T^0 peat-forming plant assemblage preserved in growth position by volcanic ash-fall: A case study from the Middle Pennsylvanian of the Czech Republic

Stanislav Opluštil, Josef Pšenička, Jiří Bek, Jun Wang, Zhuo Feng, Milan Libertín, Zbyněk Šimůnek, Jan Bureš & Jana Drábková

A Middle Pennsylvanian tuff bed (the Bělka bed) in the roof of the Lower Radnice Coal bears T^0 peat-forming vegetation preserved in growth position. This vegetation has been studied in detail at the 12 hectares large Ovčín coal deposit in the southern part of the Radnice Basin. Documentation of the fossil record in six excavations and that previously collected in the former opencast mine allowed for a detailed reconstruction of the local peat-forming lepidodendrid-cordaitalean forest structured into well-developed stories. It consists of about 33 species, which colonized the occasionally flooded planar peat swamp precursor of the Lower Radnice Coal. The canopy story of this vegetation was dominated by *Lepidodendron (Paralycopodites) simile*, *L. lycopodioides*, *Lepidophloios acerosus* and *Cordaites borassifolius*. They formed a relatively dense canopy, locally interrupted with significant gaps allowing development of a rich groundcover that together with liana-like plants represents the most diverse part of the forest. A less diverse understory composed of calamites, medullosan pteridosperms and *Psaronius* tree ferns displays a patchy distribution pattern presumably related to density of the canopy. The minimal area that sufficiently represents the pattern of this forest phytocoenosis is estimated to be about 200 m^2, although lower stories are well represented even within much smaller areas of about 60 m^2. Slight heterogeneity in the population density of dominant taxa (*Cordaites* vs. lepidodendrid lycopsids) was documented across the Ovčín coal deposit. The fossil record of the Bělka tuff bed also indicates that the coal-forest colonizing the peat swamp prior the generation of forest killed by volcanic ash fall, was destroyed, presumably due to long-lasting flooding and thus suggests that catastrophic events were probably a relatively common part of the evolution of peat-forming Pennsylvanian successions. • Key words: Pennsylvanian, T^0 plant assemblage, coal forests, volcanic ash beds, Radnice Basin.

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Fossil forests buried in growth position are quite common in Pennsylvanian successions. They usually occur on discrete horizons often associated with certain types of facies, thus indicating that their origin is related to particular environments and processes. Fundamental controls on the origin of these phenomena are related to rapid burial in a geological instant, preserving the plant relationships in space and time and removing or reducing many taphonomical biases (Opluštil *et al.* 2009a, DiMichele & Falcon-Lang 2011, Rößler *et al.* 2012). Such conditions are achieved especially by crevasse splay deposition, earthquake-induced subsidence which catastrophically drops the vegetated area beneath the water table, rapid eustatic sea-level rise, permineralization of vegetation by hot springs, or its burial by ash falls proximal to volcanic centres (DiMichele & Falcon-Lang 2011). Particular mechanisms and their "products" differ in the fidelity with which they preserve the ecosystem. Volcanic ash falls onto standing vegetation are one of the most reliable means to preserve a geological snapshot due to simple and rapid burial. Burial of vegetation by an air-fall volcanic ash avoids nearly entirely the effects of time averaging and transport of plant remains from the place of growth to the site of deposition, thus generating real T^0 plant assemblages (Johnson 2007). Such taphocoenoses often preserve even subtle ecological details, *e.g.* lianas scrambling along trees, epiphytes still attached to supportive plant (= phorophyte) or such exceptional details as an arachnid preserved on a *Cordaites* leaf (Opluštil *et al.* 2009a, Selden & Penney 2010, Pšenička & Opluštil 2013). Limited taphonomic bias makes these assemblages ideal for the analysis of tree density, spatial heterogeneity, assemblage diversity, whole-plant reconstructions, assessment of plant interactions and other ecological "parameters" that can be rarely obtained from any other type of fossil preservation (*e.g.* Opluštil *et al.* 2009a, b, Wang *et al.* 2009, DiMichele & Falcon-Lang 2011, Pšenička *et al.* 2005). Careful taphonomical analysis of T^0 assemblages thus significantly contributes to much better understanding of the fossil ecosystems they represent (Johnson 2007).

Distribution of plant remains in tuff beds is complex. Whereas lateral changes in the composition of plant fossil assemblages reflect spatial heterogeneity of vegetation cover, the vertical distribution of plant remains within a tuff includes separation of litter and ground cover from tree crown foliage, lianas and epiphytes (Burnham & Spicer 1986, Wing *et al.* 1993, Burnham 1994, Opluštil *et al.* 2009a, b). Evidence of interactions between animals and plants also may be preserved, not uncommonly (Prokop & Nel 2010, Scott & Taylor 1983, Pšenička & Bek 2009, Rößler *et al.* 2012).

Although plant-bearing volcaniclastic beds are generally rare, there are several excellent examples in Europe, Asia, North and South America and Australia. Besides several fossiliferous tuff beds of Moscovian age in the Czech Republic (Opluštil *et al.* 2007, Bureš *et al.* 2013), well-known fossiliferous tuff beds have been described also from the Late Pennsylvanian of the Puertollano Basin in central Spain (Wagner 1989), the early Permian of the Döhlen Basin and the famous petrified forest from Chemnitz in Saxony, Germany (Rößler 2006, Rößler & Barthel 1998, Rößler *et al.* 2014). Outside of Europe, early Permian plant-bearing tuff beds were described from the Wuda Coalfield in Inner Mongolia, North China (Pfefferkorn & Wang 2007, Wang *et al.* 2012) and from the late Permian in Guizhou Province in south China (He *et al.* 2013, Hilton *et al.* 2004). The Faxinal coalfield (Sakmarian) in Brazil is an example of such preservation in a Gondwanan peat-forming environment (Boardman *et al.* 2012). Example of an exceptional Cretaceous forest preserved in volcanic ash bed is that one described by Wing *et al.* (1993) from Big Cedar Ridge in Wyoming, USA. In this paper we document a well-preserved middle Moscovian (Bolsovian) plant assemblage preserved in the base of the Whetstone Horizon in the Radnice Basin located in western Bohemia, the Czech Republic.

Geology of the study area and the locality

The study locality is situated along the southern margin of the Radnice Basin in western Bohemia, about 15 km north of the town of Rokycany (Fig. 1). This about 20 km^2 basin consists of a large tectonic and erosional remnant of Carboniferous strata surrounded by smaller ones, all formerly connected with a much larger basin complex further north and westward. This about 300 km long complex of continental basins extends from western to north-eastern Bohemia and into the adjacent part of Poland (Fig. 1A). It is filled with terrestrial sediments ranging from the Middle to Upper Pennsylvanian (Fig. 2) and in the eastern part of the complex also to the Permian and locally even to the Triassic. Deposition was interrupted by several hiatuses and the Carboniferous part of the succession is characterised by alternation of grey coal-bearing strata with coal-barren alluvial red-bed sediments whereas Permian strata are dominantly red beds with intercalated grey lacustrine horizons (Fig. 2).

In the Radnice Basin only the early Moscovian (Bolsovian) Radnice Member sediments are preserved. The thickness of this basal unit strongly varies from 0 to about 200 m due to prominent basement paleotopography onto which the deposition of this unit took place (Pešek 1994). This unit consists dominantly of fluvial strata with a minor contribution of colluvial and lacustrine sediments, and was deposited in a system of tectonically established or incised river valleys on Precambrian to Ordovician basement (Opluštil 2005). Long-lasting mires developed during periods of increased subsidence and/or wetter climate in valleys or their parts protected from increased clastic input. In the Radnice Basin such conditions resulted in a development of the Radnice group of coals composed of the Lower and Upper Radnice Coals and separated by the widespread volcanigenic Whetstone Horizon (Figs 2, 3). The Lower Radnice Coal is usually around a 1 m thick ash-rich coal bed, but in the study locality can reach up to 5 m of good quality coal. The Upper Radnice Coal is generally thicker, locally over 10 m and was extensively mined.

The Whetstone Horizon and review of its fossil record

The Whetstone Horizon, which is the main object of our study because of its unique fossil record, typically consists of non-reworked, airfall volcanic ash bed at the base over-

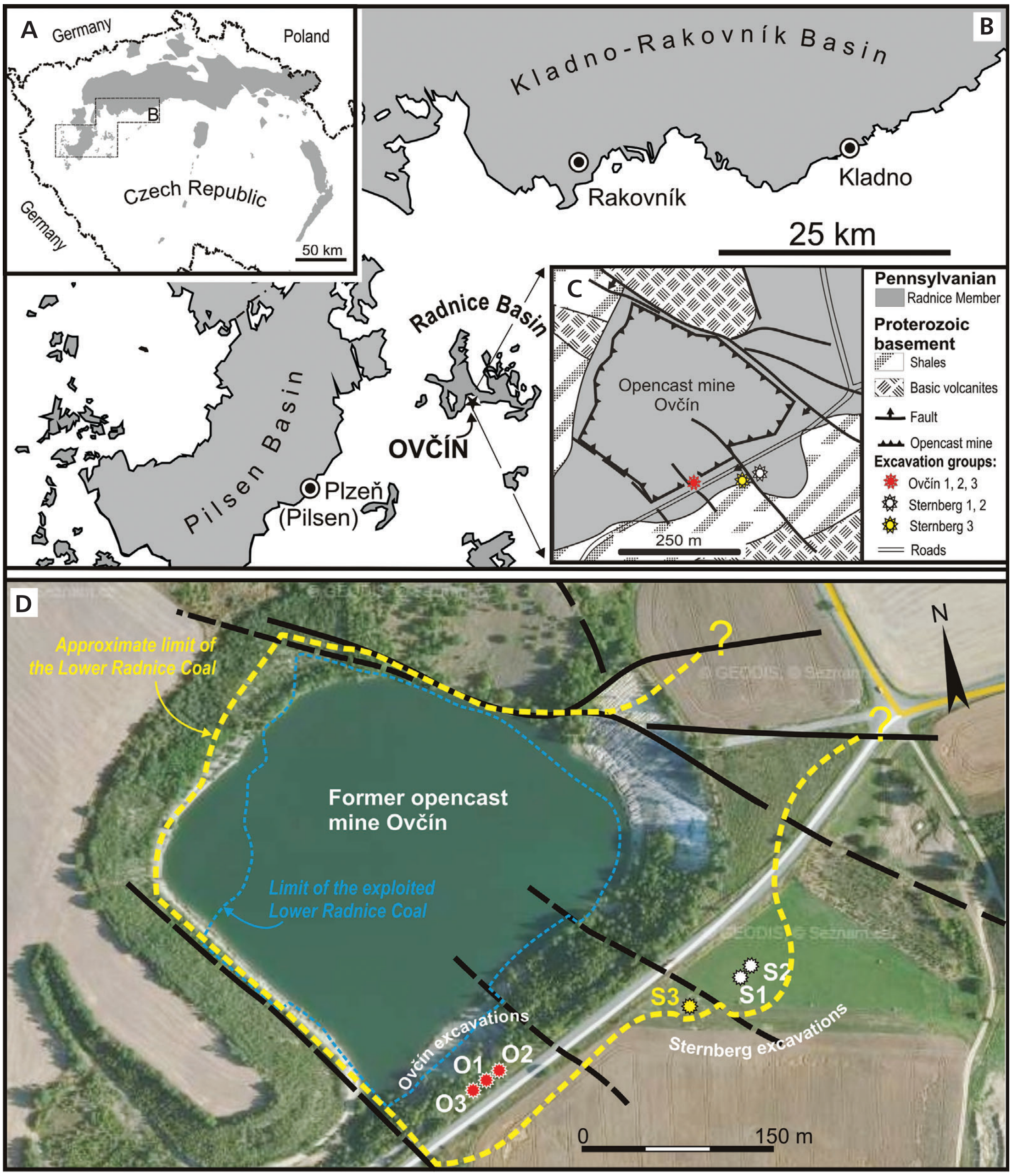


Figure 1. Position of the Ovčín coal deposit and excavations. • A – the Late Palaeozoic continental basins in the Czech Republic. • B – detail of basin complex in central and western part of the Czech Republic and position of the Ovčín locality. • C – geological map of the Ovčín coal deposit and position of the excavation groups. • D – orthophotomap of the former Ovčín opencast mine and position of the excavations.

lain by reworked volcaniclastics mixed with siliciclastic material (Mašek 1973, Opluštil *et al.* 2009a). The volcanic ash layer at the base is about 0.4 to 0.6 m massive, pale yellow to whitish tuff called "Bělka" (Figs 2, 3) composed of a kaolinite matrix with dispersed sand-sized crystals and fragments of sanidine, quartz and vermicular kaolinite as the main minerals. Radiometric dating of sanidine from the tuff using the $^{40}Ar/^{39}Ar$ method yielded an age of 309.0 ± 3.7 Ma (Hess *et al.* 1985). Sharply overlying the Bělka bed is a complex of parallel to ripple laminated tuffitic mudstones to fine grained sandstones called "Brousek" (*i.e.* "whetstone").

The Whetstone Horizon covers vast areas of the Late Palaeozoic basin complex in western and central parts of the Czech Republic. Bělka is known from mines and boreholes over a distance of about 100 km in a SW-NE direction without any prominent change in its thickness and grain size. It is preserved throughout the area of the Radnice Member wherever the sedimentary environment was favourable during the original eruption. The tuff bed is

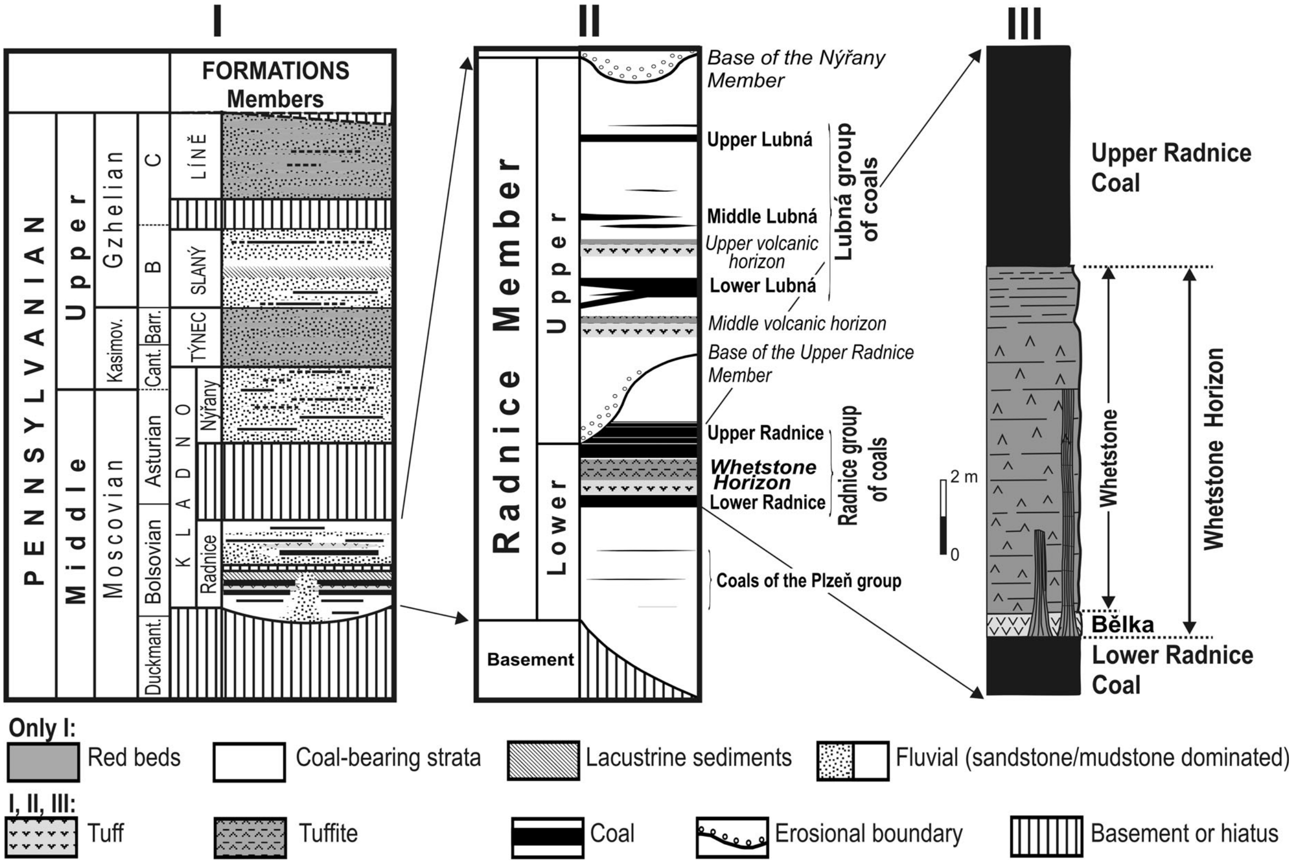


Figure 2. Stratigraphy of the late Paleozoic basins in central and western Bohemia (I), position of the Whetstone Horizon in the Radnice Member (II) and generalised section of the Whetstone Horizon (III).

missing only in colluvial and channel facies. Apart from the Bělka, thickness of the Brousek varies from one or two metres to more than 10 m in the Radnice Basin and up to 20 m in the Kladno-Rakovník Basin to the north (Mašek 1973).

