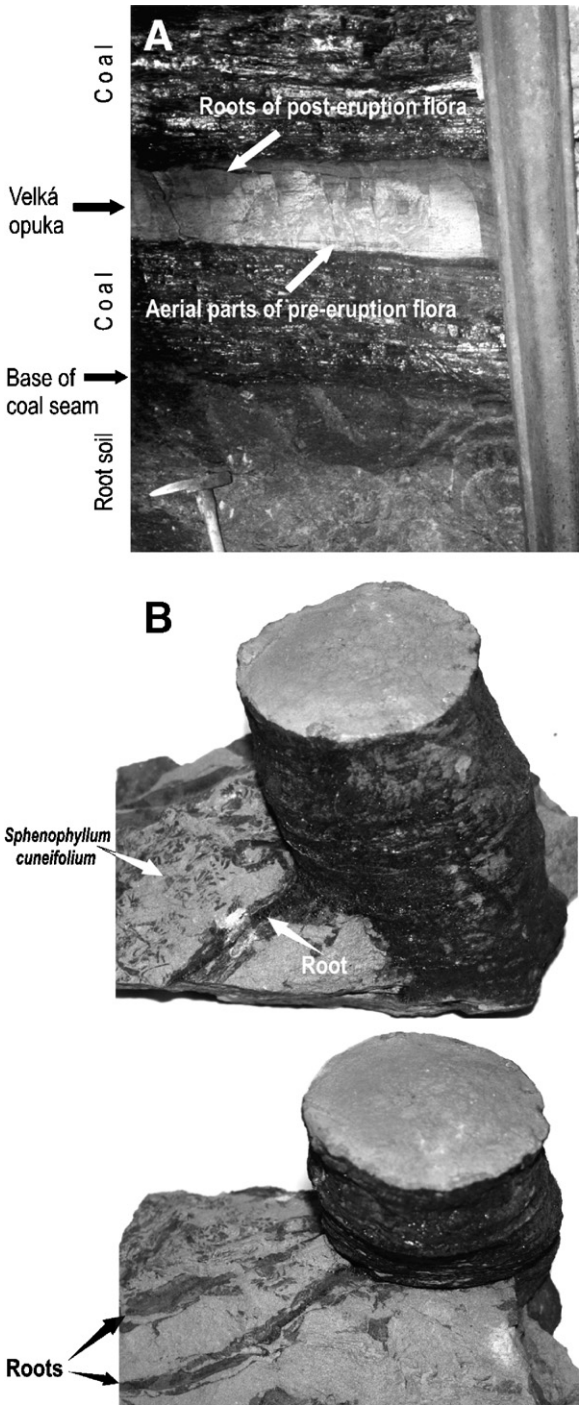


Fig. 10. A. Velká opuka tonstein near the base of the Upper Radnice Coal. Schoeller Mine, Kladno Coalfield. Coal laminae in the band belong to either pre-eruption (mostly at the base) or post-eruption (roots in upper part) flora. B. Upright calamite stem rooted in the coal. Adventitious (?) roots indicated by arrows refer for revitalisation of the plant damaged by volcanic ash fall and later rooting in the tuff bed. Note the *Sphenophyllum cuneifolium* foliage scattered around the stem. Collection of the Mining museum at Mayrau Mine in Vinařice near Kladno. Diameter of the calamite stem is 8 cm.

these opencast mines, the Z-tuff was directly underlain by the Lower Lubná Coal. Flora obtained from these opencast mines represents peat-forming elements. However, specimens stored in the National Museum, were collected in the Rako Mine during the first half of the 20th century by Němejc and miners who did not mentioned whether the Z-tuff was underlain by coal or by clastics. Both alternatives are possible, since in the part of coalfield operated by this mine, the Lower Lubná Coal was often replaced by kaolinitic mudstones to claystones with roots.

4.5. Floristic assemblages of the tonstein in coal of the Chotíkov group (Upper Westphalian D/Lower Cantabrian)

- *Characteristics of the horizon*: This is a pale green tuff, about 5 to 10 cm thick, in the roof of the lower of two seams in the middle of the Nýřany Member (Fig. 1) assigned to the Chotíkov group of coals. These about 80 cm to 1 m thick seams were exploited until 1992 in the Dobré štěstí Mine in the SE part of the Pilsen Basin.
- *Origin and characteristics of the material*: More than 75 specimens were collected at Dobré štěstí coal mine tip during a few visits in 1990–1992 (Šimůnek, 1994). All the specimens were derived from a single mining face ST 2920 (Šimůnek, 1994) which allows the area of sampling to be estimated at about 5000 m^2 or less. They are stored in the collection of the Czech Geological Survey in Prague.
- *Local palaeogeography*: The locality is situated in the SW part of the mining field of Dobré štěstí Mine near the present-day SE margin of the Pilsen Basin. The flora (of this volcanoclastic horizon) colonised mire, which formed on an extensive alluvial plain a few kilometres away from the former basin margin.
- *Taphocoenoses*: The floral assemblage was originally described by Šimůnek (1994) who identified 16 morphospecies including small epiphytic organisms (probably lichen) on a *Cordaites* leaf. After reinterpretation, about 10 biological species are now identified in the collection of studied specimens (Table 14). The most diversified plant groups are sphenopsids, ferns and pteridosperms represented by three species in each group (Fig. 13). However, the most common plant remains were *Cordaites* leaves and *Calamites* leafy shoots and stems. No lycopsids were found.
- *Interpretation*: The sampling area and relatively small number of species indicate that the described association probably represents a uniform plant assemblage characterised as mixed cordaites–calamites dominated forest with co-dominance of tree ferns and

Table 10
Species composition and estimated number of biological species of taphocoenoses of the Upper Radnice Coal preserved in the velká opuka tonstein from the excavation in the František Mine area in Otvovice near Kralupy nad Vltavou

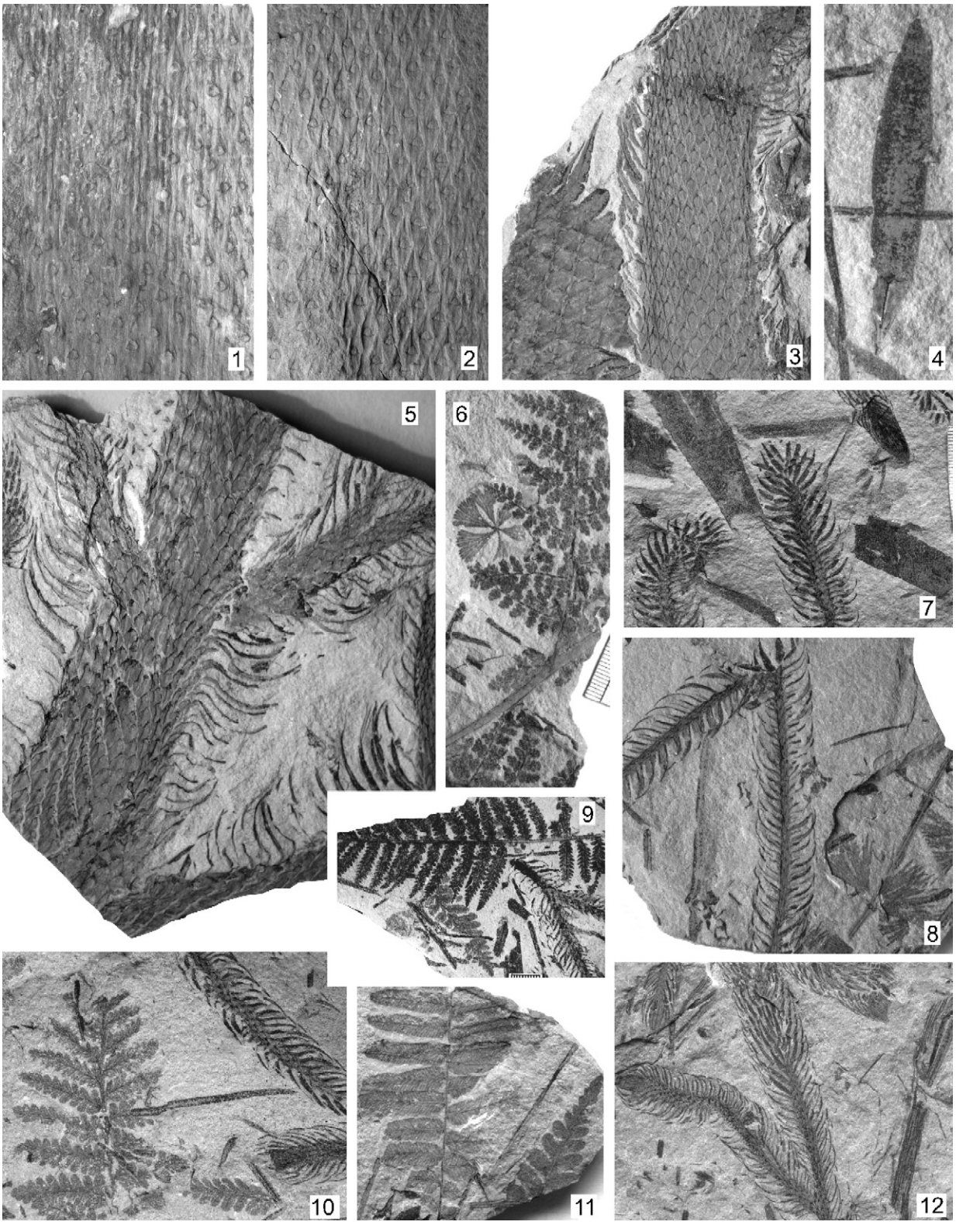
Velká opuka				Locality: Františ̌k Mine, Otvovice	
	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidocarpon majus*	T
2			Stems,	*Lepidodendron simile*	T
3			Leafy shoots	*Sigillaria diploderma*	T
4		Sub-arborescent form		*Omphalophloios feistmantelii*	S
5	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes longifolius*	
6			Stem	*Calamites* sp.	S
7		Sphenophylls		*Sphenophyllum majus*	U
8	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
9		Zygopterid ferns		*Corynepteris angustissima*	U
10				*Desmopteris longifolia*	U
11		Other ferns		*Sphenopteris* sp.	V/U
12				*Senftenbergia plumosa*	V
13	Cordaitopsida	Cordaites		*Cordaites* sp.	T
Number of morphospecies				13	
Estimated number of biological species				12	
Area of sampling				6 m^2	

pteridosperms (Fig. 13). Ground-cover consisted of *Sphenophyllum emarginatum* (Brongniart) Brongniart.

5. Discussion and interpretation

This analysis of peat-forming plant assemblages preserved in volcanoclastic horizons of the Late Palaeozoic continental basins of the Czech Republic is based on a set of specimens obtained from several localities during nearly two centuries of collecting. The methods of sampling therefore varies from the non-systematic collecting at coal mine tips or opencast mines, biased by selection of specimens, to the systematic excavation of plant-bearing tuff beds carried out by the present authors. Collections of plant fossils from particular localities therefore provide data of varying quality concerning the reconstruction of original plant assemblages. Taking into account the above mentioned "sampling background" of the revised plant fossil collections, three groups of data can be distinguished with respect to the reliability and quality of the information that they provided:

1. *Flora obtained from excavations carried out by present authors*
   This approach provides the best-quality data which allow most of the plant remains buried within a studied area to be found. Detailed identification and location of all the plant remains in the excavations reduced the bias caused by non-systematic sampling, including the preferred or random selection of particular species, or the omission of less attractive specimens. Taphocoenoses obtained from such excavations allow the reconstruction of not only the species composition of former phytocoenoses and their spatial variations, but also the distribution of individual plants and the density of vegetation cover. The obtained data also help avoid under- or over-estimation of some species and reflects the former "species richness". Among localities studied in such detail include Ovčín opencast mine, Štilec opencast mine and František in Otvovice.
2. *Collections from coal mine tips sampled by current authors during a short time span*
   This type of collection provides medium-quality data, which represents the fossil record from a larger area, usually of several thousands square metres, but still maybe representing a single plant assemblage. Careful sampling and identification of all the plant remains provide reliable information on species richness and composition of original phytocoenoses, but does not tell us anything about the spatial distribution and peculiarities of the plants and the density of the vegetation cover. Collections revised in this way include those from the coal tips of the Ida Mine, Schoeller Mine, A. Uxa Mine and Dobré štěstí Mine.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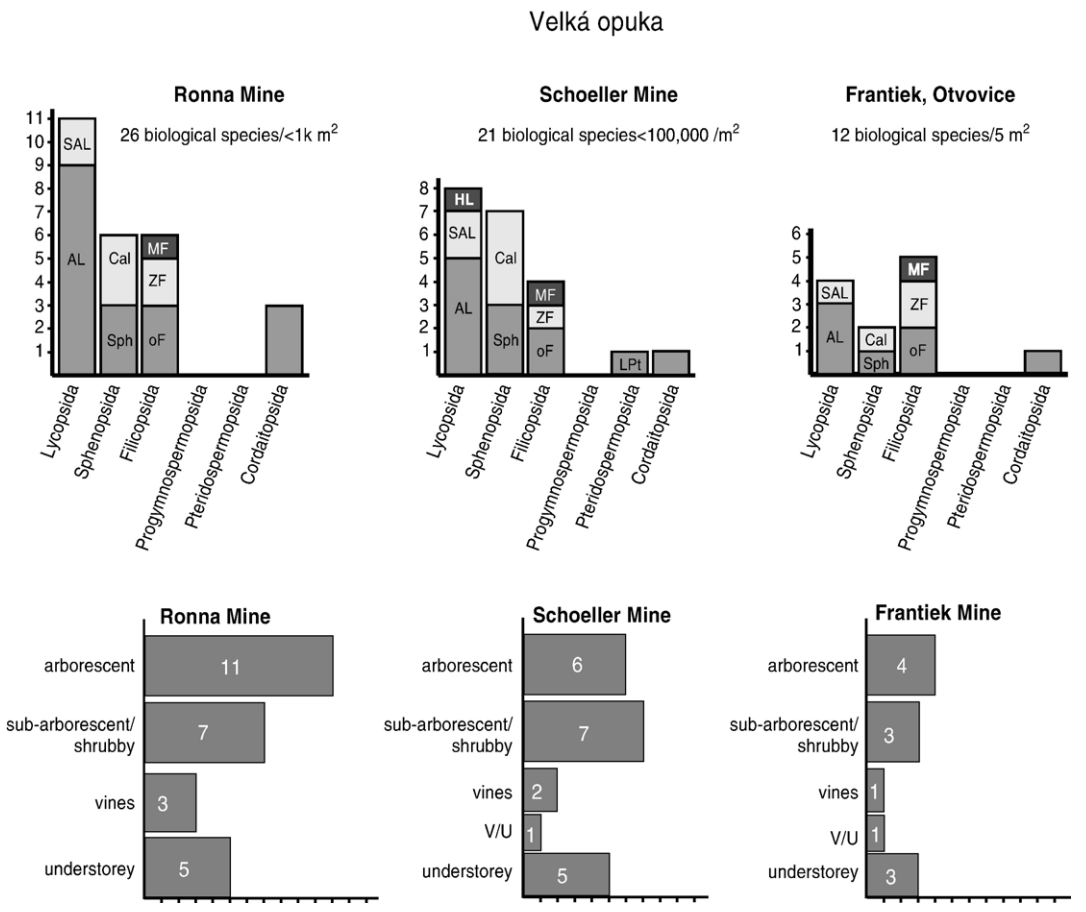

Fig. 11. Species and plant groups diversity and habitus of assemblages of the velká opuka tonstein of the Upper Radnice Coal at the studied localities in basins of central and western Bohemia. For explanation see Fig. 5.