The Bělka is interpreted as a distal, single ash-fall deposit from a high-energy volcanic eruption that buried the entire landscape over an extensive area in the western part of the Czech Republic (Fig. 4). The Brousek is considered to represent a reworked non-consolidated volcanic ash washed from surrounding topographic highs down into adjacent valleys and deposited in a shallow lake produced by compaction of peat under the Bělka load (Opluštil *et al.* 2009a).

The source of the volcanic material that comprises the Whetstone Horizon is not precisely known. However, it is speculated (Mašek 1973, Pešek 1994, Opluštil *et al.* 2009a) that the volcanic centre was very probably located about 80 to 100 km northward in North Bohemia and/or the adjacent part of Saxony, Germany. Here, thick volcanic lava and ignimbrite bodies occur between Litoměřice, Teplice and Dresden with the Altenberg Caldera as the main volcanic centre (Mašek 1973, Breiter 1997, Hoffmann *et al.* 2012). The extent of volcanic ash fall deposits is difficult to estimate. Assuming that the Altenberg Caldera was really the volcanic centre of the Whetstone Horizon, then the Bělka tuff bed covered a minimum area that lies approximately between Altenberg, at the source, and the southern limit of the Radnice Member, which is located between towns Pilsen and Kralupy nad Vltavou, about 120 and 80 km apart from Altenberg respectively. This area, which is approximately 3500 km^2, represents only a fragment of what was likely a once much larger area covered by volcanic ash, indicated by only subtle changes in Bělka thickness over a distance of 100 km between Pilsen and Kralupy nad Vltavou.

The Whetstone Horizon bears coalified plant fossils and invertebrate remains (*e.g.* Opluštil *et al.* 2007, Prokop & Nel 2010). The character of preservation and distribution of fossil remains, however, significantly differs between the Bělka and Brousek. The Bělka contains plant fragments of various sizes including aerial axes up to several metres long and locally nearly complete aerial part of plants (Šimůnek *et al.* 2009, p. 306, fig. 6). Upright coalified stems exclusively rooted in the roof of the Lower Radnice Coal and filled either by Bělka or Brousek material are very common. Their diameter ranges from only a

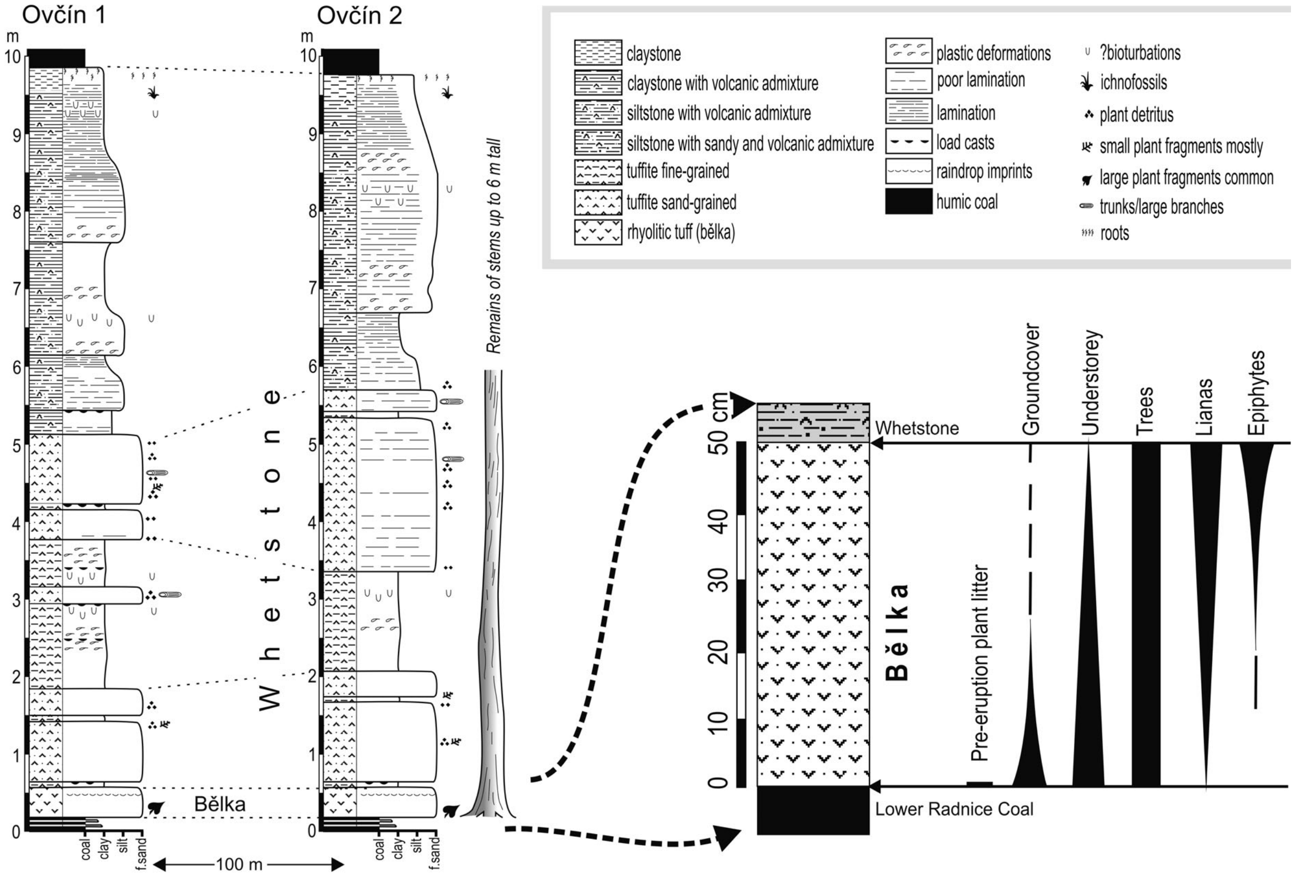


Figure 3. Sections of the Whetstone Horizon taken in the Ovčín opencast mine during its operation (according to Drábková 1986) and generalised vertical distribution of plants of various habitats/individual storeys in the Bělka tuff bed.

few millimetres to more than 1 m (Libertín *et al.* 2009; Opluštil *et al.* 2007, 2009a). The tallest stems are more than 6 m high (Drábková 1986). The Bělka plant remains are not charred and their spatial distribution is irregular reflecting the original structure of the vegetation at the time of ash deposition. Lateral patterns of spatial variation reflect the original structure and density of the vegetation whereas the vertical distribution of plant remains within the bed probably reflects plant growth habits and the timing of their deposition in the rapidly accumulating ash (Opluštil *et al.* 2009a, Pšenička & Opluštil 2013). The fossil record in the Brousek part of the horizon, which is a complex of lacustrine sediments composed of re-deposited volcaniclastics and admixed siliciclastics, apparently differs from that one of the Bělka bed. Except for the basal few centimeters of the Brousek, where some large plant fragments (especially stems) continue from the Bělka bed, the plant remains in the Brousek are much more fragmentary and often represented by plant detritus either irregularly scattered or concentrated on several discrete bedding planes or within thin beds. In the study locality nearly all plant or invertebrate fragments occur in the lower 3 to maximum 5 m of the Brousek section. In its uppermost part, there is a rich assemblage of ichnofossils indicating insect and vertebrate (both tetrapods and fish) activity, as described by Turek (1989, 1996).

Palaeoecologically, the flora preserved in the Bělka bed at the base of the Whetstone Horizon represents an *in situ* preserved plant assemblage buried in a geological instant by volcanic ash and therefore providing an instantaneous snapshot of the T^0 peat forming plant assemblage. Plant remains in the overlying Brousek represent the same pre-eruption flora as that one of the Bělka. In this case, however, most of the plants were first buried by volcanic ash at or near the site of their original growth (valley margins and potentially also adjacent hill slopes) and subsequently drifted as the unconsolidated volcanic ash was washed by rains down the valley from the surrounding hills and/or valley margin. This interpretation is in agreement with the common presence of thin discrete layers of plant detritus in the lower part of the Brousek section. The Brousek flora therefore represents an allochthonous plant assemblage preserved mostly *ex situ*. This is indicated not only by the fragmentary nature of plant remains and their distribution pattern but also by partly different plant composition compared to the underlying Bělka.

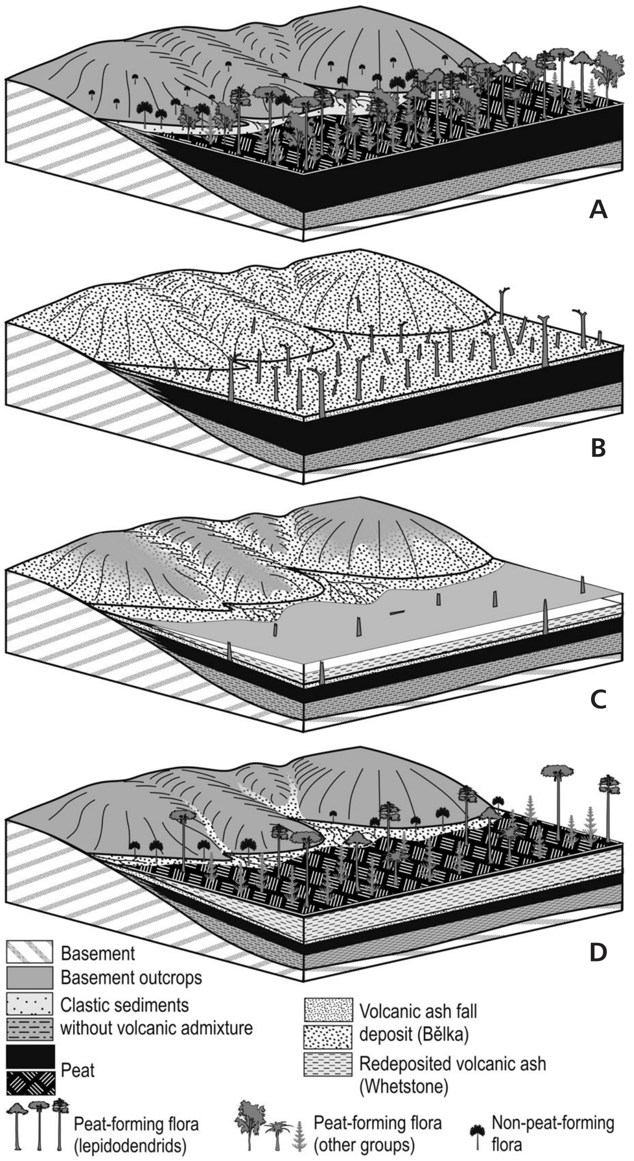


Figure 4. Genesis of the Whetstone Horizon at the Ovčín coal deposit. • A – intact coal forest colonizing peat swamp of the Lower Radnice Coal prior the volcanic eruption. • B – damaged coal forest partly buried in volcanic ash early after the eruption. The lanscape is completely covered by tephra. • C – shallow lake was produced by compaction of peat under volcanic ash load. Lake was filled by unconsolidated tephra washed down the valley from surrounding palaeohighs. • D – peat swamp (Upper Radnice Coal) re-established over the Ovčín coal deposit after lake filling by sediments.

Review of the Palynology of the Ovčín coal deposit

Palynological research at the Ovčín locality was focused mainly on palaeoecological intepretation of the plant assemblage and its reconstruction (Bek 1986, Drábková 1986, Opluštil *et al.* 2009a, b).

The spore and pollen assemblage of the Radnice coal group consists of three groups. The first group is characterised by long-ranging taxa including *Lycospora* (Ibrahim) Schopf *et al.* (Fig. 5J–O), *Calamospora* Schopf *et al.* (Fig. 6C), *Densosporites* (Berry) Butterworth *et al.*, *Laevigatosporites* Ibrahim (Fig. 5R, S), *Granulatisporites* (Ibrahim) Potonié & Kremp (Fig. 6F), *Cyclogranisporites* Potonié & Kremp, *Lophotriletes* (Naumova) Potonié & Kremp (Fig. 6E, G, I), *Triquitrites* (Wilson & Coe) Potonié & Kremp, *Raistrickia* (Schopf *et al.*) Potonié & Kremp, *Leiotriletes* Naumova (Fig. 6A, B), *Verrucosisporites* (Ibrahim) Smith & Butterworth (Fig. 6J, P) and *Apiculatisporis* Potonié & Kremp. Stratigraphically important miospores of the second group are *Cirratriradites saturni* (Ibrahim) Schopf *et al.* (Fig. 5E–H), *Endosporites zonalis* (Loose) Knox (Fig. 5Q), *Knoxisporites polygonalis* (Ibrahim) Potonié & Kremp (Fig. 5C), *Reticulatisporites muricatus* Kosanke (Figs 5D, 6O), *Anapiculatisporites minor* (Butterworth & Williams) Smith, *Punctatisporites obesus* (Loose) Potonié & Kremp (Fig. 6D, K), and genera *Vestispora* (Wilson & Hoffmeister) Wilson & Venkatachala (Fig. 5U), *Punctatosporites* Ibrahim, *Cingulizonates* Dybová & Jachowicz and *Alatisporites* Kosanke (Fig. 5V). The third group is represented by species recorded in low numbers and those are very rare and/or are described for the first time in the Carboniferous of the Czech Republic. These include the genera *Paleospora* Habib, *Fragipollenites* (Konyali) McLean, *Gorgonispora* Urban, *Kewaneesporites* Peppers, *Spackmanites* (Habib) Ravn, *Secarisporites* Neves, *Maculatasporites* Ravn, *Diaphanospora* (Balme & Hassel) Evans, *Striatomonosaccites* Bharadwaj, *Quasillinites* Ravn & Fitzgerald, *Tinulisporites* Dempsey, and the species *Punctatisporites flexuosus* Felix & Burdbridge, *Anapiculatisporites protuberatus* (Hagemann) Ravn, *Tricidarisporites arcuatus* Neville *in* Neves *et al.*, and *Tantillus triquetrus* Felix & Burdbridge.

In the Lower Radnice Coal dominance of *Lycospora orbicula* (Potonié & Kremp) Smith & Butterworth (22% on average, max. 75 per cent) is palaeoecologically significant. These microspores were produced by cones of the *Flemingites*-type born on the arborescent lycopsid *Lepidodendron simile sensu* Němejc, the macrofossils of which are found at the study locality. Subdominants include monolete spores of the *Sphenophyllum myriophyllum*-type; *i.e.* *Laevigatosporites* and *Latosporites*. Also relatively abundant are spores of probable ferns such as *Oligocarpia* Goeppert and *Senftenbergia* Corda represented by the spores *Leiotriletes*, *Granulatisporites*, *Raistrickia*, *Apiculatisporites* and *Punctatisporites* (Fig. 6D). The parent plants producing *Savitrisporites* (Fig. 5B), *Dictyotriletes castaneaeformis* and the *Lophotriletes*-types remain unknown.

The palynological spectrum of the Upper Radnice Coal is dominated by arborescent lycopsids of the same type as those found in the Lower Radnice Coal. Also relatively abundant are spores of *Sphenophyllum myriophyllum*

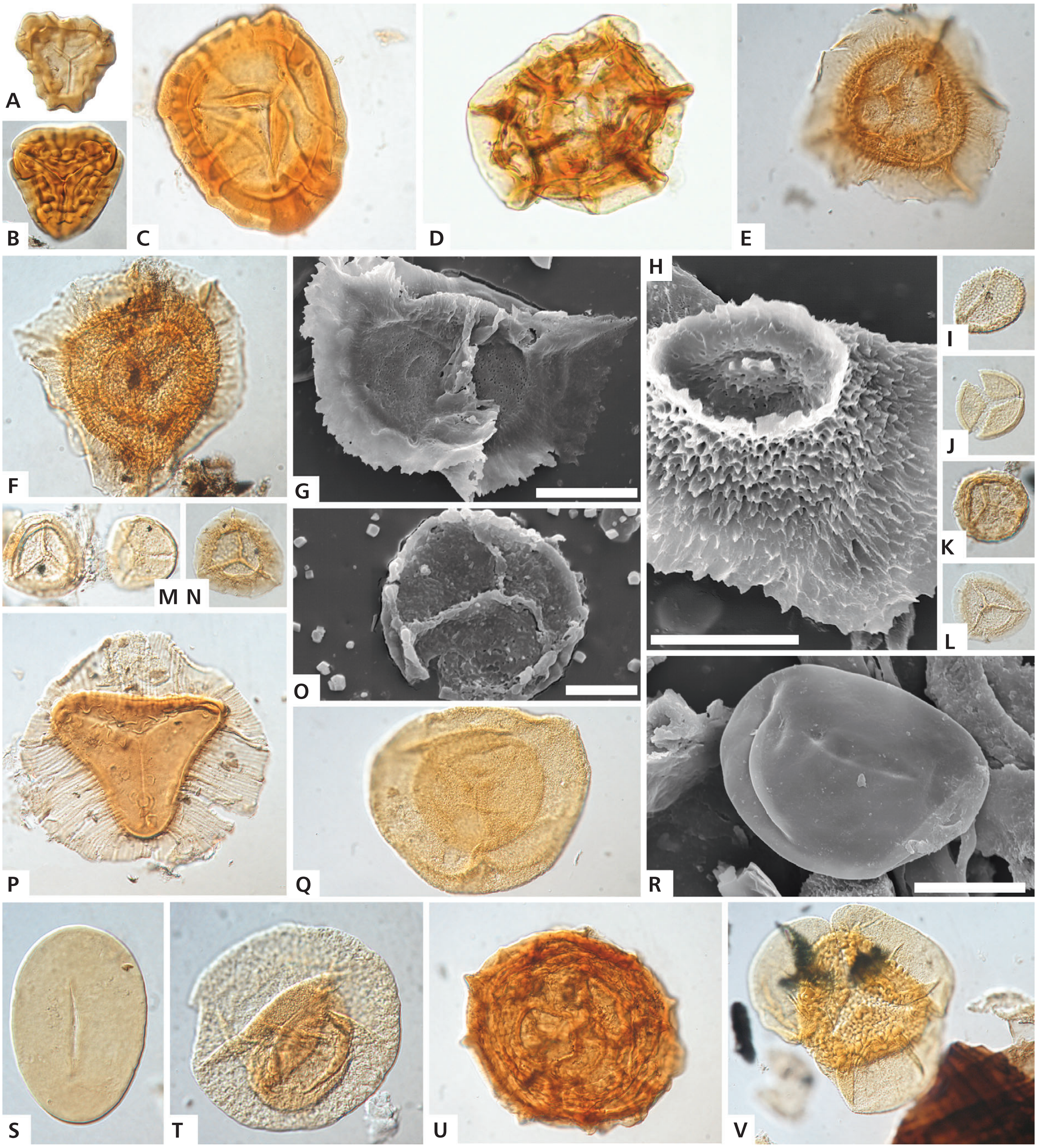


Figure 5. All photomicrographs of miospores in light microscope × 500. • A – *Westphalensisporites irregularis*; B – *Savitrisporites nux*; C – *Knoxisporites polygonalis*; D – *Reticulatisporites muricatus*; E, F – *Cirratriradites saturni*. • G – *Cirratriradites saturni*. Proximal surface, SEM, scale bar 20 µm. • H – *Cirratriradites saturni*. Part of the distal surface with circular foveolae. SEM, scale bar 12 µm. • I – *Microspinosporites orbiculus*; J – *Lycospora parva*; K – *Lycospora rotunda*; L – *Lycospora pellucida*; M – *Lycospora pellucida* (left) and *Lycospora parva* (right); N – *Lycospora noctuina*. • O – *Lycospora rotunda*. SEM. Proximal surface, scale bar 7 µm. • P – *Reinschospora magnifica*; Q – *Endosporites zonalis*. • R – *Laevigatosporites desmoinesensis*. SEM, scale bar 23 µm. • S – *Laevigatosporites desmoinesensis*; T – *Florinites mediapudens*; U – *Vestispora magna*; V – *Alatisporites pustulatus.*

Table 1. List of miospore and pollen genera from the Radnice coal group of the Ovčín coal deposit.

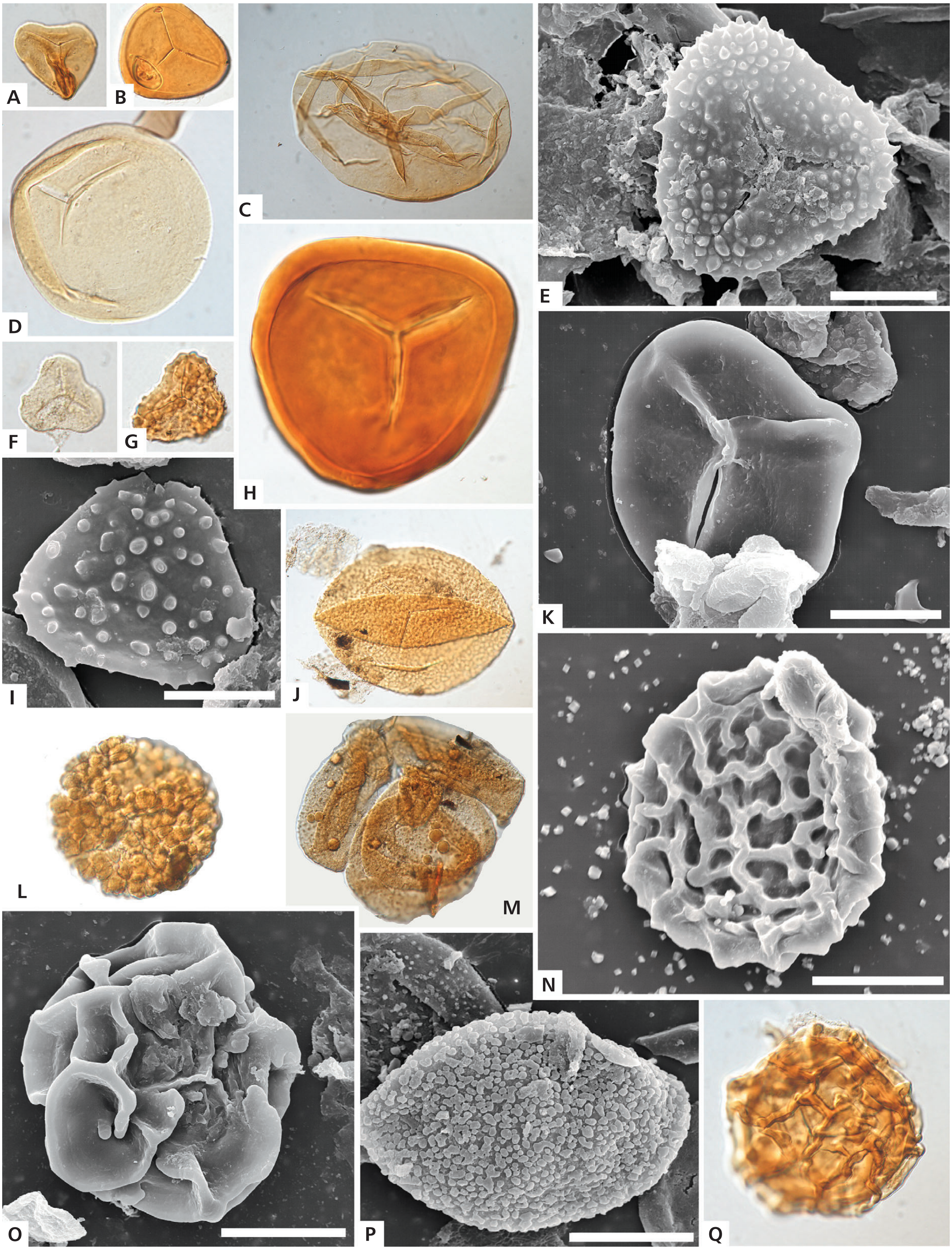
Acanthotriletes (Naumova) Potonié & Kremp
Ahrensisporites Potonié & Kremp
Alatisporites Kosanke, Fig. 5V
Anacanthotriletes Ravn
Anapiculatisporites (Potonié & Kremp) Smith & Butterworth
Apiculatasporites (Ibrahim) Smith & Butterworth
Apiculatisporis Potonié & Kremp
Calamospora Schopf, Wilson & Bentall, Fig. 6C
Cappasporites Urban
Cingulizonates (Dybová & Jachowicz) Butterworth, Jansonius, Smith & Staplin
Cirratriradites Wilson & Coe, Fig. 5E–H
Converrucosisporites Potonié & Kremp
Convolutispora Hoffmeister, Staplin & Malloy, Fig. 6L
Crassispora (Bharadwaj) Sullivan, Fig. 6M
Cristatisporites (Potonié & Kremp) Butterworth, Jansonius, Smith & Staplin
Cyclogranisporites Potonié & Kremp
Densosporites (Berry) Butterworth, Jansonius, Smith & Staplin
Diaphanospora (Balme & Hassel) Evans
Dictyotriletes (Ibrahim) Smith & Butterworth, Fig. 6N, Q
Endosporites Wilson & Coe, Fig. 5Q
Florinites Schopf, Wilson & Bentall, Fig. 5T
Foveosporites Balme
Fragilipollenites Konyali
Gorgonispora Urban
Granulatisporites (Ibrahim) Potonié & Kremp, Fig. 6F
Guthoerlisporites Bhardwaj
Illinites (Kosanke) Helby
Knoxisporites (Potonié & Kremp) Neves & Playford, Fig. 5C
Laevigatosporites Ibrahim, Fig. 5R, S
Latensina Alpern
Latosporites Potonié & Kremp
Leiotriletes (Naumova) Potonié & Kremp, Fig. 6A, B
Lophotriletes (Naumova) Potonié & Kremp
Lundbladispora Alpern
Lycospora (Ibrahim) Potonié & Kremp, Fig. 5J–O
Maculatasporites Ravn
Microreticulatisporites (Knox) Potonié & Kremp
Microspinosporites Bek, Fig. 5I
Mooreisporites Neves
Paleospora Habib
Pityosporites (Seward) Manum
Planisporites (Knox) Potonié
Punctatisporites (Ibrahim) Potonié & Kremp, Fig. 6D, H, K
Pustulatisporites (Knox) Potonié & Kremp
Quasillinites Ravn & Fitzgerald
Raistrickia (Schopf, Wilson & Bentall) Potonié & Kremp
Reinschospora Schopf, Wilson & Bentall, Fig. 5P
Reticulatisporites (Ibrahim) Potonié & Kremp; Figs 5D, 6O
Reticulitriletes (Mädler) Ravn
Savitrisporites Bharadwaj; Fig. 5B
Secarisporites Neves
Spackmanites (Habib) Ravn
Spencerisporites (Chaloner) Drábková, Bek & Opluštil
Striatomonosaccites Bhardwaj
Tantillus Felix & Burdbridge
Tinulisporites Dempsey
Tricidarisporites Sullivan & Marschall
Triquitrites (Wilson & Coe) Potonié & Kremp
Verrucosisporites (Ibrahim) Smith & Butterworth, Fig. 6J, P
Vestispora (Wilson & Hoffmeister) Wilson & Venkatachala, Fig. 5U
Westphalensisporites Alpern, Fig. 5A

Crépin, 1880 and *S. priveticense* Libertín, Bek & Drábková, 2014, whereas spores of all other main plant groups occur in lower numbers. The plant affinity of about 8% of all palynomorphs found is unknown.

Material and methods

Data presented in this paper were obtained from about 6.0 × 5.6 m (~33.5 m^2) rectangular excavation called "Sternberg Excavation 3" (S3), located about 50 m from the eastern edge of the former open cast mine Ovčín (Fig. 1D), which extracted both coals of the Radnice group from 1979 to 1986. The purpose of our excavation, undertaken in summer season of 2009, was to expose the Bělka bed and to study carefully its plant fossil content in order to obtain data for palaeoecological reconstruction of the buried plant assemblage. Therefore, between 1.5 and 2.5 m of overburden, composed of lower part of the Brousek section, was removed down by an excavating machine to a level just above the Bělka tuff bed. The basal fossiliferous parts of the Brousek were carefully split and searched for identifiable plant remains. These were collected for later comparison with the plant assemblage buried *in situ* by the volcanic ash of the Bělka tuff bed. The exposed Bělka surface was divided into 1 m^2 units, marked off with string, that formed an XY-coordinate system, permitting the relative locations of plant fossils to be recorded accurately. The tuff bed was then carefully quarried in slabs about 0.1 m thick, which were further split to find as many fossils as possible. Fossil remains found in each square unit were identified and their precise position was drawn onto a sheet of graph paper.

Figure 6. All photomicrographs of miospores in light microscope × 500. A – *Leiotriletes gulaferus*; B – *Leiotriletes convexus*; C – *Calamospora microrugosa*; D – *Punctatisporites obliquus.* • E – *Lophotriletes microsaetosus*. Distal surface. SEM, scale bar 12 µm. • F – *Granulatisporites microgranifer*; G – *Lophotriletes microsaetosus*; H – *Punctatisporites obesus*; • I – *Lophotriletes* cf. *granoornatus.* Distal surface. SEM, scale bar 15 µm. • J – *Verrucosisporites microtuberosus*. • K – *Punctatisporites obesus*. Proximal surface. SEM, scale bar 30 µm. • L – *Convolutispora* cf. *tessellata*; M – tetrade of *Crassispora kosankei*. • N – *Dictyotriletes mediareticulatus*. SEM, scale bar 33 µm. • O – *Reticulatisporites muricatus.* Proximal surface. SEM, scale bar 40 µm. • P – *Verrucosisporites microtuberosus*. Distal surface. SEM, scale bar 30 µm. • Q – *Dictyotriletes mediareticulatus*.


A
B
C
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Q

Each individual species was recorded on a separate graph-paper sheet for each of the sampling units. All the findings were numbered and photographed and samples for later re-evaluation were taken to lab in the West Bohemian Museum in Pilsen (WBMP), where all the material collected from the excavation is housed and available for scientific study. The most important specimens, especially large or well-preserved remains, were recovered as a block or set of blocks, fixed and moved to the lab for preparation and further study. Although it was possible to identify taxonomically most of the specimens during excavation, some isolated pteridosperm or cordaitalean axes or decorticated lycopsids were difficult to identify directly. Therefore samples of these specimens were also taken to the lab in the WBMP for later determination. Special attention was paid to the contact of the Bělka bed with the Lower Radnice Coal, which preserves mostly plant litter in various stages of decay and therefore sometime difficult to identify. This is further obscured by thin muddy coatings, which must be washed off in the lab. In addition, 5 to 10 mm at the base of the Bělka bed is usually overfull by fossils representing partly plant litter but mostly small herbaceous plants, which were buried soon after the onset of the volcanic ash fall. For the above-mentioned reasons, one to two centimetre thick blocks of the basal part of the Bělka were often taken and searched for fossils in the WBMP lab.

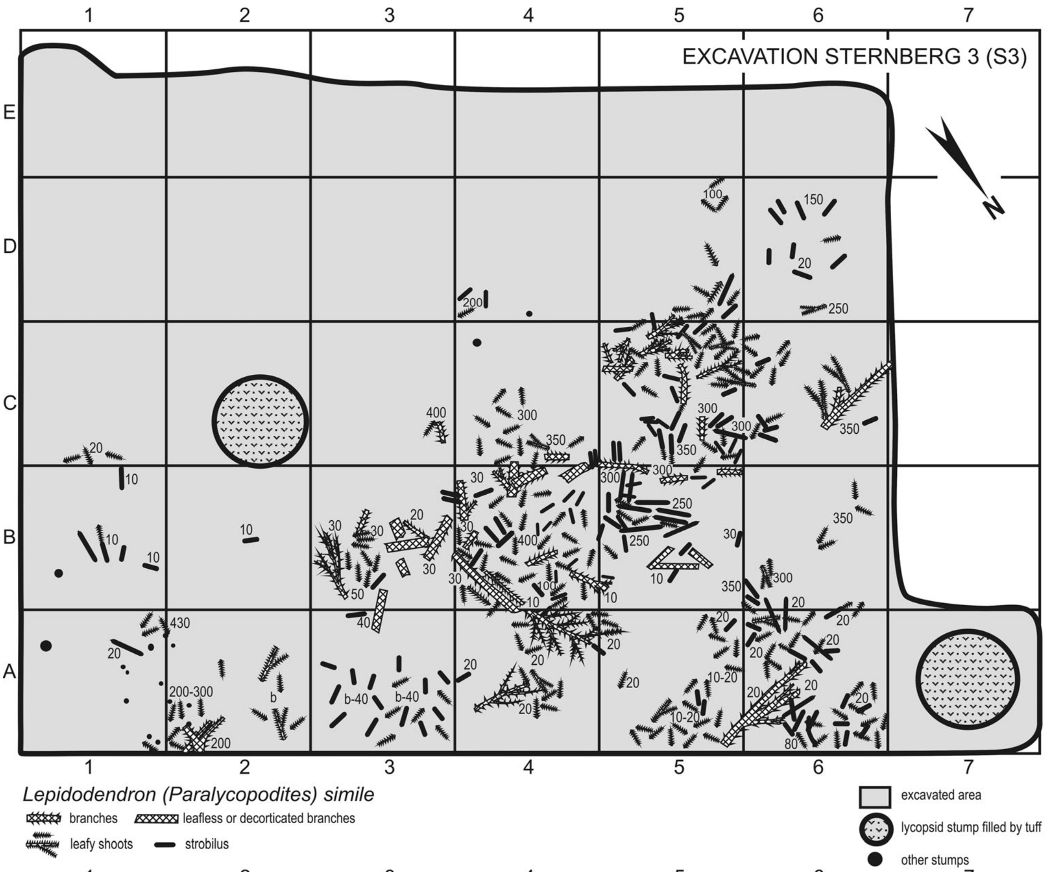
In the second step, material stored in the WBMP was prepared, fixed and re-determined if necessary. The results were used to upgrade the data recorded on the sheets of graph paper on which were recorded the positions of the fossils found in the excavation. Subsequently all these data-containing sheets of graph paper were scanned and re-drawn in CorelDRAW. For each species a separate layer representing the whole excavated area was constructed. Small plant fragments and mostly herbaceous plants were indicated by icons, whereas larger specimens were redrawn from photographs to the corresponding layer and square units. Information on height above the tuff base of each finding or group of findings and axis diameter were finally added. Resulting graphical processing/treatment of the field data served as a basis for 3D reconstruction of the vegetation cover and interpretation/estimation of some ecological parameters of the plant assemblage, especially density of vegetation, distribution pattern and life strategy. Some unusually complete specimens will be used to improve whole plant reconstruction of the various species, which will be published elsewhere. Heights of cordaitaleans and lepidodendrid lycopsid trees were calculated using the formulae derived by Niklas (1994). Although lycopsids possessed little wood, their thick periderm rind probably had similar mechanical properties to the wood of cordaitaleans (*e.g.* DiMichele & Phillips 1994). Therefore we used for these plants an allometric equation for "woody" species. Another parameter, adopted from modern ecological studies is estimation of so-called minimal area, which is minimal area that can be considered to represent the plant assemblage and that captures all the characteristic species (Cain 1938, Kent & Coker 1992, Opluštil *et al.* 2009b). The area is usually estimated by graphing the number of species against a series of progressively larger quadrat areas, successively doubled in size. As the area enlarges the number of species increases. The area where the curve becomes flat is considered as the minimum area. We estimated this parameter while recognizing that our excavation was much smaller than the minimum area of modern forest assemblages, which varies usually between 200 and 500 m^2 (Mueller-Dombois & Ellenberg 1974). To make this estimate more reliable we brought into this analysis the results from five previous excavations of similar size located nearby (Fig. 1D), which were done between 2002 and 2006. These previous excavations are grouped into two clusters tens to a few hundred metres apart. Excavation cluster "Ovčín" consists of three adjacent excavations designated O1, O2 and O3. Cluster "Sternberg" comprises two adjacent excavations designated S1 and S2 (Opluštil *et al.* 2009a, b). For details of estimation of the minimal area see Opluštil *et al.* (2009a).