3. *Historical collections formed by previous authors*
These collections consist of specimens taken by previous authors from localities which are now mostly inaccessible. The number of species is usually lower compared to the above mentioned groups, but the area of sampling is much larger. Specimens were derived from probably more than one uniform plant assemblage. Data are of limited value, providing only incomplete information on the composition of former plant assemblages. Neither the structure and spatial

Plate VI. Some species of the Upper Radnice Coal from the František Mine in Otvovice, SW of Kralupy and Vltavou. Velká opuka, Radnice Member, (Bolsovian).

1. *Sigillaria diploderma*, (0.75×)
2. *Omphalophloios feistmantelii*, sterile part of the stem, (0.6×)
3. Branch of *Lepidodendron simile* (sensu Němejc 1947), (0.5×)
4. *Lepidocarpon majus*, (0.7×)
5. *Lepidodendron simile* (*sensu* Němejc 1947), (0.7×)
6. *Sphenopteris* sp. and *Sphenophyllum majus*, (0.8×)
7. Leaves of *Cordaites* sp. and leafy shoots of *Lepidodendron simile* (*sensu* Němejc 1947), (0.5×)
8. Leafy shoots of *Lepidodendron simile* (*sensu* Němejc 1947) and *Sphenophyllum majus*, (0.75×)
9. Association of three species: *Senftenbergia plumosa*, *Pecopteris aspidioides* and leafy shoots of *Lepidodendron simile* (*sensu* Němejc 1947), (0.5×)
10. *Pecopteris aspidioides* and leafy shoots of *Lepidodendron simile* (*sensu* Němejc 1947), (0.5×)
11. *Desmopteris longifolia* and *Pecopteris aspidioides*, (0.7×)
12. Leafy shoots of *Lepidodendron simile* (*sensu* Němejc 1947) and small Calamite stem, (0.5×).

Table 11
Species composition and estimated number of biological species of taphocoenoses of the Upper Radnice Coal preserved in the velká opuka tonstein from the Ronna Mine in Kladno

Velká opuka — Lokality: Ronna Mine

	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidocarpon majus*	
2			Stems	*Asolanus* sp.	T
3				*Lepidodendron acutum*	T
4				*Lepidodendron longifolius*	T
5				*Lepidodendron ophiurus*	T
6				*Lepidodendron simile*	T
7				*Lepidophloios laricinum*	T
8				*Sigillaria diploderma*	T
9				*Sigillaria feistmantelii*	T
10				*Sigillaria pachyderma*	T
11		Sub-arborescent forms		*Spencerites havlenae*	S
12				*Omphalophloios feistmantelii*	S
13	Sphenopsida	Calamites	Leafy shoots	*Annularia radiata*	S
14				*Asterophyllithes grandis*	S
15				*Asterophyllithes longifolius*	S
16			Cones	*Palaeostachya ettingshausenii*	
17				*Palaeostachya pedunculata*	
18				*Palaeostachya elongata*	
19			Stem	*Calamites* sp.	
20		Sphenophylls		*Sphenophyllum majus*	U
21				*Sphenophyllum pseudoaquense*	U
22				*Sphenophyllum cuneifolium*	U
23	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
24		Zygopterid ferns		*Corynepteris angustissima*	U
25				*Corynepteris corraloides*	U
26		Other ferns		*Sphenopteris cf. crepinii*	V
27				*Hymenotheca globulifera*	V
28				*Sphenopteris stipullata*	V
29	Cordaitopsida	Dicranophytopsids		*Dicranophyllum dominii*	S
30		Cordaites		*Cordaites* sp. 1	T
31				*Cordaites* sp. 2	T
Number of morphospecies				31	
Estimated number of biological species				26	
Area of sampling				~ 1 km^2	

distribution of the plants, nor the richness of the individual species can be recognised. This group, however, includes most of the studied localities: Doubrava–Blatnice, Svinná, Obránců míru Mine and Malé Přílepy. The Krčelák–Lubná Coalfield, Prago Mine and Ronna Mine localities are of similar nature, however, part of the material was collected by some of the present authors. Thus, additional information on the character of the plant assemblages was obtained.

5.1. Comparison of plant assemblages of volcanoclastic horizons

A widespread fossiliferous tuff beds represent a record of a brief volcanic events that produced large quantities of volcanic ash which buried all the life over a vast area. The present analysis of floras preserved in such beds, either intercalated or overlying coal seams, has permitted the study of the structure of plant

assemblages that colonised the fossil mires. Comparison of plant assemblages of a particular tuff beds provides a unique opportunity to study differences and peculiarities in composition mire assemblages, whereas the comparative study of the floras from particular volcanoclastic horizons allows the persistence of plant assemblages and individual species in time to be traced, and the characterisation of their ecological demands.

5.1.1. Vegetation pattern of plant assemblages of the Whetstone Horizon

Plant fossils preserved in "bělka" at the base of the Whetstone Horizon represent coal-forming phytocoenoses of the Lower Radnice Coal. This coal is characterised by an increased ash content either dispersed or concentrated into thin discrete bands, indicating that it originated as a permanently to intermittently flooded planar eutrophic mire (Opluštil et al., 1999). Areas with a permanently exposed surface were probably rare, since there is no clear indication of the existence of domed mires. However, planar, only occasionally flooded mires with temporarily exposed surface could locally exist.

The list of species identified in the tuff bed at the base of the Whetstone Horizon, including those found at localities not investigated here, is estimated to represent about 95 biological taxa. However, species diversity at individual localities varies between 5 and 40 biological species, averaging at about 21 species (at the analysed localities). Taxon richness is usually related to the area of sampling and number of samples, and this depends on the methods of sampling used (see Section 5). Taphocoenoses derived from areas of more than 1 km^2 usually display the highest diversity related probably to the existence of several ecologically controlled assemblages.

Data obtained from excavations at the Ovčín and Štilec localities indicate no significant difference in the number of taxa between each excavation. Most species were found within an area of less than 50 m^2 at Ovčín and within less than 5 m^2 at Štilec. In contrast, associations derived from large areas are usually taxonomically rich due to ecological heterogeneity of the mire within this area. Thus the number of species in a "homogenous" part of the Lower Radnice Coal mire vegetation varied between 5 and 28. This represents part of the assemblage adapted to a particular ecological conditions.

Various types of plant assemblage have been found at the studied localities (Figs. 8 and 9 and Table 15). Most of them display variations of basic arborescent lycopsid forest pattern, with dense and taxonomically diversified stories, and ground-cover composed of ferns and small sphenopsids. Such assemblages existed at Ovčín, Obránců míru Mine, Doubrava–Blatnice and Svinná. Doubrava–Blatnice is unique for the occurrence of several "exotic" elements that have not been found elsewhere, e.g. the ferns *Sonapteris barthelii*, *Urnatopteris sp.*, *Rhodeites gutbieri*, *Discopteris doubravensis* or *D. kettneri*. Only few localities yielded a different non-lycopsid assemblage. Unusual, Medullosans-dominated mire phytocoenosis was encountered at Malé Přílepy, including some species of the genera *Praecallipteridium* and *Palaeoweischelia*. This is in contradiction with generally accepted ideas that pteridosperms colonised usually non-mire environments like levees or clastic floodplain (e.g. the assemblage from the A. Uxa Mine was characterised by the predominance of *Calamites* and tree ferns, whereas lycopsids were poorly represented. A monotonous and poorly structured assemblage was encountered at the Štilec opencast mine, consisting of only five herbaceous plant species that formed a dense, not more than 1.5 m tall ground-cover.

Concerning the complexity of the assemblage and its synecological relationships, the most apparent contrast is between the assemblages from the Ovčín and Štilec localities (Figs. 8 and 9 and Table 15) which probably represent opposite stages of plant succession. That from Štilec is interpreted as a pioneer assemblage that re-colonised a shallowed "lake" which developed on a former mire. Species that colonised this wet mire had a herbaceous reed-like habit, whereas arborescent lycopsids, typical of permanently flooded mires (DiMichele et al., 2002) did not occur. Moreover, most of the species found at Štilec have not been reported from any other locality (*Calamites n.* sp., *Dendraena pinnatilobata*, *Kidstonia heracleensis* and *Spencerites n.* sp.). In contrast, the assemblage from Ovčín is rich in species and diversity of growth forms. It indicates the coexistence of nearly 30 species with different living strategies that permitted a reduction of competition-stress and the fully exploitation of the colonised habitat. Therefore, the Ovčín assemblage is considered as the climax or pre-climax stage of the planar eutrophic mire succession.

Besides the species that occurred only at one locality, there are also several species which have been found at most of the studied localities, such as *Sphenophyllum myriophyllum*, *S. cuneifolium* and *Corynepteris angustissima*. Among lycopsids, the most common species are *Lepidodendron simile* and *Lepidodendron mannabachense*.

5.1.2. Vegetation pattern of plant community of the velká opuka tonstein

Species preserved in the velká opuka tonstein represent the plant assemblage of the Upper Radnice Coal mire. This mire covered a much larger area and so

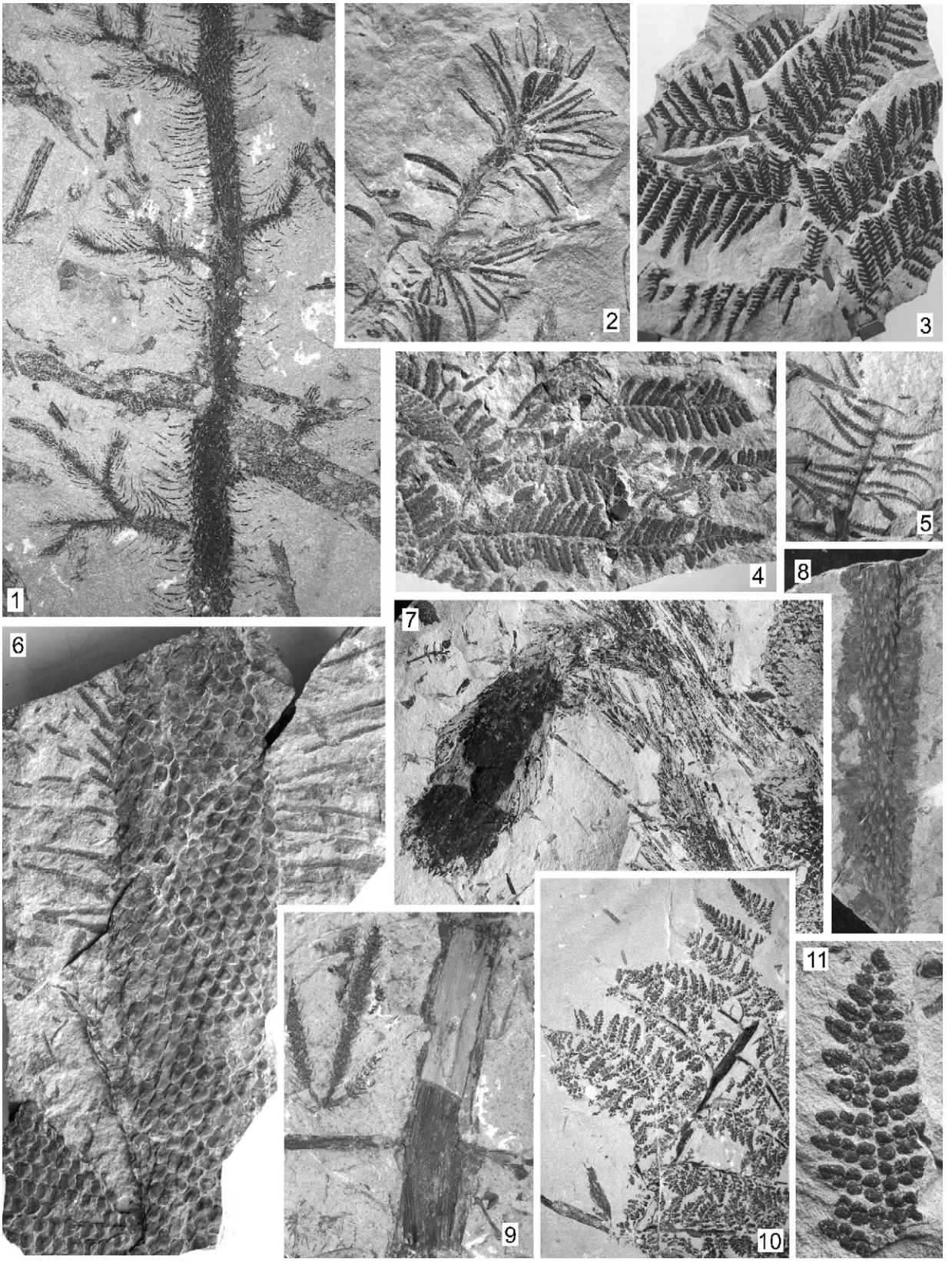
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Table 12
Species composition and estimated number of biological species of taphocoenoses of the Upper Radnice Coal preserved in the velká opuka tonstein from the Schoeller Mine in the Kladno Coalfield

Velká opuka — Locality: Schoeller Mine, Kladno

	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidocarpon majus*	
2			Stems	*Lepidodendron acutum*	T
3				*Lepidodendron longifolius*	T
4				*Lepidodendron ophiurus*	T
5				*Lepidodendron lycopodioides*	T
6				*Lepidophloios laricinum*	T
7		Sub-arborescent forms		*Spencerites havlenae*	S
8				*Omphalophloios feistmantelii*	S
9		Herbaceous forms		*Selaginella labutii n.* sp.	U
10	Sphenopsida	Calamites	Leafy shoots	*Annularia radiata*	S
11				*Asterophyllites grandis*	S
12				*Asterophyllites eqauisetiformis*	S
13				*Asterophyllites longifolius*	S
14			Cones	*Palaeostachya distachya*	
15				*Palaeostachya* sp.	
16			Stems	*Calamites sachsei*	
17				*Calamites* sp.	
18		Sphenophylls		*Sphenophyllum myriophyllum*	U
19				*Sphenophyllum pseudoaquense*	U
20				*Sphenophyllum cuneifolium*	U
21	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
22		Zygopterid ferns		*Corynepteris angustissima*	U
23		Other ferns		*Sphenopteris cf. crepinii*	V
24				*Renaultia* sp.	V/U
25	Pteridospermopsida	Lyginodendrid pteridosperms		*Eusphenopteris nummularia*	V
26	Cordaitopsida	Cordaites		*Cordaites* sp.	V
Number of morphospecies				26	
Estimated number of biological species				21	
Area of sampling				< 100 000 m^2	

represents a greater heterogeneity of sedimentary environments and consequently of ecological conditions compared to the Lower Radnice Coal (Fig. 7). Besides the permanently or temporarily flooded parts of the mire with standing water, there were also areas with exposed or only occasionally flooded peat surface. These

Plate VII. Plant association of the Upper Radnice Coal from the Ronna Mine in Kladno. Velká opuka, Radnice Member, (Bolsovian).

1. *Lepidodendron ophiurus* (*sensu* Němejc 1947), (0.5×)
2. *Lepidodendron acutum*, (0.5×)
3. *Senftenbergia plumosa*, (0.4×)
4. *Pecopteris aspidioides*, (0.4×)
5. *Corynepteris angustissima*, (0.25×)
6. *Omphalophloios feistmantelii*, part of the fertile zone, (0.5×)
7. Leafy shoot of *Lepidodendron longifolius* terminated with cone of *Achlamydocarpon cernuus*, (0.5×)
8. *Spencerites havlenae*, (0.5×)
9. *Calamites* sp. with *Palaeostachya* sp., (0.5×)
10. *Sphenopteris cf. crepinii*, (0.3×)
11. *Eusphenopteris cf. nummularia*, (1×).