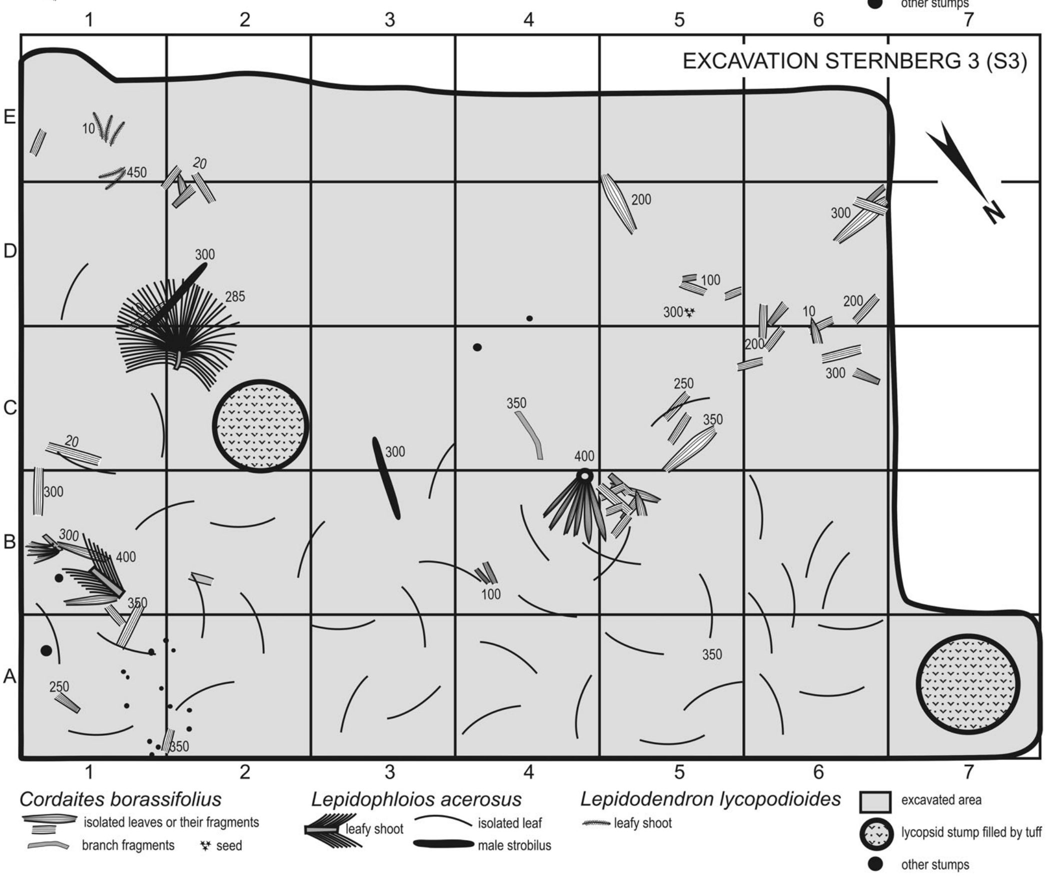
Results

Composition of the plant assemblage and species diversity in the Bělka tuff bed of the S3 excavation

Within 33.5 m^2 of the excavated area we identified 33 taxa, which are estimated to represent at least 25 biological species (Tables 2, 3). The most diverse are lycopsids represented by 7 species followed by pteridosperms and filicopsids with 6 species in each group. Sphenopsids are represented by 5 species whereas cordaitaleans only by 1 species. Estimation of biological (whole plant) species is based on the fossil taxa representing organs that best characterise the diversity of particular plant groups (Cleal 2005). Lepidodendrid lycopsids are best identified by leafy shoots and/or bark compressions and are represented by *Lepidodendron simile sensu* Němejc (1947) *non* Kidston (1909), *Lepidophloios acerosus* Lindley & Hutton (1831), *Lepidodendron*

Figure 7. Distribution of fossil remains of the most important arborescent taxa (*Lepidodendron simile*, *L. lycopodioides*, *Lepidophloios acerosus* and *Cordaites borassifolius*) as uncovered in the S3 excavation in the Bělka tuff bed. Numbers indicate height (in mm) above the top of the Lower Radnice Coal.


EXCAVATION STERNBERG 3 (S3)
N
Lepidodendron (Paralycopodites) simile
branches
leafless or decorticated branches
leafy shoots
strobilus
excavated area
lycopsid stump filled by tuff
other stumps


EXCAVATION STERNBERG 3 (S3)
N
Cordaites borassifolius
isolated leaves or their fragments
branch fragments
seed
Lepidophloios acerosus
leafy shoot
isolated leaf
male strobilus
Lepidodendron lycopodioides
leafy shoot
excavated area
lycopsid stump filled by tuff
other stumps

lycopodioides Sternberg (1821) and *Sigillaria* sp. (Tables 2, 3). The most common is *L. simile* (Fig. 7), which occurred as branches and leafy shoots (Fig. 8A–C) often in organic connection with bisporangiate *Flemingites*-type cones (Fig. 8D–H). The length of these bisporangiate cones varies from 40 to 170 mm due to differences in maturity or position on the plant. Much less common *Lepidophloios acerosus* was represented only by few leafy shoot fragments (Fig. 9A), two up to 0.5 m long male cones (Fig. 9B) and isolated grass-like leaves several tens of centimetres long (Fig. 7). The associated cones (*Lepidostrobus* sp.) were found in one of the previous excavations (S2) in organic connection with *Halonia*-type branches of *L. acerosus* (Opluštil *et al.* 2009a). The even less common lycopsid *Lepidodendron lycopodioides* was represented only by a few leafy shoots (Fig. 7). The arborescent genus *Sigillaria* (Fig. 10) occurred as a single poorly preserved and partly decorticated axis, several centimetres broad, resembling *Sigillaria diploderma* Corda, 1845 (Fig. 9D); this specimen was the only identified remain of *Sigillaria* found in all the Ovčín excavations.

Subarborescent lycopsids are represented by a single species, *Spencerites havlenae* Drábková, Bek & Opluštil, 2004 (Figs 9C, 10), found only as two isolated specimens.

Herbaceous lycopsids are represented by *Selaginella* cf. *gutbieri* (Goeppert) Thomas, 1997 and a new species of bisporangiate herbaceous lycopsid (Figs 9E, 10). The first was represented by several small cone fragments and rare leafy shoots and the second as a nearly complete plant attached to a prostrate (fallen) lycopsid stem obliquely penetrating from the coal seam roof up to the base of the Brousek (Pšenička & Opluštil 2013).

Sphenopsids are represented by "arborescent" calamites and herbaceous sphenophylls. Calamitalean stems attributable mainly to *Stylocalamites* Weiss, 1884 and much less commonly *Calamitina* indicate two species (Figs 11D, E, 12), associated, however, with three types of foliage. The most common calamitalean foliage is *Asterophyllites* cf. *grandis* (Fig. 11A, B), which probably represents foliage of the most common stem, *Stylocalamites* sp., although these species have not been found in organic connection. The two remaining species *A. equisetiformis* and *A. longifolius* (Fig. 11C) occurred on very few specimens. A single specimen of C*alamariophyllum* sp. (Fig. 11F) found in the excavation shows *Calamariophyllum* leaves attached to nodes of a *Calamitina*-type stem. Sphenophylls (Figs 12, 13) are represented by *S.* cf. *cuneifolium* Sternberg (Fig. 12D, E), *S. priveticense* Libertín, Bek & Drábková, 2014 (Fig. 12A–C) and *Bowmanites pseudoaquensis* Libertín, Bek & Drábková 2008. All were found with organically attached cones. Most of the remains are relatively small fragments of leafy or naked axes or isolated leaf whorls. Also probably of sphenophyll affinity is a small cone (Fig. 12F) found isolated and resembling the permineralised species *Bowmanites trisporangiatus*.

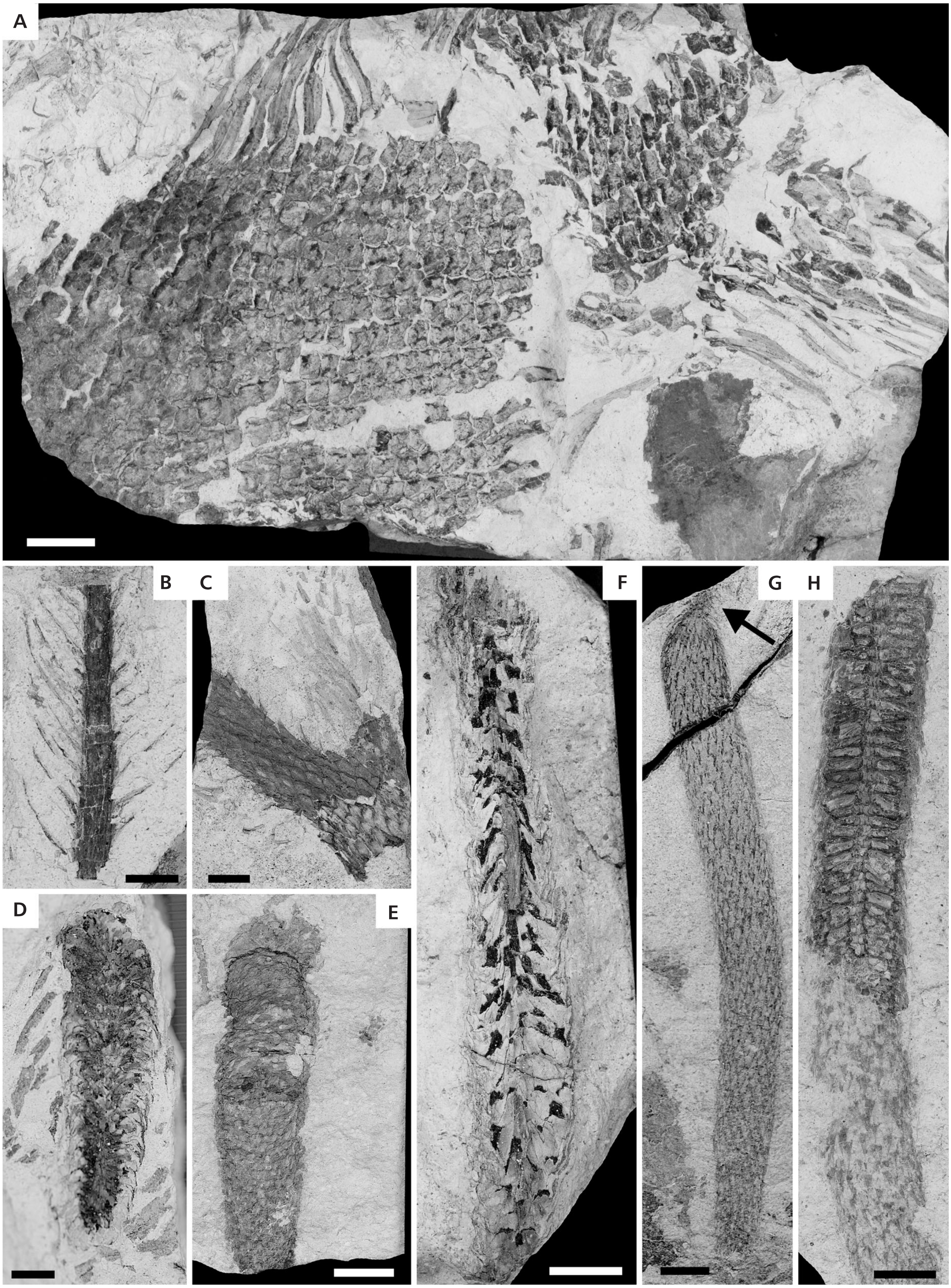
Among filicopsids, zygopterid ferns are the most diverse (Figs 14, 15), represented predominantly by *Corynepteris angustissima* (Sternberg) Němejc, 1938 (Fig. 15A, B) with subordinate numbers of *Desmopteris longifolia* (Sternberg *in* Goeppert) Stur, 1885 (Fig. 15C). A single specimen of *Rhodeites gutbieri* (Ettingsahusen) Němejc, 1936 (emended by Pšenička & Schultka 2009) (Fig. 15D) was found in the Bělka tuff bed. Leptosporangiate ferns (Fig. 10) are represented by *Oligocarpia lindsaeoides* and poorly preserved foliage of *Sphenopteris* sp. Very rare is also foliage of *Pecopteris aspidioides* Sternberg, 1825 (Fig. 10) as the only representative of marratialean ferns.

Medullosan pteridosperms are represented by foliage of *Laveineopteris loshii* (Brongniart) Cleal, Shute & Zodrow, 1990 (Figs 13, 16A) accompanied by five species of lyginodendrids (Table 2, Figs 10, 14): *Eusphenopteris*

Figure 8. Remains of *Lepidodendron* (*Paralycopodites*) *simile* sensu Němejc, 1947 and its cones preserved in the Bělka tuff bed of the S3 excavation. • A – branch with attached S-shaped leaves (scale bar 10 mm). • B – terminal shoot (scale bar 5 mm). • C – dichotomizing branch with attached leaves (scale bar 10 mm). • D – small bisporangiate *Flemingites*-type of cone (scale bar 5 mm). • E – bisporangiate *Flemingites*-type of cone preserved partly in 3D (scale bar 10 mm). • F – partly deformed bisporangiate *Flemingites*-type of cone (scale bar 5 mm). • G – leafy shoot of *L. simile* in organic connection (arrow) with *Flemingites*-type of cone (scale bar 10 mm). • H – *Flemingites*-type of cone with well preserved sporangia (scale bar 5 mm).

Figure 9. Lycopsid remains from the Bělka of the S3 excavation. • A – leafy shoot of *Lepidophloios acerosus* (scale bar 100 mm). • B – nearly complete *Lepidostrobus* sp. cone which belongs to *Lepidophloios acerosus* (scale bar 40 mm). • C – remain of fertile axis of subarborescent lycopsid *Spencerites havlenae* (scale bar 10 mm). • D – partly decorticated sigillariean stem (scale bar 5 mm). • E – sterile part of epiphytic bisporangiate herbaceous lycopsid (scale bar 10 mm).

Figure 10. Distribution of fossil remains of *Pecopteris aspidioides*, *Oligocarpia lindsaeoides*, *Sphenopteris* sp., *Sigillaria* sp., *Spencerites havlenae*, *Eusphenopteris nummularia*, *Selaginella* cf. *gutbieri* and herbaceous bisporangiate lycopsid found in the S3 excavation in the Bělka tuff bed. Numbers indicate height (in mm) above the top of the Lower Radnice Coal.