Table 13
Species composition and estimated number of biological species of taphocoenoses of the Lower Lubná Coal preserved in the Z-tuff in the Lubná–Rako area SW of Rakovník

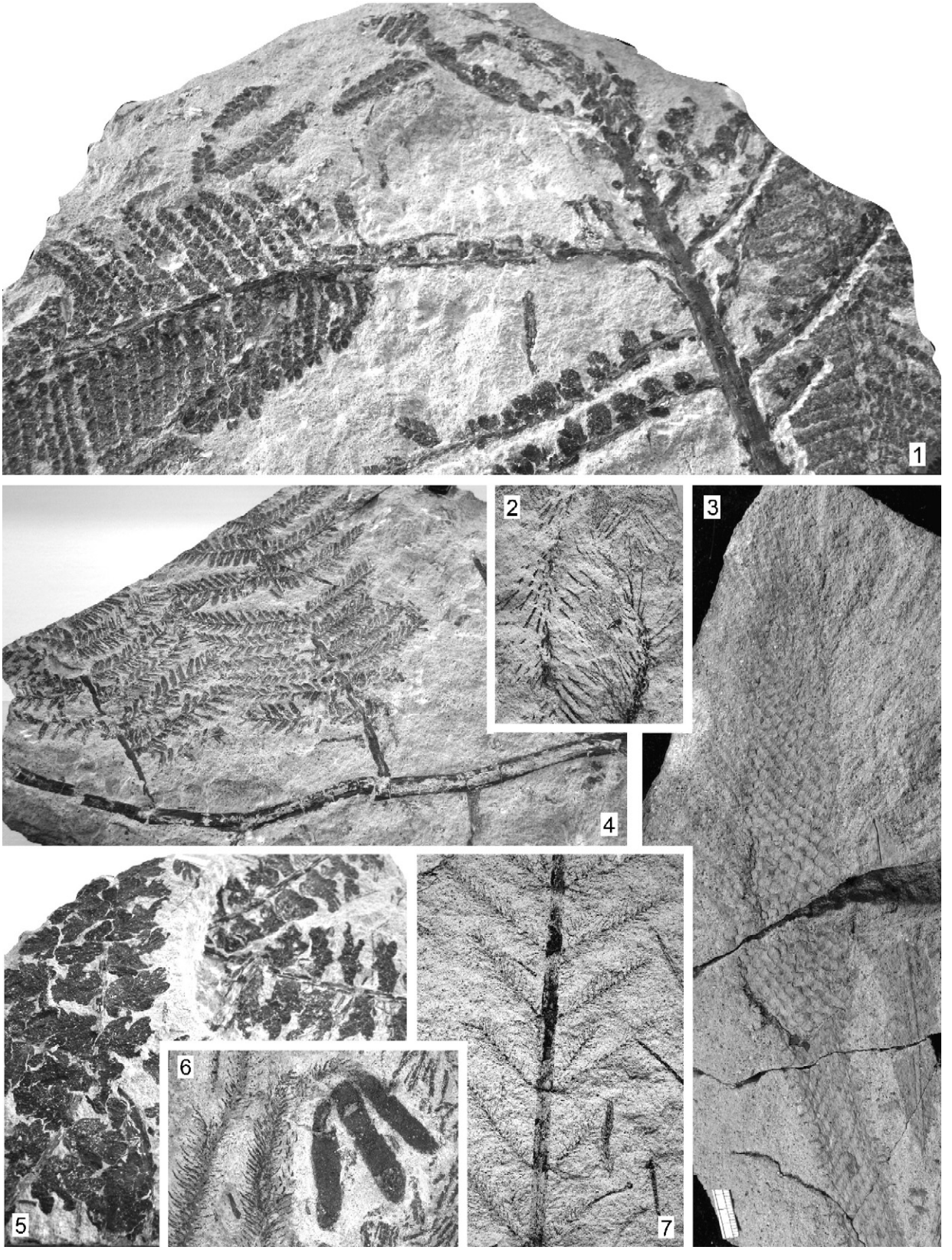
Z-tuf				Locality: Lubná - Rako	
	Plant groups			Species/habits	
1	Lycopsida	Arborescent forms	Cone	*Lepidocarpon majus*	T
2				*Flemingites* sp.	
3			Stem	*Lepidodendron cf. simile*	T
4		Sub-arborescent form		*Omphalophloios feistmantelii*	S
5	Sphenopsida	Calamites	Leafy shoots	*Asterophyllithes cf. equisetiformis*	
6				*Asterophyllithes cf. longifolius*	
7			Cones	*Palaeostachya cylindrica*	S
8				*Palaeostachya elongata*	S
9				*Palaeostachya raconensis*	S
10				*Cingularia typica*	S
11		Sphenophylls		*Sphenophyllum cuneifolium*	U
13	Filicopsida	Marattialean ferns		*Pecopteris aspidioides*	S
14		Other ferns		*Sphenopteris* sp.	V/U
15	Progymnospermopsida			*Lesleya* sp.	S
16				*Saaropteris guthoerlii*	S
17				*Rhacopteris elegans*	S
18				*Palaeopteridium macrophyllum*	S
19				*Discinites hlizae*	
20				*Discinites major*	
21	Pteridospermopsida	Medullosalean Pteridosperms		*Alethopteris lonchitica*	S
22				*Paripteris linguaefolia*	S
23				*Macroneuropteris scheuchzeri*	S
24	Cordaitopsida	Dicranophyllopsids		*Dicranophyllum* sp.	S
Number of morphospecies				24	
Estimated number of biological species				18	
Area of sampling				~ 2 km^2	

exposed areas might have been gently elevated, as indicated by the very low ash content (Opluštil et al., 1999). Palynological investigation of this coal in the Kladno Coalfield revealed a succession from a lycospore phase in the lower part of the coal, through a densospore phase in its middle part, to a lycospore phase in the upper part, and then followed by the roof shale interpreted as lacustrine sediment (Opluštil, 2003). The velká opuka tonstein is located in the lower part of the coal, just below the transition from the lycospore to the densospore phase. The mires of these phases probably differed in the water table level, the lycospore phase representing times when the water table was near or just above the peat surface, whereas the densospore phase represents drier conditions, with significant water table fluctuation (Smith, 1962; Opluštil et al., 1999).

In all, about 60 biological species were identified in the velká opuka. Some of these species (e.g. *Noeggerathia foliosa*, *N. intermedia*, etc.) were found only at localities which have not been studied in detail because of insufficient numbers of specimens. Only three localities yielded a satisfactory set, i.e. several tens of specimens at least. They significantly differ in the size of the sampling area, ranging from about 5 m^2 at František to a few square kilometres at the Ronna and Prago Mines. Surprisingly, the taxonomic diversity at all three localities varies only a little between 13 and 20 species. This suggests a more or less uniform plant assemblage, the basic pattern of which occupied an area

Plate VIII. Plant association of the Lower Lubná Coal from the Lubná Coalfield, mostly Rako Mine, Z-tuff, Radnice Member, (Bolsovian).

1. *Palaeopteridium macrophyllum*, (0.2×)
2. *Dicranophyllum* sp., (0.5×)
3. *Omphalophloios feistmantelii,* apical part of the fertile zone with shed sporangia in the lower part. Associated with *Lepidocarpon majus*. (0.3×)
4. *Alethopteris lonchitica*, (0.2×)
5. *Saaropteris guthorlii*, (0.25×)
6. *Lepidodendron cf. simile* (*sensu* Němejc 1947). Leafy shoots terminated by cones *Flemingites* sp., (0.3×)
7. *Asterophyllithes* sp. with isolated sporophylls of *Omphalophloios feistmantelii*, (0.25×).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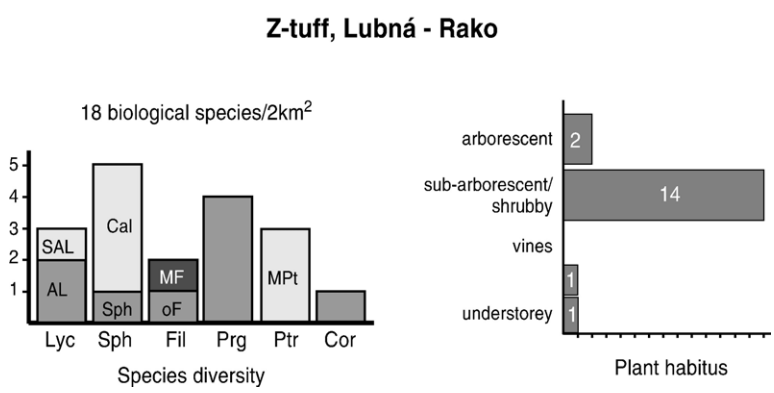

Fig. 12. Species and plant groups diversity and habitus of assemblages of the Lower Lubná Coal mire preserved in the Z-tuff in the Lubná–Rako area.

of a few tens of square metres. The area occupied by this assemblage is controlled by ecologically uniform conditions.

The assemblages of particular localities of the velká opuka tonstein are well-diversified and structured into various growth forms (Fig. 11). They are dominated by arborescent lycopsids with co-dominant calamites. Cordaites are sub-dominant whereas medullosans are absent from the studied localities. Only rarely, some neuropterids and alethopterids occurred among the specimens from other coal mines. Ground-cover plants were represented by zygopterid ferns, sphenophylls and probably also by small calamites. The most common species of this horizon are *Corynepteris angustissima, Sphenopteris cf. crepinii, Lepidodendron ophiurus, L. longifolius* and *Calamites cf. suckowii*.

5.1.3. Comparison of plant communities of studied volcanoclastic horizons

Taphocoenoses preserved in the studied tuff beds represent floras of five stratigraphically different horizons from two palaeogeographically different areas: central and western Bohemian area, and the Intra-Sudetic Basin in the Lusatian area. Stratigraphically they span an interval from the Duckmantian to the Cantabrian. These stratigraphic and palaeogeographic differences were taken into account when comparing the plant assemblages of these horizons. The most interesting results were provided by the comparison of the plant assemblages from the three stratigraphically related horizons of the Radnice Member (Bolsovian) from the central and western Bohemian area. These involve the Whetstone Horizon in the roof of the Lower Radnice Coal, the velká

Table 14
Species composition and estimated number of biological species of taphocoenoses of the Chotíkov Coal preserved mined at the Dobré štěstí Mine in the Pilsen Basin

Tuff of the coal of the Chotíkov group — Locality: Dobré štěstí Mine, Dobřany

	Plant groups			Species/habits	
1	Sphenopsida	Calamites	Leafy hoots	*Annularia stellata/mucronata*	
2			Cones	*Calamostachys tuberculata*	
3			Stems	*Calamites cisti*	S
4				*Calamites* sp.	S
5		Sphenophylls		*Sphenophyllum emarginatum*	U
6	Filicopsida	Marattialean ferns		*Pecopteris polypodioides*	S
7				*Pecopteris nýřanensis*	S
8				*Pecopteris unita*	S
9	Pteridospermopsida	Lyginodendrid Pteridosperms		*Dicksonites plueckenetii*	V
10				*Eusphenopteris nummularia*	V
11		Medullosalean Pteridosperm		*Neuropteris cf. plicata*	S
12	Cordaitopsida	Cordaites		*Cordaites* sp.	T
Number of morphospecies				12	
Estimated number of biological species				10	
Area of sampling				< 5000 m^2	

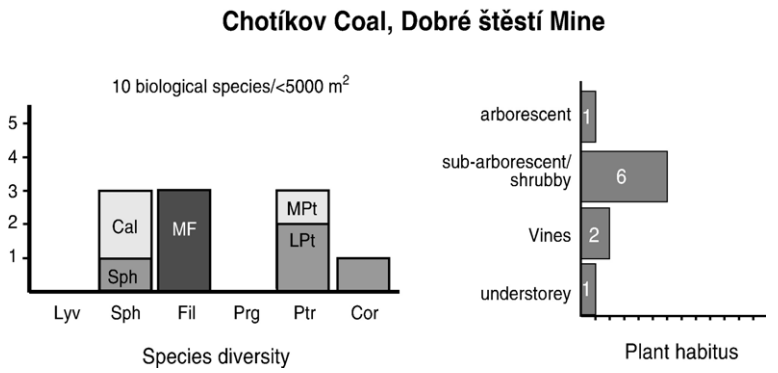

Fig. 13. Species and plant groups diversity and habitus of plants preserved in tonstein of the Chotíkov Coal mire in the Pilsen Basin.

opuka tonstein in the Upper Radnice Coal, and Z-tuff in the roof of the Lower Lubná Coal (Fig. 1). These tuff beds are usually between 10 and 20 m apart, separated by fluvial to lacustrine sediments. Comparing the total number of species, there is no significant difference between the Whetstone and velká opuka plant assemblages, whereas the lower diversity of the Z-tuff is related to the statistically small set of specimens in the collections compared to the Whetstone Horizon. This difference, however, disappears when comparing the list of species from the individual localities of the Whetstone Horizon with the Z-tuff collection.

Taxonomically, the flora of all these horizons is generally similar, but differ in the absence or presence of some species or even genera. Thus the assemblage of the Lower Radnice Coal preserved at the base of the Whetstone Horizon is characterised by the apparent absence of *Omphalophloios feistmantelii*, a sub-arborescent lycopsid plant that is very common in the two younger horizons, the velká opuka and Z-tuff. The absence of this species in the assemblage of the Lower Radnice Coal is in good agreement with the palynology of this coal, which completely lacks the spores of this plant (densospores). In the Kladno Coalfield, these spores first appear at the base of the Upper Radnice Coal but become abundant above the velká opuka where they spread rapidly over the whole mire due to lowering of the water table (Opluštil et al., 1999). The absence of *O. feistmantelii* in the Lower Radnice Coal and its presence in the overlying Upper Radnice Coal indicates that this species had to spread to central and western Bohemia sometime between the formation of these two seams. However, this interval consists mostly of re-deposited volcanic ash mixed with siliciclastic sediments deposited in a shallow lake produced by compaction of peat after the initial load of tuff bed (Opluštil et al., 1999). Rapid deposition indicated by up to 6 m tall upright stems permits the conclusion that immigration of *O. feistmantelii* to central and western Bohemia took place in a very short interval of probably a few hundred years.

There are several other species which are responsible for the differences in plant assemblages preserved in these three volcanoclastic horizons. Among them, *Lepidodendron mannabachense*, *L. lycopodioides*, *Sphenophyllum myriophyllum*, *Palaeopteridium macrophyllum* and *Cordaites borassifolius* are typical elements of the Lower Radnice Coal assemblage, which do not occur in the velká opuka in the Upper Radnice Coal. *Lepidodendron mannabachense* has not been reported from the velká opuka at all, but the spores of this plant (*Lycospora loganii*) are locally common in the Upper Radnice Coal (Bek and Opluštil, 2004). Another apparent difference is the general absence of medullosans in the velká opuka and their rich diversity in the Whetstone Horizon and Z-tuff (Figs. 8 and 12). *Laveineopteris loshii* is the most common representative of this plant group.

The assemblage of the velká opuka also differs by the presence of several species absent in the Whetstone Horizon: *Lepidodendron ophiurus* (sensu Němejc, 1947), *Lepidodendron acutum*, progymnosperm plants *Noeggerathia foliosa* and *N. intermedia* (not found at the studied localities). In contrast, there are several species which are common for assemblages of all three coals, e.g. *Lepidophloios laricinus*, *L. acerosus*, *Sphenophyllum cuneifolium* and *Pecopteris aspidioides*.