A
B
C
D
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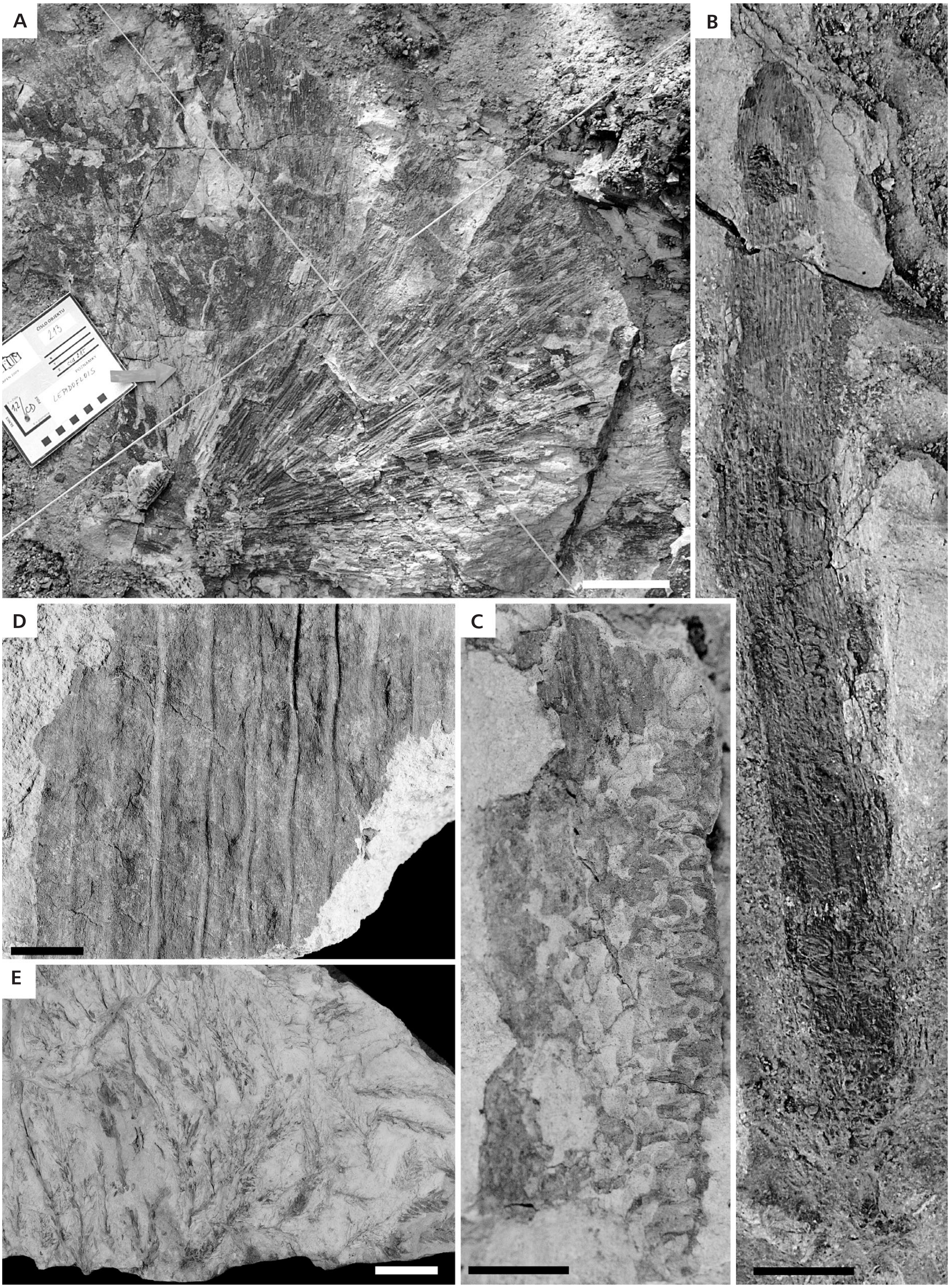
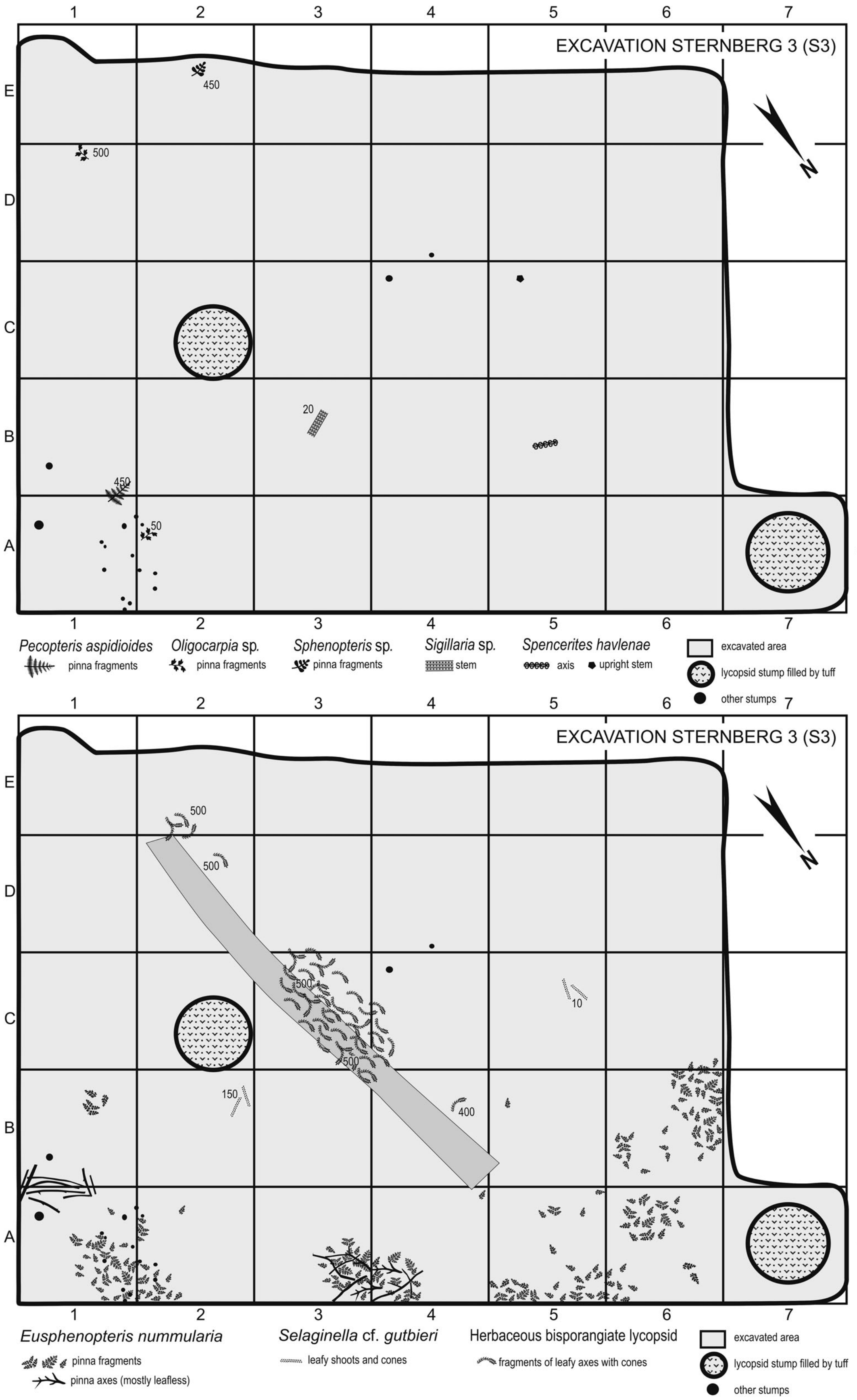
H


A
B
D
C
E


EXCAVATION STERNBERG 3 (S3)
1 2 3 4 5 6 7
A B C D E
N
500
450
20
50
Pecopteris aspidioides
pinna fragments
Oligocarpia sp.
pinna fragments
Sphenopteris sp.
pinna fragments
Sigillaria sp.
stem
Spencerites havlenae
axis
upright stem
excavated area
lycopsid stump filled by tuff
other stumps
EXCAVATION STERNBERG 3 (S3)
500
150
400
10
Eusphenopteris nummularia
pinna fragments
pinna axes (mostly leafless)
Selaginella cf. gutbieri
leafy shoots and cones
Herbaceous bisporangiate lycopsid
fragments of leafy axes with cones
excavated area
lycopsid stump filled by tuff
other stumps

nummularia (Gutbier) Novik, 1947 (Fig. 16B), *Sphenopteris mixta* Shimper, 1869 (Fig. 16C), *Palmatopteris furcata* (Brongniart) Potonié, 1891 (Fig. 16D), *Sphenopteris spinosa* Goeppert and *Mariopteris muricata* (Brongniart) Zeiller, 1879. *Palmatopteris furcata* (Brongniart) Potonié, 1891, which is less common than the dominant *E. nummularia*, was concentrated in two spots around the NE corner of the excavation, an area of less than 1 m in breadth, suggesting only one plant (two fronds found). Large fronds fragments of *S. mixta* occupied about 3 m^2 near the excavation centre 1 to 5 cm above the base of the tuff bed suggesting burial of the whole plant (Figs 14, 16C). *Mariopteris muricata* (Brongniart) Zeiller, 1879 is represented only by an ultimate pinna fragment found near the excavation margin, which suggests that the plant itself grew outside the uncovered area. *Sphenopteris spinosa* occurred also as small tiny frond fragments found in the middle of the excavation.

Cordaitaleans are represented by isolated leaves, found sparsely scattered in various parts of the excavation and only rarely attached to branches (Figs 7, 17). Leaf cuticles are identical with those described by Šimůnek *et al.* (2009) from type specimen of *C. borassifolius* (Sternberg) Unger, 1850. Associated are rare findings of isolated seeds of the *Cardiocarpus*-type. Naked branch fragments were reliably identified as belonging to cordaitaleans only where the central artisia-type of pith hollow was found (Fig. 17B, C). Those without this key-taxonomic feature were impossible to distinguish from pteridosperm axes or other unidentifiable fragments that still make up a significant part of the fossil record. This was partly confirmed by the observation that some of these "unidentifiable axes" under SEM showed the presence of rays and tracheids sometimes with pitting typical of cordaitalean plants (Fig. 17D). Remaining axes are of various diameters (ranging from about few centimetres to about 25 cm) and length between 10 and >400 cm. Their identification remains difficult or impossible because of an absence of diagnostic features due to a decortication and/or partial decomposition. The axes are mostly randomly oriented and located at various levels above the tuff base. Fragments of the largest diameter, potentially stems, often obliquely penetrate the tuff bed and end in the overlying Brousek (tuffite) (Opluštil *et al.* 2009a, pl. III). Various degrees of decomposition (from relatively fresh to decomposed without any structure) and random orientation indicate that this part of fossil record represents both plant litter or plants that died and had fallen prior the eruption as well as plants that were well alive and standing when the volcanic ash began to fall. The latter entered into the fossil record as branches broken off due to volcanic ash loading or as the whole plants were levelled for the same reason. This is in agreement with the generally high degree of decomposition observed under SEM on specimens from the basal part of the tuff (Fig. 18A), whereas specimens from the upper part of the tuff bed are usually anatomically very well preserved (Fig. 18B).

During the excavation of the tuff bed, several upright decorticated lycopsid and cordaitalean stems were found. The diameter of most of them varies between 1 and 8 cm (2–3 cm in average); however, two of them are 60 and 80 cm in diameter. These large stems end in basal part of the tuffite bed (Brousek) and are filled by tuff (not by Brousek) (Fig. 18C), which clearly indicates they were stumps already prior to the volcanic eruption. Remaining small stems were identified as calamitaleans (Fig. 18D), ferns (*Corynepteris angustissima*) and sphenophylls (*Sphenophyllum priveticense*), rooted in the roof of coal.

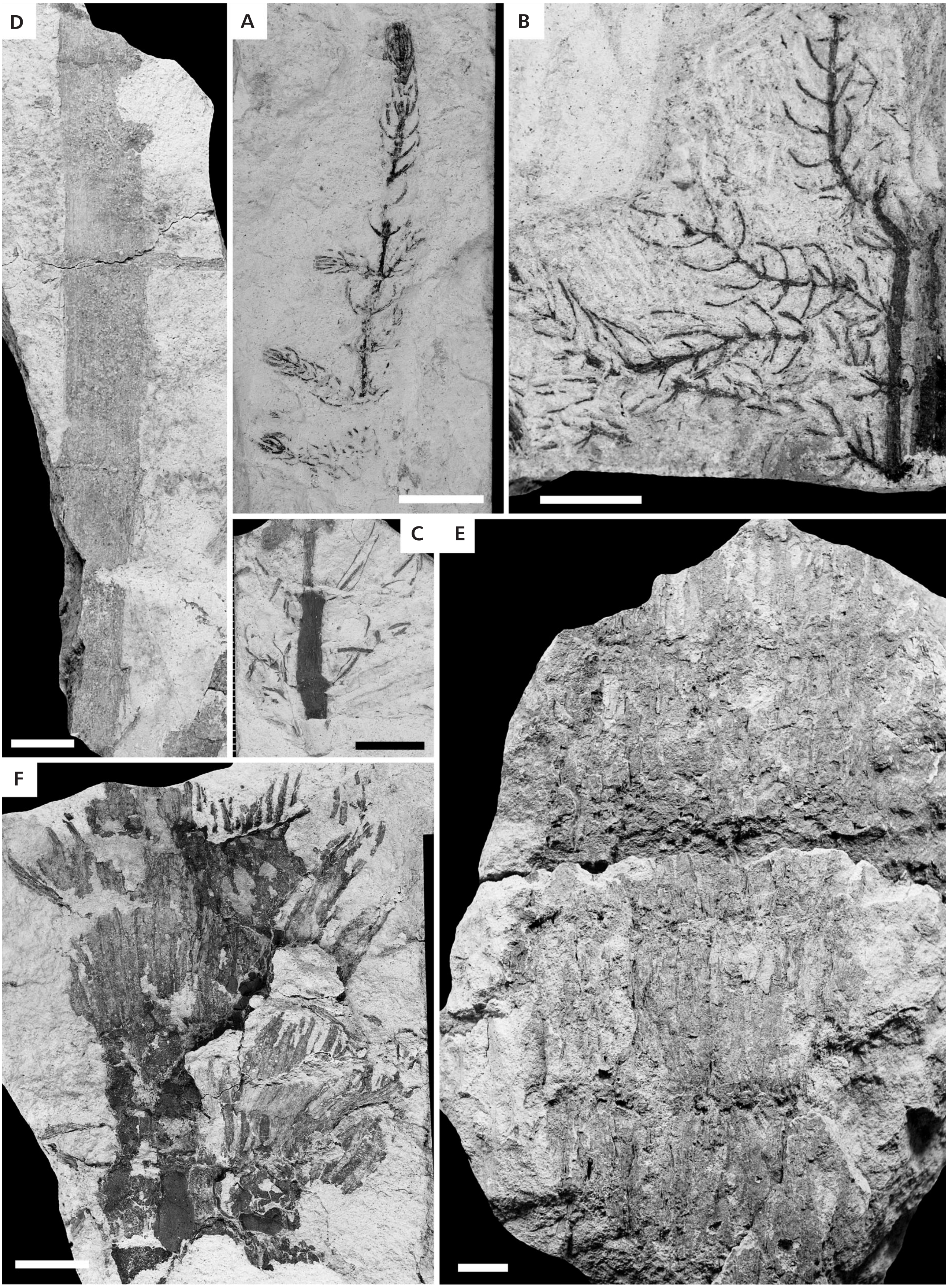
Discussion on structure of the plant assemblage uncovered in the S3 excavation

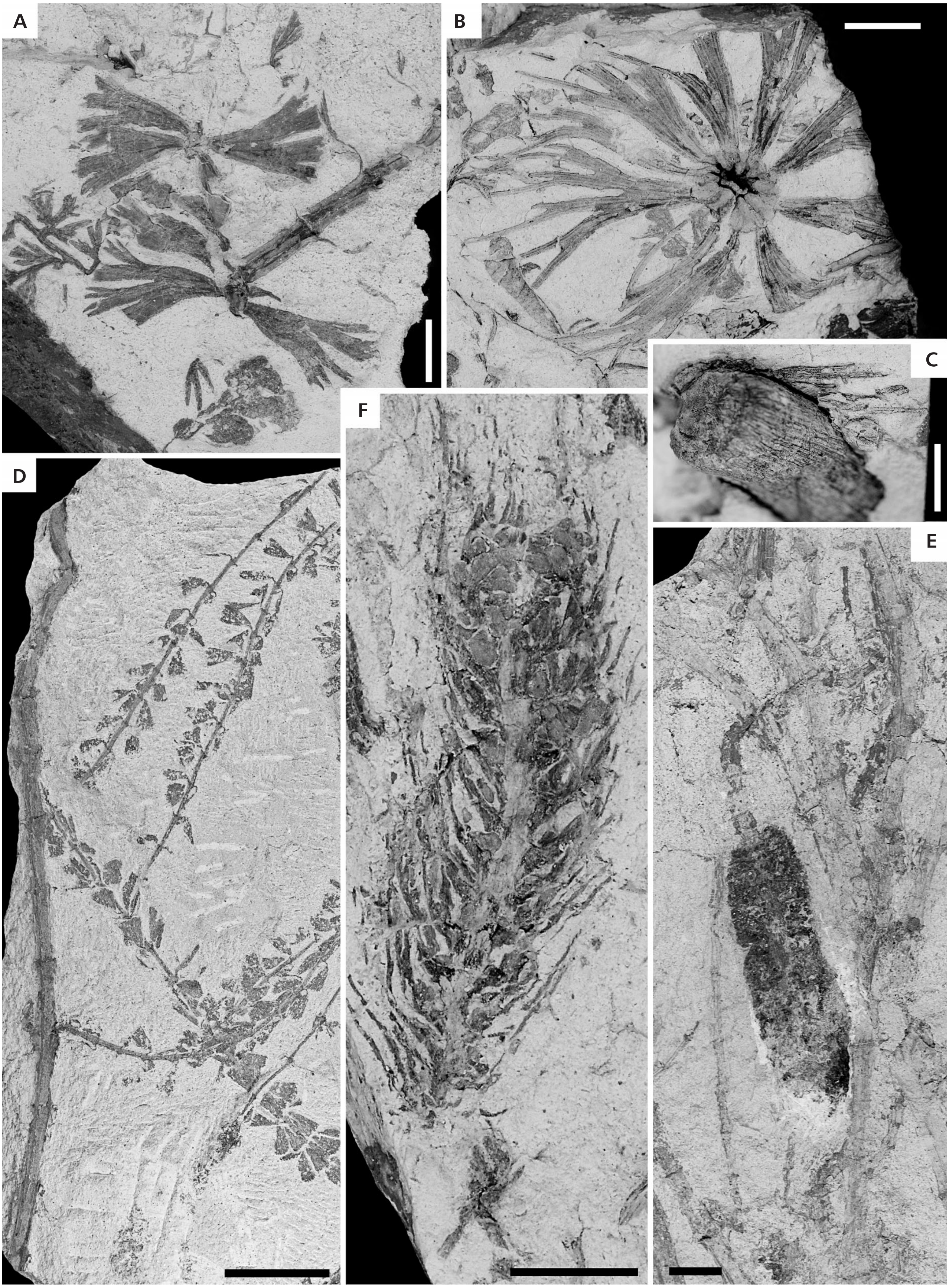
Plants found in the excavation represent a wide spectrum of growth forms. This suggests the existence of taxa of different life strategies, which together formed a diversified and well-structured forest phytocoenosis. Based on our

Figure 11. Sphenopsid remains found in the S3 excavation. • A – apical part of *Calamites* foliage *Asterophyllithes* cf. *grandis* (scale bar 10 mm). • B – *Calamites* foliage *Asterophyllithes* cf. *grandis* (scale bar 10 mm). • C – *Asterophyllithes longifolius* (scale bar 10 mm). • D – *Stylocalamites*-type of stem with one branch (scale bar 10 mm). • E – the *Calamitina*-type of stem in advanced stage of decay (scale bar 10 mm). • F – the *Calamariophyllum* associated with *Calamitina*-type of stem.

Figure 12. Sphenophyllalean remains from the Bělka tuff bed of the S3 excavation. • A, B – *Sphenophyllum priveticense* (scale bar 5 mm). • C – 3D preservation of axis of *Sphenophyllum priveticense* (scale bar 5 mm). • D – *Sphenophyllum cuneifolium* (scale bar 30 mm). • E – ?*Bowmanites cuneifolius* (scale bar 10 mm). • F – *Bowmanites* sp. (scale bar 5 mm).

Figure 13. Distribution of fossil remains of selected plant taxa uncovered in the S3 excavation in the Bělka tuff bed. Numbers indicate height (in mm) above the top of the Lower Radnice Coal.


D
A
B
C
E
F


A
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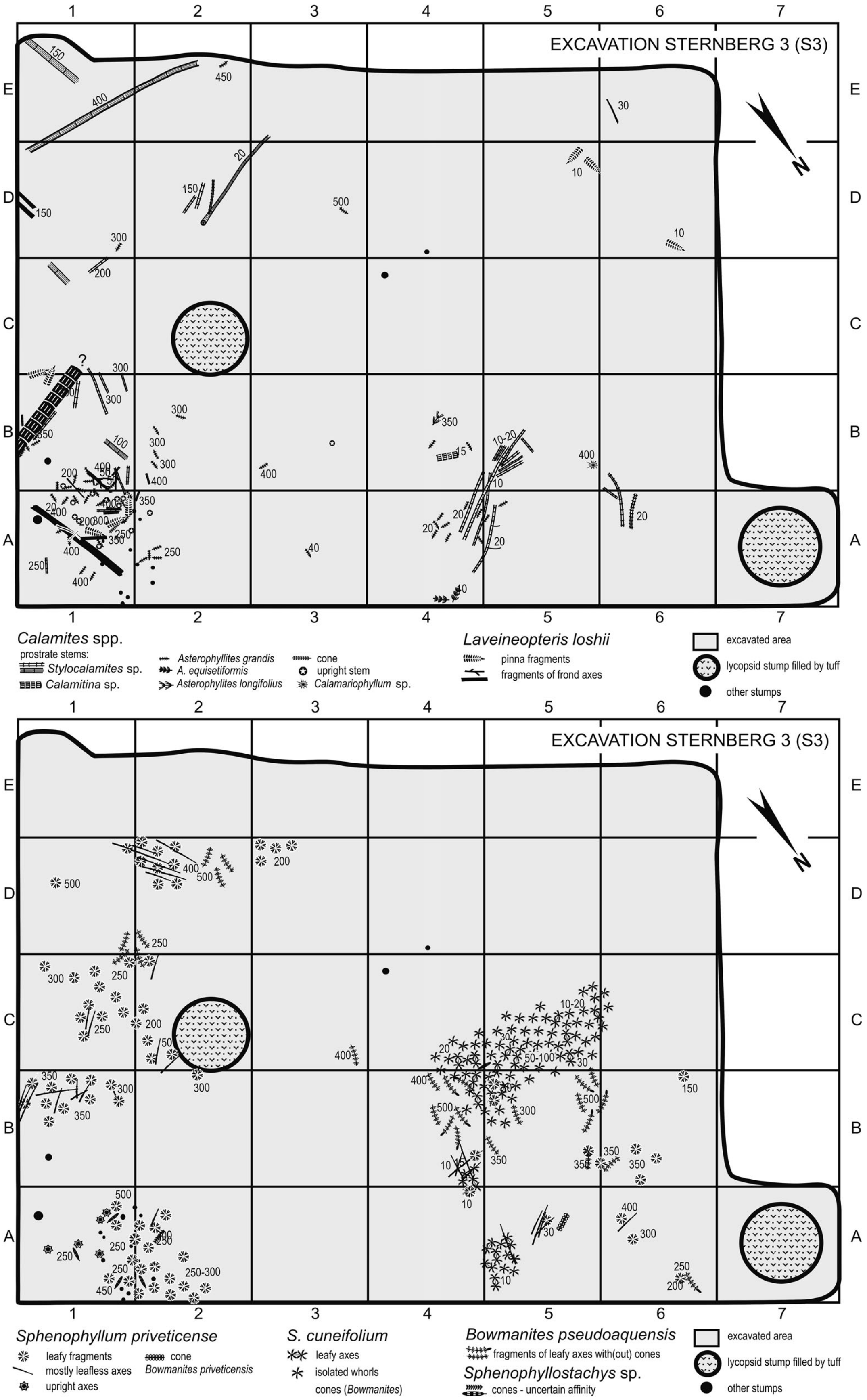

EXCAVATION STERNBERG 3 (S3)
Calamites spp.
prostrate stems:
Stylocalamites sp.
Calamitina sp.
Asterophyllites grandis
A. equisetiformis
Asterophyllites longifolius
cone
upright stem
Calamariophyllum sp.
Laveineopteris loshii
pinna fragments
fragments of frond axes
excavated area
lycopsid stump filled by tuff
other stumps
EXCAVATION STERNBERG 3 (S3)
Sphenophyllum priveticense
leafy fragments
mostly leafless axes
upright axes
cone
Bowmanites priveticensis
S. cuneifolium
leafy axes
isolated whorls
cones (Bowmanites)
Bowmanites pseudoaquensis
fragments of leafy axes with(out) cones
Sphenophyllostachys sp.
cones - uncertain affinity
excavated area
lycopsid stump filled by tuff
other stumps

observations from this and previous excavations and/or published data (*e.g.* Opluštil *et al.* 2009a or Pšenička & Opluštil 2013 for an overview) we subdivided particular plant species into four basic groups, which occupied different stories (Table 3) in the former peat-forming phytocoenoses: (1) canopy; (2) understory; (3) lianas and epiphytes and (4) ground cover and occasional climbers (the latter initially grow as ground cover). This subdivision is, however, rather arbitrary, and no sharp boundaries existed between the individual stories.

The following discussion on structure of vegetation cover results from an assumption that plants were buried *in situ.* In such a case, the distribution of small ground-cover plants almost faithfully outlines the original site of growth whereas the distribution of crown remains of arborescent species can be used only as a proxy to estimate the crown diameter due to dispersal of falling leaves, shoots and branches.

Canopy

Canopy taxa in the S3 excavation include four arborescent lycopsids (*Lepidodendron simile*, *L. lycopodioides*, *Lepidophloios acerosus* and *Sigillaria* sp.) and *Cordaites borassifolius* (Table 3). Their remains together covered about 53% of the excavation, however, the area occupied by particular species differs significantly (Figs 19–21). The most widespread were branches, leafy shoots and cones of *L. simile*, which covered about 14.2 m^2 (*i.e.* 42%) of 33.5 m^2 of the excavated area (Table 3, Figs 5, 18). Absence of an appropriate stump or erect lycopsid stem(s), however, suggests that the parent plant(s) grew outside the excavation area but its crown overlapped its adjacent NW part. It is estimated that crown had to reach about 5–6 m in diameter since the canopy fragments occurred up to 3 m from the excavation margin. This size is consistent with observations from previous excavations (Opluštil *et al.* 2009a, b). The tree was evidently in full sexual maturity as proved by tens of bisporangiate *Flemingites*-type cones often organically attached to leafy shoots (Fig. 8G). These cones indicate that *L. simile* belongs to anatomically defined lepidodendrid genus *Paralycopodites* which bears two opposite rows of lateral branches with cones resulting in continuous reproduction once the plant reached sexual maturity (DiMichele & Phillips 1994). The second most common canopy taxon was *Cordaites borassifolius* the remains of which covered 1.5 m^2, *i.e.* 4.4% of the studied area on two opposite sides of the excavation (Figs 7, 20). No corresponding upright stem was discovered and therefore we assume that one parent plant grew behind the western or northern excavation limit (next to *L. simile*) and another probably several meters east of the excavated area. The former tree was mature, as indicated by the presence of rare isolated *Cardiocarpus* seeds. Third in order of canopy taxa is *Lepidophloios acerosus*. Its leafy shoots and cones covered only 0.8 m^2, *i.e.* 2.4% of the excavation, although loose leaves were very sparsely scattered over an area of about 12.5 m^2 (Table 3, Figs 7, 20). No corresponding upright stem occurred in the excavated area, which indicates that the parent tree grew probably near the eastern margin of excavation S3. Similarly the least represented canopy species *Lepidodendron lycopodioides* grew few meters south of the excavation as indicated by several terminal leafy shoots found near the SE edge of the S3 excavation (Fig. 7).

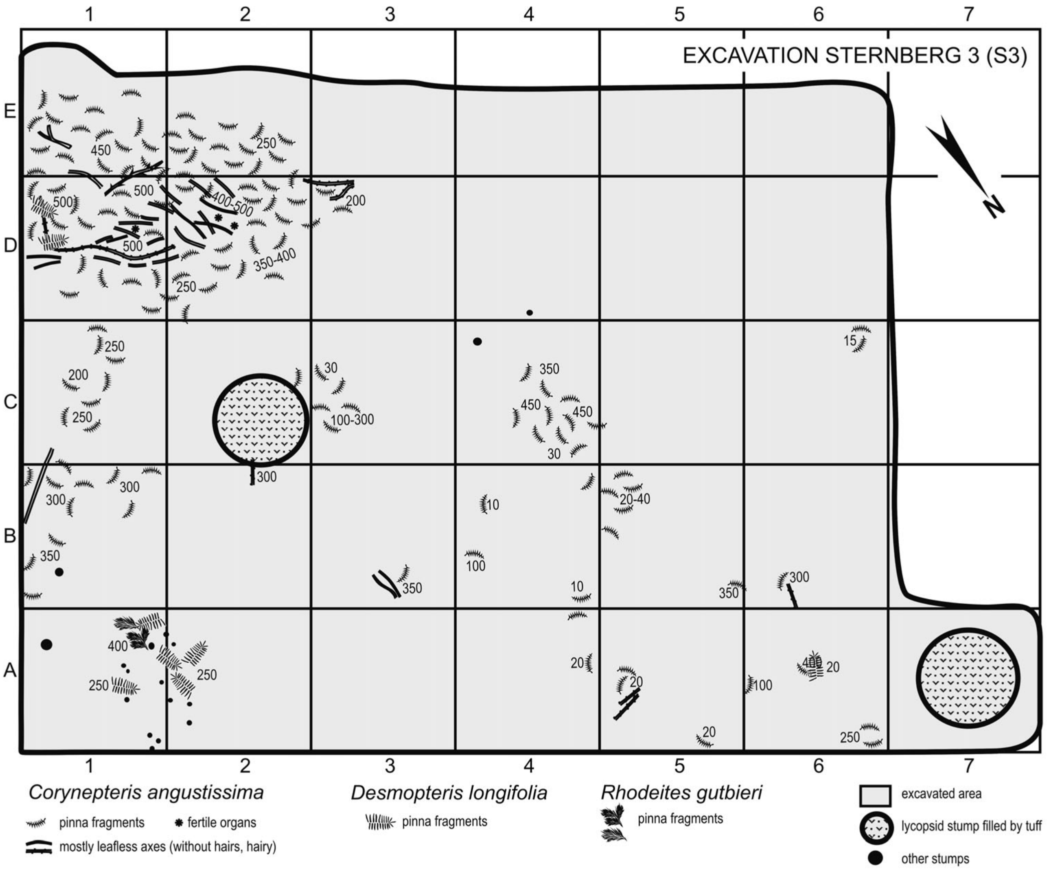
Remains of lycopsids are preserved mostly as coalified compressions in the Bělka bed, however, part of tissues is often permineralised and anatomically preserved, as already observed by Corda (1845). Here-described examples represent fragments of a vascular cylinder with primary xylem tissue and outer cortex of terminal shoots of *Lepidodendron simile* (Fig. 18E, F). This species produced small bisporangiate cones, which suggests that it corresponds to anatomically defined genus *Paralycopodites* (DiMichele 1980). Secondary xylem usually does not develop in the terminal shoots, in this case most likely from deciduous lateral branch systems, which is in agreement with the general pattern of determinate growth of these plants (*e.g.* Eggert 1961, Němejc 1963). Cortical zones have not been observed.

Absence of parent stems of canopy taxa does not allow application of the Niklas (1994) formula as a proxy for calculation of tree heights. However, similar calculations for the same plant species discovered in surrounding excavations suggest that in all cases canopy occupied level between 15 and 23 m above the ground (Opluštil *et al.* 2009a, b).

Understory ("shrubs")

This level includes medium-size plants (probably between 2 and 7 m in height) represented by medullosan pteridosperms (*Laveineopteris loshii*) and calamitaleans (Table 3, Fig. 19). Remains of *L. loshii* are scattered in the NE and near SW corners as small, mostly ultimate pinna and rachis fragments over an area of about 1 m^2 (Fig. 13). Associated in the B1 is a small upright stem about 80 mm in diameter showing an aerial root mantle, which potentially might represent parent stem of the *L. loshii* foliage. It is assumed that this species was relatively a small tree, and that a main

Figure 14. Distribution of fossil remains of selected ferns and pteridosperm species uncovered in the S3 excavation in the Bělka tuff bed. Numbers indicate height (in mm) above the top of the Lower Radnice Coal.