5.2. Comparison of the Radnice Member flora of peat and clastic substrates

The lists of species obtained from the tuff beds of the Radnice Member were further compared to the flora preserved in mudstones of the same unit. This comparison revealed substrate preference of particular taxa; i.e. which species preferred the peat substrate of mires,

Table 15
Lateral changes in species composition of plant assemblages of the Lower Radnice Coal preserved in the Whetstone Horizon of the studied localities

Species	Štilec	A. Uxa	M. Přílepy	Ovčín	Prago	Svinná	Doubrava	Zbuch
Lepidodendron simile				■		■	■	
Lepidodendron mannabachense					■	■	■	
Lepidodendron longifolium						■	■	■
Lepidodendron ophiurus						?		
Lepidodendron lycopodioides				■		■	■	
Lepidophloios laricinus		■		?		?		■
Lepidophloios acerosus				■		■		
Asolanus camptotaenia						■		■
Sigillaria pachyderma						■		
Sigillaria undulata						■		
Sigillaria trigona						■		
Sigillaria rugosa						■		■
Sigillaria rhytidolepis						■		
Polysporia robusta					■	■		
Spencerites havlenae				■		■		
Spencerites n. sp.	■							
Calamites suckowii		■				■		
Calamites n. sp.	■							
Sphenophyllum majus				■		■	■	
Sphenophyllum cuneifolium		■			■	■	■	■
Sphenophyllum myriophyllum		■		■	■	■	■	
Sphenophyllum pseudoaquense				■	■			
Sphenophyllum brasense				■		■		
Pecopteris aspidioides		■		■		■	■	
Pecopteris pennaeformis		■						
Corynepteris angustissima	■	■		■		■	■	■
Corynepteris winslowii							■	
Desmopteris longifolia		■		■		■	■	■
Sphenopteris cf. Crepinii		■					■	■
Desmopteris alethopteroides	■					■		
Senftenbergia plumosa				■	■	■		
Dendraena pinnatiloba	■							
Kidstonia heracleensis	■							
Diplotmema acutiloba								■
Oligocarpia lindsaeoides				■		■		
Crossotheca nyranensis							■	
Sonapteris barthelii							■	
Rhodeites gutbieri							■	
Rhodeites subpetiolata							■	
Urnatopteris sp.							■	
Discopteris kettneri							■	
Discopteris doubravensis							■	
Zeilleria zodrowii							■	
Zeilleria avoldensis							■	
Zeilleria frenzlii							■	
Palaeopteridium macrophyllum							■	
Rhacopteris bipinata		■			■			

Table 15 (*continued*)

Species	Štilec	A. Uxa	M. Přílepy	Ovčín	Prago	Svinná	Doubrava	Zbůch
Alethopteris distantinevosa			■		■	■		■
Alethopteris lonchitica			■					
Paripteris linguaefolia			■					
Macroneuropteris scheuchzeri						■	■	
Lonchopteris sp.						■		
Laveineopteris bohemica			■					
Laveineopteris loshii			■	■	■	■	■	■
Palaeoweischelia defrancei			■					
Praecallipteridium bohemica			■					
Sphenopteris cf. mixta				■				
Dicksonites irregularis			■					
Eusphenopteris nummularia		■		■	■	■	■	
Eusphenopteris spinosa			■					■
Palmatopteris furcata				■		■		
Cordaites borassifolius			■	■		■	■	

which the siliciclastic subtrates of flood plain environment, and which were tolerant to both.

Most of the compared species (usually taxonomically easily identifiable) appeared in both types of substrates (Table 16). There might be differences in the richness of their occurrence, although some species are common in both types (e.g. *Lepidodendron simile*, *L. acutum*, *Lepidophloios laricinus*, *L. acerosus*, *S. cuneifolium*, *S. myriophyllum*, *Pecopteris aspidioides*, *Senftenbergia plumosa* etc.). *Lepidodendron mannabachense* occurs in both types of substrate; its leafy shoots and fructifications are common fossils in the Whetstone Horizon (Lower Radnice Coal, Plate 3) whereas bark compressions/impressions have not yet been found here. No evidence of that lycopsid has yet been observed in the velká opuka in the Upper Radnice Coal except for its spores. However, bark and leafy shoots of *Lepidodendron mannabachense* appear again in the roof shale of this coal.

Only a few species preferred one type of substrate. Specialists on peat substrates include *Lepidodendron longifolius*, *L. ophiurus* (sensu Němejc, 1947), *L. lycopodioides*, *Omphalophloios feistmantelii*, *Spencerites havlenae*, *Laveineopteris loshii* and *Cordaites borassifolius*. Purely clastic substrates were preferred by *Lepidodendron aculeatum*, *Calamites undulatus* and *Laveineopteris bohemica* (Table 16).

There is also a difference in growth habit in the assemblages from peat and clastic substrates. Those from clastic substrates are dominated by larger species of arborescent lycopsids, *Calamites* and *Cordaites*. Peat-forming species of these genera are usually represented by taxa of smaller habit compared to the species from clastic substrates. The diameter of trunk of "coal-forming" lepidodendrons (e.g. *Lepidodendron ophiurus*, *L. lycopodioides*, *L. longifolium* etc.) is usually not larger than 20 to 30 cm and their height is estimated to be about 15 to 20 m maximum, whereas trunk of *Lepidodendron aculeatum*, a giant of clastic floodplain, often reaches more than 1 m in diameter and was probably over 30 m high. Similarly, calamites of peat subtrates are mostly smaller plants with compressed pit casts only several centimetres wide. Most of them were probably not higher than 5 m whereas *Calamites undulatus* Sternberg, the most common arborescent sphenopsid of the clastic substrates of the Radnice Member, could reach a height of up to 10 m or more. The same scenario is followed by *Cordaites*. Excavations at the Ovčín locality indicate that *Cordaites borassifolius*, the most common species of the Whetstone Horizon, was only about 15 to 20 m tall tree but some *Cordaites* species of the clastic substrates could have been fairly large trees. Moreover, species diversity of *Cordaites* in the peat substrates is generally lower in comparison to the clastic substrates.

5.3. Comparison of plant assemblages of fossiliferous tuff beds with plant assemblages derived from coal-balls

Results of analysis of peat-forming assemblages preserved in volcanoclastic beds of Westphalian and

Table 16
Stratigraphic distribution of taxa buried in the three studied volcanoclastic beds and siliciclastics of the Radnice Member and their substrate preference

Plant groups	Species	Peat substrates			Clastic substrates
		WH	VO	Z-tuff	
		LRC	*URC*	*LLC*	
Lycopsida	*Lepidodendron aculeatum*	?			
	Lepidodendron mannabachense				
	Lepidodendron acutum				
	Lepidodendron simile				
	Lepidodendron longifolium				?
	Lepidodendron ophiurus				
	Lepidodendron lycopodioides	?			?
	Lepidophloios laricinus				
	Lepidophloios acerosus				
	Sigillaria diploderma				
	Omphalophloios feistmantelii				?
	Spencerites havlenae				
	Polysporia robusta				
Sphenoppsida	*Calamites undulatus*				
	Calamites suckowii			?	
	Sphenophyllum majus			?	
	Sphenophyllum cuneifolium				
	Sphenophyllum myriophyllum				
	Sphenophyllum pseudoaquense				
Filicopsida	*Pecopteris pennaeformis*				
	Pecopteris aspidioides				
	Corynepteris angustissima				?
	Desmopteris longifolia				
	Sphenopteris crepinii				
	Senfenbergia plumosa				
	Hymenotheca globulifera				
	Zeilleria avoldensis				
	Zeilleria frenzlii				
Progymnospermopsida	*Noeggerathia foliosa*				
	Palaeopteridium macrophyllum				
	Rhacopteris bipinnata	?			?
	Saaropteris guthorlii				
Pteridospermopsida	*Alethopteris distantinervosa*				
	Alethopteris lonchitica				
	Paripteris linguaefolia				
	Macroneuropteris scheuchzeri	?			
	Laveinopteris bohemica				
	Laveinopteris loshii	?			
	Sphenopteris mixta	?			?
	Eusphenopteris nummularia				
	Palmatopteris furcata				
Cordaitopsida	*Cordaites borassifolius*	?			