EXCAVATION STERNBERG 3 (S3)
N
Corynepteris angustissima
pinna fragments
fertile organs
mostly leafless axes (without hairs, hairy)
Desmopteris longifolia
pinna fragments
Rhodeites gutbieri
pinna fragments
excavated area
lycopsid stump filled by tuff
other stumps

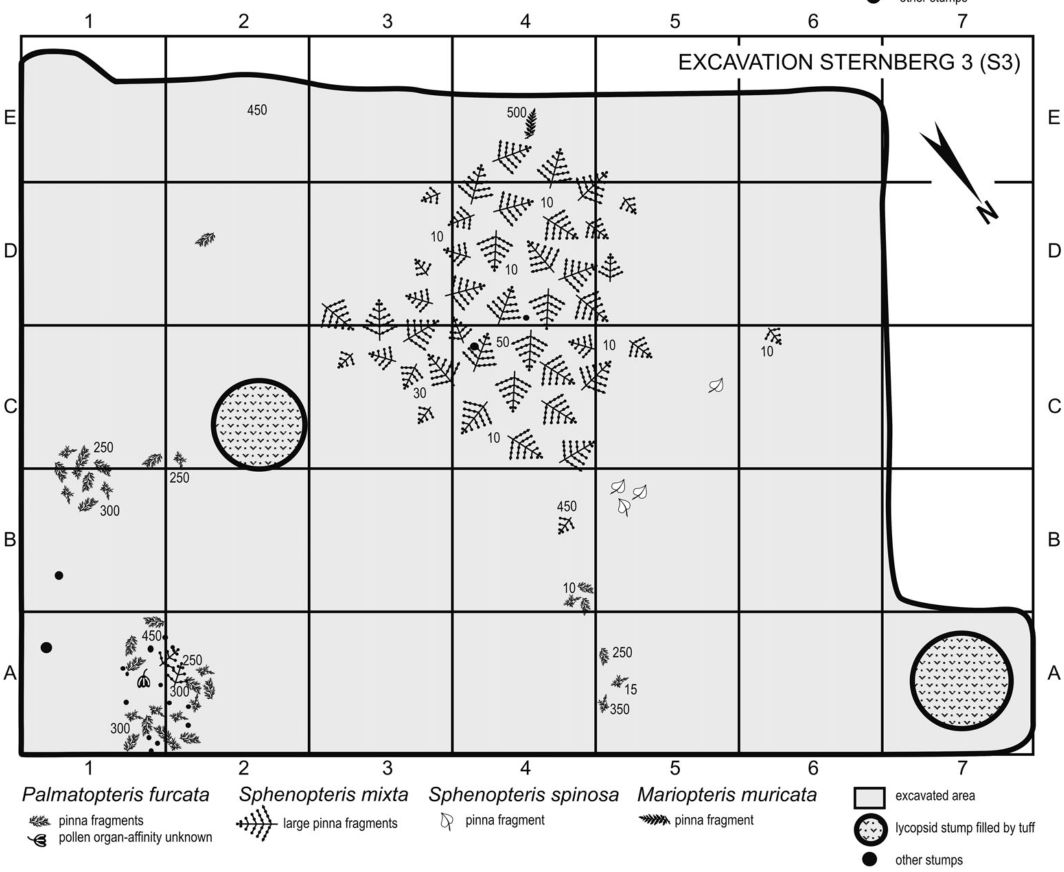

EXCAVATION STERNBERG 3 (S3)
N
Palmatopteris furcata
pinna fragments
pollen organ-affinity unknown
Sphenopteris mixta
large pinna fragments
Sphenopteris spinosa
pinna fragment
Mariopteris muricata
pinna fragment
excavated area
lycopsid stump filled by tuff
other stumps

Table 2. The list of taxa found in the excavations held at the Ovčín coal deposit. Species highlighted in grey occurred in all or most excavations and are considered as typical elements of the Ovčín coal forest.

	Plant groups			Species	O1	O2	O3	S1	S2	S3
1	**Lycopsida**	Arborescent forms	Cone	*Flemingites* sp.			+	++	++	++
2				*Lepidostrobus* sp.	+		+	++	++	+
3				*Lepidocarpon majus*		+				
4			Stems	***Lepidodendron simile***	+	+	++	++	++	++
5				*Lepidodendron lycopodioides*	++	++	++	+		+
6				*Lepidodendron longifolium*					+	
7				***Lepidophloios acerosus***	+	+	+	++	++	+
8				*Sigillaria* sp.						+
9		Sub-arborescent forms		*Spencerites havlenae*	+	+	++	+		+
10		Herbaceous forms		*Selaginella* cf. *gutbieri*		+	+			+
11				Herbaceous bisporangiate lycopsid					+	++
12	**Sphenopsida**	Calamites	Leafy shoots	*Asterophyllites longifolius*		+	+			+
13				*Asterophyllites equisetiformis*		+	+			+
14				*Asterophyllites* cf. *grandis*	+	+	+			+
15				*Asterophyllites* sp.				+		
16				*Calamariophyllum* sp.		+	+			+
17			Cones	*Palaeostachya gracillima*	+	+		+		
18				*Palaeostachya distachya*	+	+	+			
19			Stems	***Stylocalamites* sp.**	++	++	++	++	++	++
20				*Calamitina* sp.(*C.*cf. *goeppertii*)	+	+	+		+	+
21		Sphenophylls		***Sphenophyllum priveticense***	++	+	++	++	+	++
22				*Bowmanites pseudoaquensis*	+		+	+	++	+
23				*Sphenophyllum cuneifolium*			+			++
24	**Filicopsida**	Marattialean ferns		***Pecopteris aspidioides***	+	++	+	+	++	+
25		Zygopterid ferns		***Corynepteris angustissima***	++	++	++	+	+	++
26				*Desmopteris longifolia*	++	+	++	+		+
27				*Rhodeites gutbieri*						+
28		Other ferns		*Hymenotheca* sp.	+		++	+		
29				*Senftenbergia plumosa*		+	+			
30				*Sonapteris bekii*	+					
31				*Oligocarpia lindsaeoides*	+	+	+			+
32				*Sphenopteris* sp.				+		+
33	**Pteridospermopsida**	Medullosalean pteridosp.		*Laveineopteris loshii*	++	++	+	++		+
34		Lyginodendrid Pteridosperms		*Sphenopteris mixta*	++		++	+	+	++
35				*Mariopteris muricata*				++	+	+
36				*Palmatopteris furcata*	++	+	++	+		+
37				*Sphenopteris spinosa*	+		+			+
38				***Eusphenopteris nummularia***	+	++	++	+	++	++
39	**Progymnospermopsida**			*Adiantites* sp.		+				
40	**Cordaitopsida**	Cordaites	Cones	*Cordaitanthus* sp.	+		+		+	
41			Seeds	*Cardiocarpus* sp.	+		+	+		+
42			Leaves	***Cordaites borassifolius***	++	+	++	++	++	+
43			Pith casts	*Artisia* sp.	+	+	+	+	+	+
Number of species				Excavations separately	27	26	32	24	17	33
				Excavation groups	36	27	33			
Estimated number of biological species				Excavations separately	**20**	**18**	**22**	**18**	**13**	**25**
				Excavation groups	**24**	**20**	**25**			
Area of sampling (m^2)				Excavations separately	21	22.5	50	25	25	33.5
				Excavation groups	93.5	50	33.5			

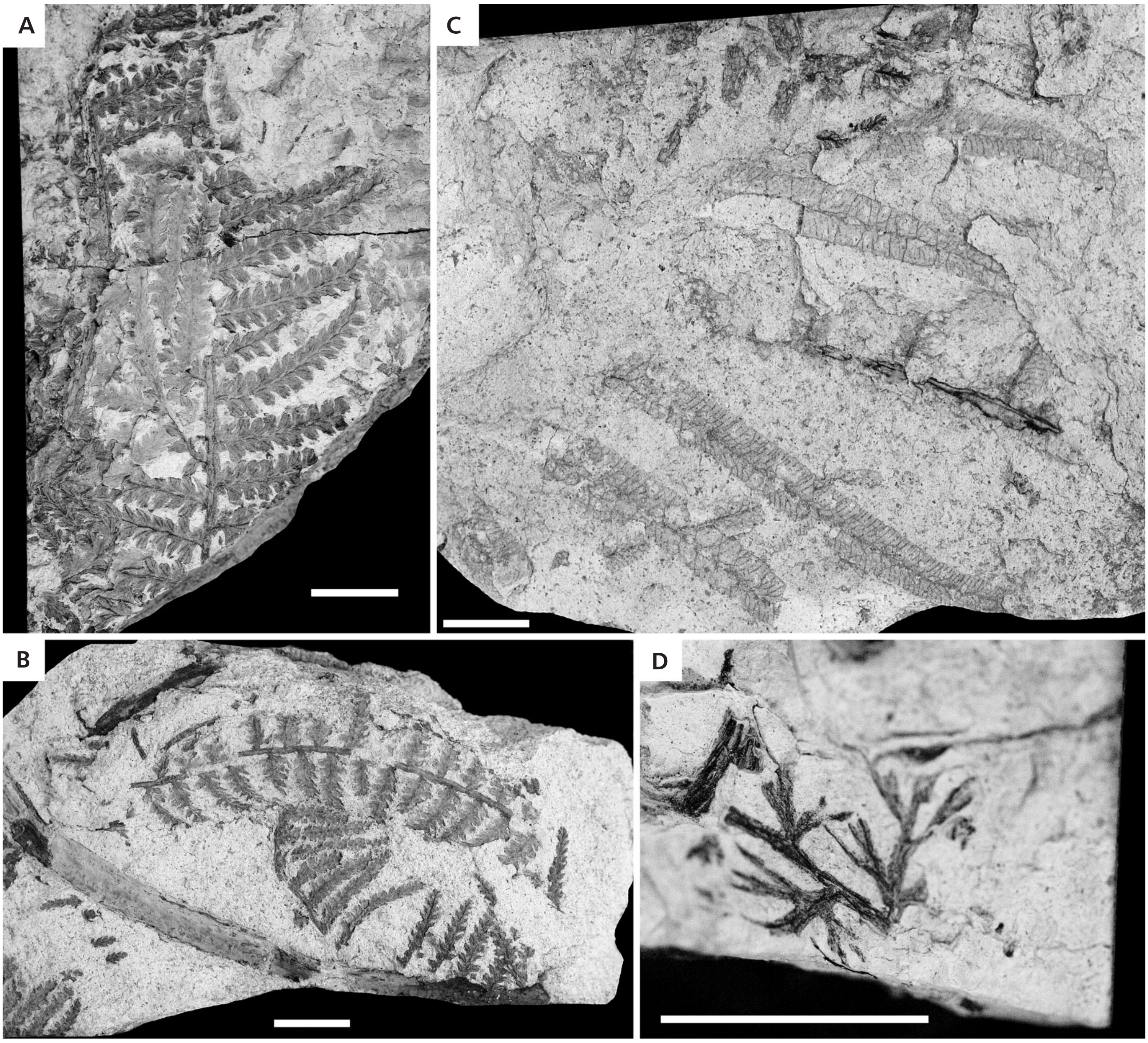


Figure 15. Fern remains found in the Bělka tuff bed of the S3 excavation. • A, B – zygopterid fern *Corynepteris angustissima* (scale bar 10 mm). • C – zygopterid fern *Desmopteris longifolia* (scale bar 10 mm). • D – small fragment of probably a zygopterid fern *Rhodeites gutbieri* (scale bar 10 mm).

stem 80 mm wide may well have been that of a fully mature plant. Paralel explanation that it was a small, pre-reproductive, juvenile plant does not seem correct since Shute & Cleal (2002) suggested that juvenile *Laveineopteris* had cyclopterid rather than pinnate foliage. However, no cyclopterids have been found. Instead presence of mostly naked rachises and rareness of foliage suggest that either foliage was present only in distal part of fronds reaching mostly outside the excavation. Ruled out cannot be also a possibility that the parent plant may have been growing outside the excavation with some fronds overlapping the excavation margin. This is probably also the case for a minor occurrence of such foliage in D5–6 near the SW corner, which also lacks a corresponding upright stem. Therefore it is assumed that the parent plant grew south of the excavation.

Calamitalean remains are represented by naked axes with distinct nodes and internodes of two types. More common but generally smaller axes (usually between 1 and 3 cm thick) are assigned to *Stylocalamites*, whereas up to 8 cm thick axes belong to the *Calamitina*-type. They are associated (not organically connected) with the foliage *Asterophyllithes* cf. *grandis*, *A. equisetiformis* and *A. longifolius*. *Stylocalamites* axes occur usually in clusters along the northern and eastern margin of the excavation. The largest concentration was discovered in A1–2 and B1. It consists of >10 upright stems between 7 and 20 mm in diameter (Fig. 13) and similar amount of prostrate naked

Table 3. Interpreted growth habit, surface area, percentage cover, and normalized contribution to percent cover of each biological species in the S3 excavation.

Species	Habit	Area (m^2)	Percentage cover (%)	Normalised contribution (%)
"*Lepidodendron*" *simile*	Canopy	14.2	42.4	25.1
Corynepteris angustissima	Ground cover	5.7	17.0	16.3
Sphenopteris mixta	Ground cover	4.05	12.1	11.5
Stylocalamites sp., *Calamitina* sp.	Understory	3.25	9.7	9.2
Eusphenopteris nummularia	Liana	2.8	8.4	8.0
*Sphenophyllum priveticense**	Ground cover	2.75	8.2	7.8
Sphenophyllum cuneifolium	Ground cover	1.51	4.5	4.3
Cordaites borassifolius	Canopy	1.48	4.4	4.2
Herbaceous bisporangiate lycopsid	Liana/epiphyte	1.03	3.1	2.9
*Bowmanites pseudoaquensis***	Liana	0.83	2.5	2.4
Lepidophloios cf. *acerosus*	Canopy	0.8***	2.4	2.3
Laveineopteris loshii	Understory	0.86	2.6	2.6
Palmatopteris furcata	Liana	0.8	2.4	2.3
Sigillaria sp.	Canopy	0.3	0.1	0.1
Desmopteris longifolia	Ground cover	0.12	0.4	0.3
Lepidodendron lycopodioides	Canopy	0.06	0.2	0.2
Sphenopteris spinosa	Ground cover	0.05	0.1	0.1
Spencerites havlenae	Understory	0.05	0.1	0.1
Selaginella cf. *gutbieri*	?Liana/epiphyte	0.03	0.1	0.1
Oligocarpia lindsaeoides	Liana	0.02	0.1	0.1
Mariopteris muricata	Liana	0.02	0.1	0.1
Pecopteris aspidioides	Understory	0.02	0.1	0.1
Sphenopteris sp.	Ground cover	0.01	0.1	0.1
Rhodeites gutbieri	Ground cover	0.01	0.1	0.1
				Total = 100.0%

* Reported as *Sphenophyllum* cf. *majus* in earlier papers (Opluštil *et al*. 2007, 2009a, b)
** Reported as *Sphenophyllum pseudoaquense* in earlier papers (Opluštil *et al*. 2007, 2009a, b)
*** Isolated leaves omitted. Area covered including isolated leaves = 12.5 m^2

stems and associated foliage fragments. A similar but smaller group of prostrate and >1 m long incomplete calamite stems occurred in units A4–5 a B4–5. The plants, however, were rooted north of the excavation. The largest but still incomplete axes were nearly 2 m long and 4 cm in diameter. The large *Calamitina*-type of stem (Fig. 11E) was identified in B1 and B4 units, which are vertically situated 380 and 100 mm respectively above the roof of the Lower Radnice Coal. The B1 stem is slightly decomposed suggesting it was dead before the eruption. The latter one, from B4, bears leaves of *Calamariophyllum*-type (Fig. 11F).

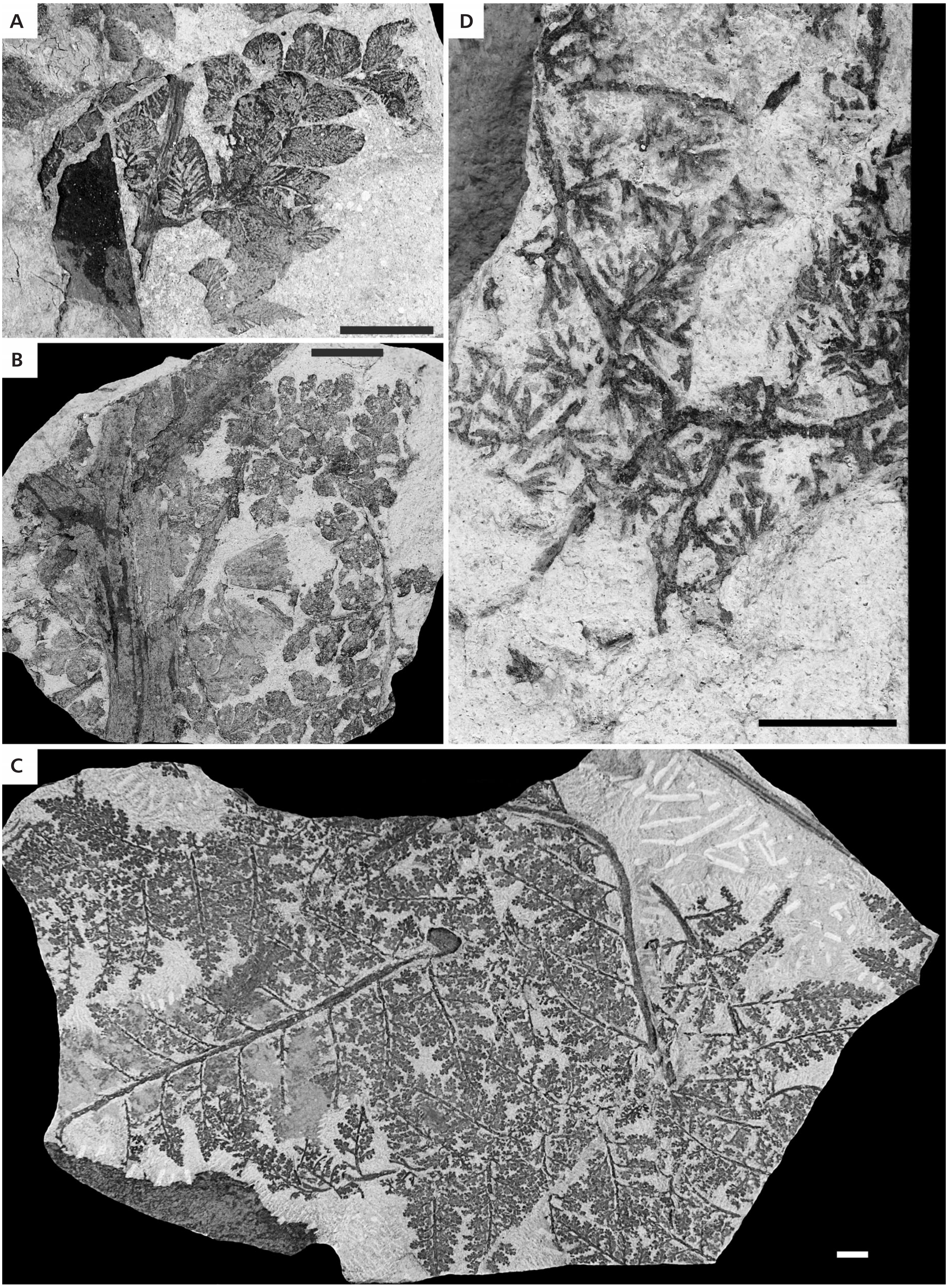
Psaronius, a marattilean tree fern bearing foliage of *Pecopteris* (*Lobatopteris*) *aspidioides* type and common in most other excavations is represented in the S3 excavation only by a small pinna fragment in A1–B1. The plant evidently grew outside the excavated area.