LRC – Lower Radnice Coal, URC – Upper Radnice Coal, LLC – Lower Lubná Coal, WH – Whetstone Horizon, VO – velká opuka, ▒ – dominant preference of only one type of substrate.
Occurrence: ? — doubtfull or exceptional, ····· rare, ——— common, ▬ abundant.

Early Stephanian age from the continental basins of the Czech Republic allow comparison with coal-ball data from paralic basins (e.g. DiMichele et al., 2002). However, direct comparison of species is impossible because of the different mode of preservation. Only diversity and vegetation patterns of the assemblages can be compared.

Peat-forming assemblages of the Radnice Member coals (Bolsovian) and those of the paralic basin mires (e.g. Galtier, 1997; Lyons et al., 1997; DiMichele et al., 2002) provide various ecologically controlled vegetation patterns of the same arborescent lycopsid-dominating plant assemblage. An interesting exception is the pteridosperm-dominated assemblage described from Spain indicating a different sedimentary conditions (Galtier, 1997) perhaps similar to those of some localities of the Whetstone Horizon (e.g. Malé Přílepy). In most other cases the Westphalian coal-ball assemblages display tree lycopsids dominating pattern like in the most cases of here performed localities.

DiMichele et al. (2002) mentioned that the floras of the most important coal seams of the Illinois Basin, appear to be homogeneous over a vast area whereas significant lateral differences in composition have been observed within the same stratigraphic horizon of mires of the Radnice Member. This might be due to differences in the area of the mires; those of the Radnice Member were small, not larger than a few square kilometres in average, and mires over 20 km^2 were uncommon (Fig. 7). The distance from the mire margin to its centre only rarely exceeded 3 km. Individual mires were separated either by fluvial channels, clastic floodplain or, most often, by basement palaeohighs. In contrast, mires of Illinois and other paralic basins occupied area of several thousand square kilometres and central parts of the mires could provide homogeneous conditions.

5.4. Ecological structure in the studied mires (successional patterns of mires)

This revision of volcanoclastic taphocoenoses from different localities revealed a co-existence of various ecologically-controlled peat-forming assemblages and their pattern of variation. Most of them represent modifications of principally the same basic arborescent lycopsid-dominated assemblage. Pattern variations concern enrichment in some of the other plant elements (pteridosperms, cordaites, progymnosperms) indicative of a slightly different habitat. However, some of the associations may represent assemblages with very different ecological demands, as corroborated by palynological analysis of whole-seam profiles (e.g. Smith, 1962; Opluštil et al., 1999). They revealed alternating densospore and lycospora phases, interpreted either as a record of succession from wetter planar rheotrophic to drier domed ombrotrophic stage of mire development, or as an oscillation between mires with a standing water table and mires with exposed, only an occasionally flooded peat surface.

The *Lycospora* phase is correlated with the lepidodendrid framework of peat-forming plant assemblage, whereas the *Densospora* phase represents an assemblage dominated by *Omphalophloios* lycopsids of sub-arborescent habit. DiMichele and Phillips (e.g. 1994) also noted that the Westphalian lepidodendrids had partitioned wetland habitats along generic lines, where *Lepidodendron* and *Lepidophloios* colonised the wettest standing water habitats, whereas *Diaphorodendron* preferred exposed to partially submerged peat substrates, and *Paralycopodites* grew on variably exposed to submerged peat. However, current studies at the Ovčín locality proved the co-existence of various lepidodendrid genera within a small area: *Lepidophloios acerosus*, *Lepidodendron mannebachense* (=*Lepidodendron* s.s.), *Lepidodendron simile sensu* Němejc (1947) (? *Paralycopodites* with *Flemingites*-type of fructifications) and *Lepidodendron lycopodioides* (the affinity of which to anatomically-defined genera remains still poorly constrained). Consequently, high-resolution environmental interpretations of Westphalian wetland habitats have to distinguish not only lepidodendrid genera but even individual species.

Taphocoenoses of the studied localities differ in the dominance of particular plant groups, which most probably indicate environmental variations. As stated earlier, most of the studied taphocoenoses were dominated by lepidodendrid lycopsids (localities: Ovčín, Svinná, Obránců míru, Ronna, Schoeller and František mines) with co-dominance or sub-dominance of other basic plant groups, most often with sphenopsids and ferns. A purely lepidodendrid forest assemblage without ground-cover indicating open water table conditions (DiMichele and Phillips, 1994) has not been proved at any of the studied localities. On the contrary, lepidodendrids usually comprise only a part of a high-diversified assemblage with a complex structural pattern, including well-developed ground-cover and shrubs, and should rather be called mixed assemblages. A few localities provided evidence for the existence of assemblages dominated by other plant groups (non-lycopsid). The mire of the Malé Přílepy Coalfield was dominated

by pteridosperms (mostly medullosans) whereas assemblages from the A. Uxa Mine or Štilec opencast mine were characterised by a predominance of calamites and ferns. Phytocoenoses of the 3rd Žd'árky Coal from the Ida Mine consisted of a mixed pteridosperm–cordaites–fern–calamites dominated assemblage.

6. Conclusion

A study of the taphocoenoses of volcanoclastic horizons has proved the co-existence of various plant assemblages. Most of them are lepidodendrid forests with well-developed and highly-diversified ground-cover and shrubs, indicating only a gently raised water table above the peat surface. Only a few assemblages show a different domination pattern in which other plant groups are more diversified and numerically more frequent than the lycopsids. Most of them are mixed assemblages with co-dominance of two or more basic plant groups. For examples, a mixed pteridosperm–cordaites–fern–calamites assemblage occurs in the 3rd Žd'árky Coal from the Ida Mine in the Intra-Sudetic Basin, and a calamites–fern dominated assemblages occurs in the Lower Radnice Coal at the localities A. Uxa Mine and Štilec. The only assemblage characterised by a predominance of only one basic plant group is the pteridosperm-dominated assemblage of the Lower Radnice Coal from the Malé Přílepy locality.

Species diversity and structural complexity of the assemblages at individual localities vary significantly from low to highly-diversified phytocoenoses with a complex structural pattern. The simplest assemblage, which consists of five ground-cover plant species, was encountered at the Štilec opencast mine. It probably represents an initial stage of hydroseral succession. On the opposite, the diversified lepidodendrid forests with a complex structural pattern and synecological relationships among plants with different life-strategies probably represent a climax (or pre-climax) member of this succession. Such phytocoenoses have been found at localities Ovčín, František Mine or Svinná Coalfield. An environmental complement of this assemblage is another lycopsid assemblage dominated by *O. feistmantelii*, which colonised relatively drier peat substrates of planar mires.

A comparison of the floras of the tuff beds in this study has revealed the persistence of similar lycopsid-dominated assemblages in the continental basins of central and western Bohemia during the Bolsovian. They differ in species composition and/or frequency of occurrence of individual taxa. They have allowed a comparison of the peat-forming flora preserved in tuffs with the flora of the clastic substrates recorded in floodplain mudstones or roof shales. Most of the taxa occur in both types of substrates. Some of these species however display a tendency to prefer one type of substrate and only a few species were adapted predominantly to one type of substrate. Peat substrates were preferred especially by *Cordaites borassifolius, Lepidodendron lycopodioides*, *L. longifolius*, *L. ophiurus*, *Omphalophloios feistmantelii*, *Spencerites havlenae* and *Laveineopteris loshii*. A strong preference for clastic substrates was typical for *Lepidodendron aculeatum*, *Calamites undulatus* and *Laveineopteris bohemica*.

The study of plant assemblages preserved in volcanoclastic horizons clearly provides great potential for further progress in understanding Pennsylvanian wetland ecosystems.

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