Remains of plants included in the understory category covered about 4.3 m^2, *i.e.* 12.8% of the excavated area, which is much less than in any previous excavation (Figs 19–21). It is the most poorly represented story of the forest and is also low in species diversity. Understory plants display a patchy distribution.

Lianas and/or epiphytes

Recognizing true lianas and epiphytes in the fossil record is problematic because of a very limited potential for these

Figure 16. Remains of some pteridosperm species discovered in the Bělka of the S3 excavation. • A – medullosan pteridosperms *Laveineopteris loshii* foliage (scale bar 10 mm). • B – lyginodendrid pteridosperm *Eusphenopteris nummularia* (scale bar 10 mm). • C – lyginodendrid pteridosperm *Sphenopteris mixta* (scale bar 10 mm). • D – lyginodendrid pteridosperm *Palmatopteris furcata* with a typical frond architecture (scale bar 10 mm).


A
B
C
D

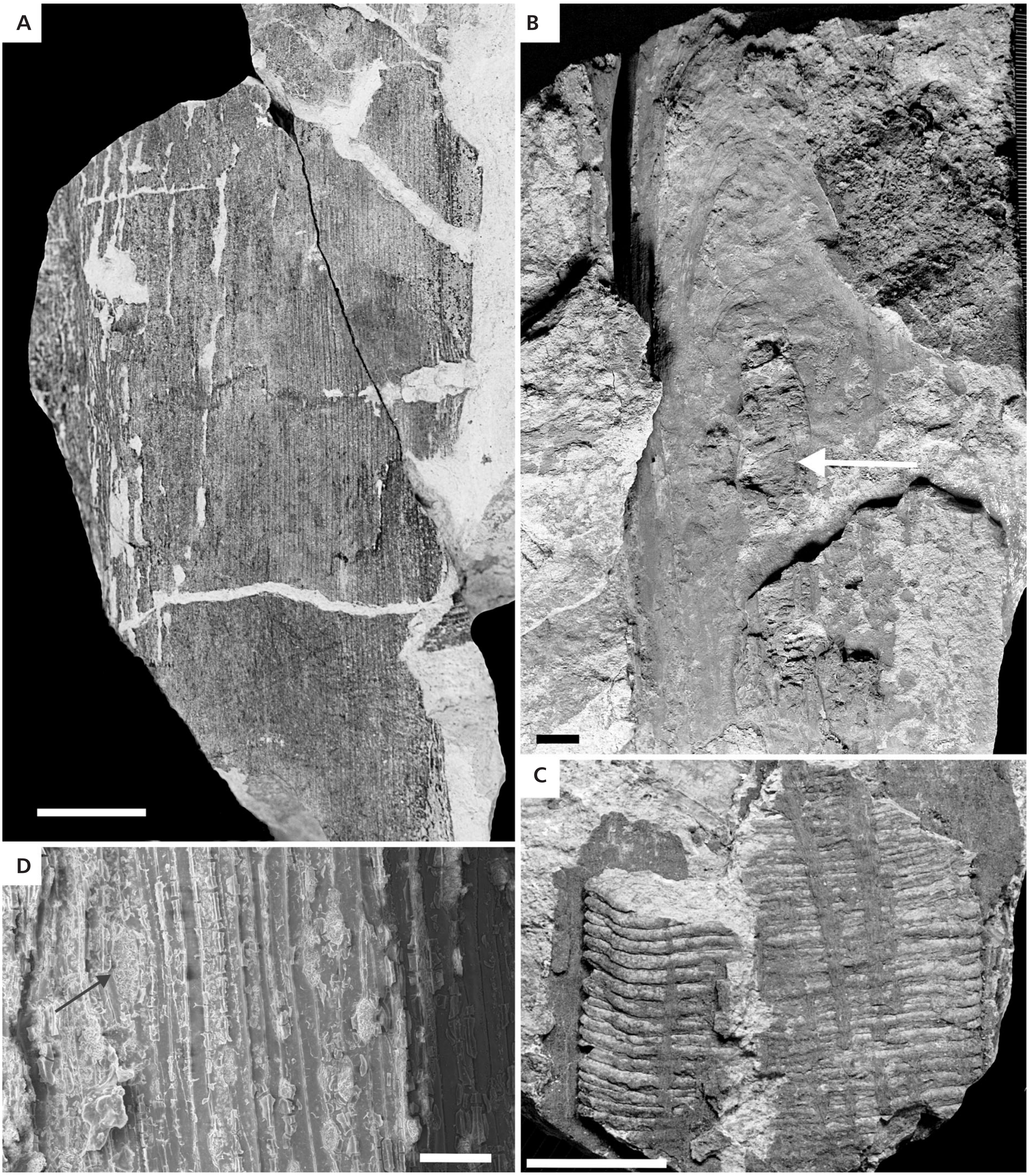


Figure 17. Cordaitalean remains found in the Bělka bed of the S3 excavation. • A – fragment of isolated leave of *C. borassifolius* (scale bar 10 mm). • B – branching point on Cordaites-stem/branch with preserved arthisia-type of pith hollow (arrow), scale bar 10 mm. • C – arthisia-type of pith hollow (scale bar 10 mm). • D – longitudinal anatomical structures of cordaitalean branch with tracheids and rays (arrow) as seen under SEM on unmacerated specimen (scale bar 0.1 mm).

plants to be preserved in growth position. Instead taphonomical processes before burial result in fragmentation and mixing of plants with a variety of habits, making the separation of lianas and epiphytes from other growth forms difficult (Burnham 2009, Pšenička & Opluštil 2013). Therefore the interpretation of these life forms is mostly based on

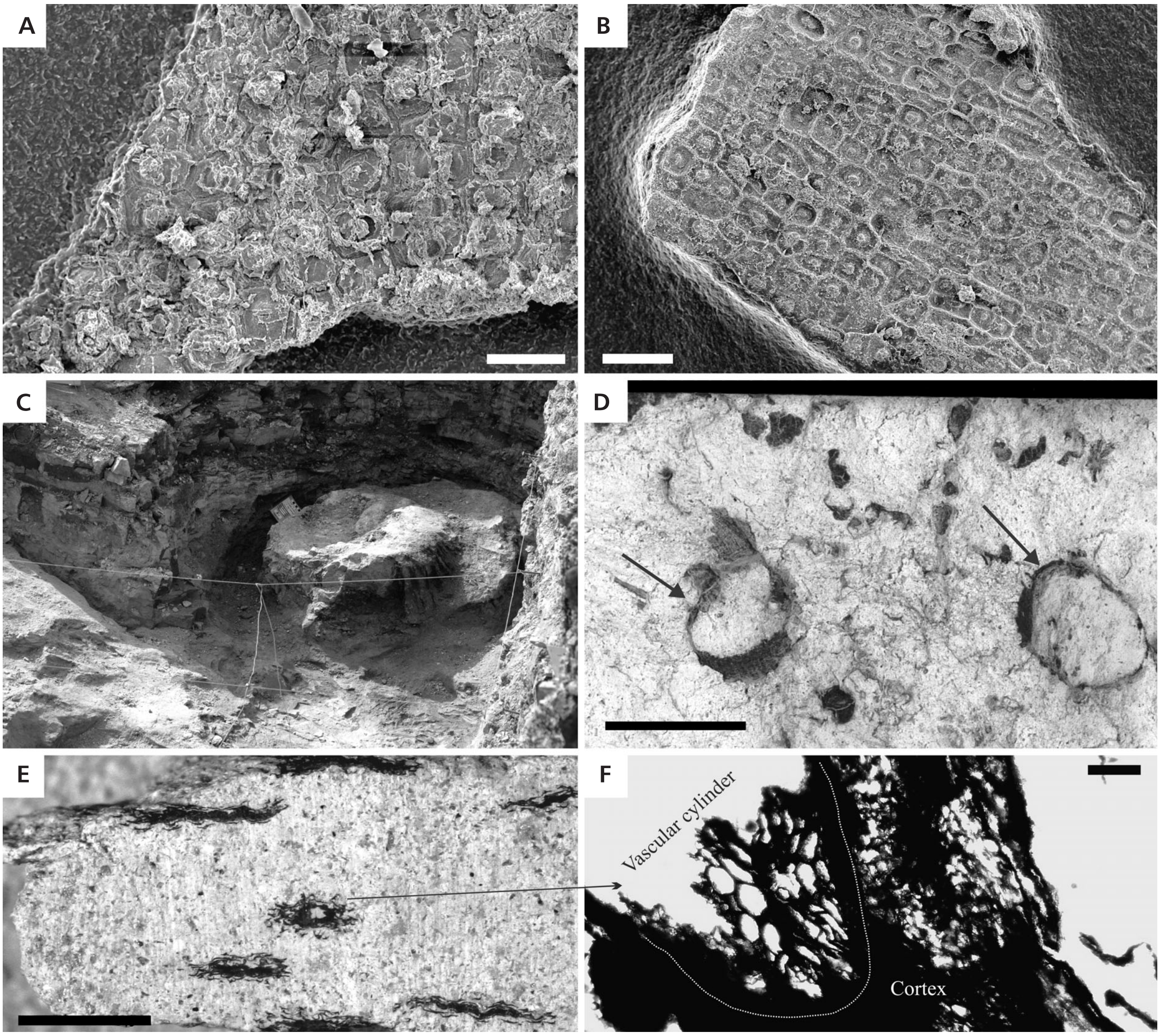


Figure 18. A – parenchymatic tissue from lowermost part of tuff; SEM (scale bar 0.1 mm). • B – the same type of parenchymatic tissue from upper part of tuff; SEM (scale bar 0.2 mm). • C – large stump terminated at the base of the Whetstone tuffite bed (Brousek) and filled by tuff. • D – small upright stems identified as calamites (arrows) (scale bar 10 mm). • E – cross-section of partly anatomically preserved terminal branch of *Lepidodendron* (*Paralycopodites*) *simile* entombed in the Bělka tuff bed, scale bar 5 mm. • F – detail of vascular cylinder with primary xylem tissue and outer cortex, scale bar 0.1 mm. All the specimens were found in the S3 excavation.

a range of indirect evidence including anomalous wood anatomy, small stem diameter relative to length and size of supported foliage, and presence of organs adapted to climbing, such as hooks, spines, and grappling structures (*e.g.* Kerp & Krings 1998, DiMichele *et al.* 2006, Burnham 2009), rather than on direct observations (Opluštil *et al.* 2009a, Gradzinski & Doktor 1995).

Interpretation of these life forms in this paper is based both on published data (in the case of *Eusphenopteris nummularia*, *Palmatopteris furcata* and *Mariopteris muricata*) and our own observations from this and previous excavations (Opluštil *et al.* 2009a, b). The latter include presence of climbing aids, such as hooks on the stem and pinnules, thin stems and specific features of anatomy in case of *Bowmanites pseudoaquensis*, *Oligocarpia* sp. and *Sonapteris* sp. (Libertín *et al.* 2008, Pšenička & Bek 2001, Pšenička *et al.* 2005). However, also important is the vertical distribution of plant fossils (Pšenička & Opluštil 2013) within the deposit; remains of lianas and epiphytes are mostly concentrated to the upper(most) part of the Bělka tuff bed. Here they were buried in the later phase of volcanic ash fall as parts of canopy (branches and leafy shoots) were broken off due to volcanic ash loading carrying with them any attached lianas and epiphytes. Typical representatives and potential candidates for lianas and even for epiphytes are the two different species of herbaceous lycopsids (*Selaginella* cf. *gutbieri* and the second species is an unidentified herbaceous bisporangiate lycopsid) the remains of which predominantly occur in the upper part of the Bělka bed in association of canopy elements derived from arborescent lycopsids. Moreover, in this particular excavation, we discovered a nearly complete plant of a bisporangiate herbaceous lycopsid attached (in a unit C3) (Fig. 22) to a large lycopsid stem obliquely penetrating the tuff bed up to the base of the overlying tuffite (Brousek) (see Pšenička & Opluštil 2013). A few smaller remains of the same species occurred about one meter up and down the stem. Although the base of tree remained uncovered, position of the stem in the tuff bed indicates it was rooted in the roof of coal and probably was levelled by the volcanic ash load. In any case, the tree with the epiphyte grew behind the northern margin of the excavation.

The second potential epiphytic plant is *Selaginella* cf. *gutbieri*. Its few tiny fragments were found in the upper part of the tuff bed in association with *L. simile* leafy shoots at two places (B2 and C5) about 3 m apart. This suggests that *S.* cf. *gutbieri* grew in the distal part of tree crown on terminal shoots of the host plant (Pšenička & Opluštil 2013).

Eusphenopteris nummularia (Fig. 16B), *Palmatopteris furcata* (Fig. 16D) and *Mariopteris muricata*, arranged in descending order of their abundance, are lyginopterid pteridosperms generally interpreted as having a climbing habit based on slim axes that cannot provide sufficient support to these plants as well as some additional features that further suggest their lianescent habit (DiMichele *et al.* 2006, Opluštil *et al.* 2009a, Boersma 1972, Burnham 2009, Krings *et al.* 2003, Cleal 2008, Kerp & Krings 1998). The most common of them is *Eusphenopteris nummularia*. Remains of its foliage and rachises cover 2.8 m^2 (*i.e.* 8.4% of the excavated area) along the northern margin of the excavation, overlapping well with the distribution of canopy taxa remains (Figs 10, 19). A patchy distribution pattern of its remains points to the conclusion that about two or three plants grew on trees (see the chapter Canopy) located just behind the northern and eastern margin of the excavation. Less common *Palmatopteris furcata* has a similar distribution pattern and therefore partially overlaps with *E. nummularia* and canopy taxa. *Mariopteris muricata* is represented only by a single ultimate pinna fragment near the southern margin (E4), which suggests that this is a dispersed fragment and the plant itself grew outside the excavation.

Bowmanites pseudoaquensis is interpreted as a liana-like sphenopsid based on direct observation from excavation S2 where nearly a complete plant was found encircled around a lycopsid stem (Opluštil 2009a). In addition deeply incised leaves of the main axes end in hooks further indicating a climbing habit for this species (Libertín *et al.* 2008). Remains of leafy axes display a patchy distribution mostly concentrated in an area covered by fragments of canopy species except for a small occurrence in the D2 unit. Nearly all the remains occurred in upper part of the Bělka bed, 350–500 m above its base. The fragmentary nature of the remains suggests that they represent only pieces of axes broken off during the volcanic ash fall while the main part of the plant was probably buried together with the parent plant branches. This could happen after the volcanic ash settled down and the area changed into a shallow lake. Dead but still standing tree torsi and liana/epiphyte plants were quickly decomposed in the humid tropical climate and re-deposited volcanic ash.

Oligocarpia sp. is represented by few tiny fragments of leafy shoots found 50 and 500 mm above the tuff base in two different parts of the excavation. Their remains either occupy the area covered by fragments of canopy taxa or occur in close proximity. Position of pinna fragments near the excavation margin led us to the conclusion that one or two plants grew in the excavated area or quite nearby.

Ground cover and occasional climbers

Into this story we included eight species, which together cover about 12 m^2, *i.e.* 36% of the excavated area (Fig. 21). Their remains are concentrated between the excavation centre and its SE corner (Fig. 19). This area only slightly overlaps with that occupied by remains of canopy species, which we consider to be indirect evidence that these species are ground cover elements generally not requiring trees for climbing. In detail, however, this story includes both true ground cover species and occasional climbers, which crept along the forest floor as a part of the ground cover until they found a plant to provide support for climbing (Opluštil *et al.* 2009a).

The most common of this group of plants is *Corynepteris angustissima* (Figs 14, 15A, B), which covered 5.7 m^2, *i.e.* 17% of the excavation area (Table 3, Fig. 20). This fern formed rhizomes covered by appendages and grew in the plant litter layer and/or the mire surface. Foliage-bore hairy phyllophores, rachises and pinnules (Pšenička 2005) that gave the plant the ability to climb upward, as discovered in one of previous excavations (Opluštil *et al.* 2009a). Although its remains occurred in various parts of the excavation including the area dominated by canopy taxa fragments, the largest concentration of up to >1m long axes and foliage, including fertile organs, was found in the SE corner of the excavation. These remains most probably represent a group of several plants. Few other plants were scattered in the centre and NW part of the excavation.

The second most common species of this story is *Sphenopteris mixta* (Fig. 16C), which occupied about 3 m^2 (12%) in the centre of the excavation (Table 3, Fig. 14). The specimens represent either complete aerial parts of the

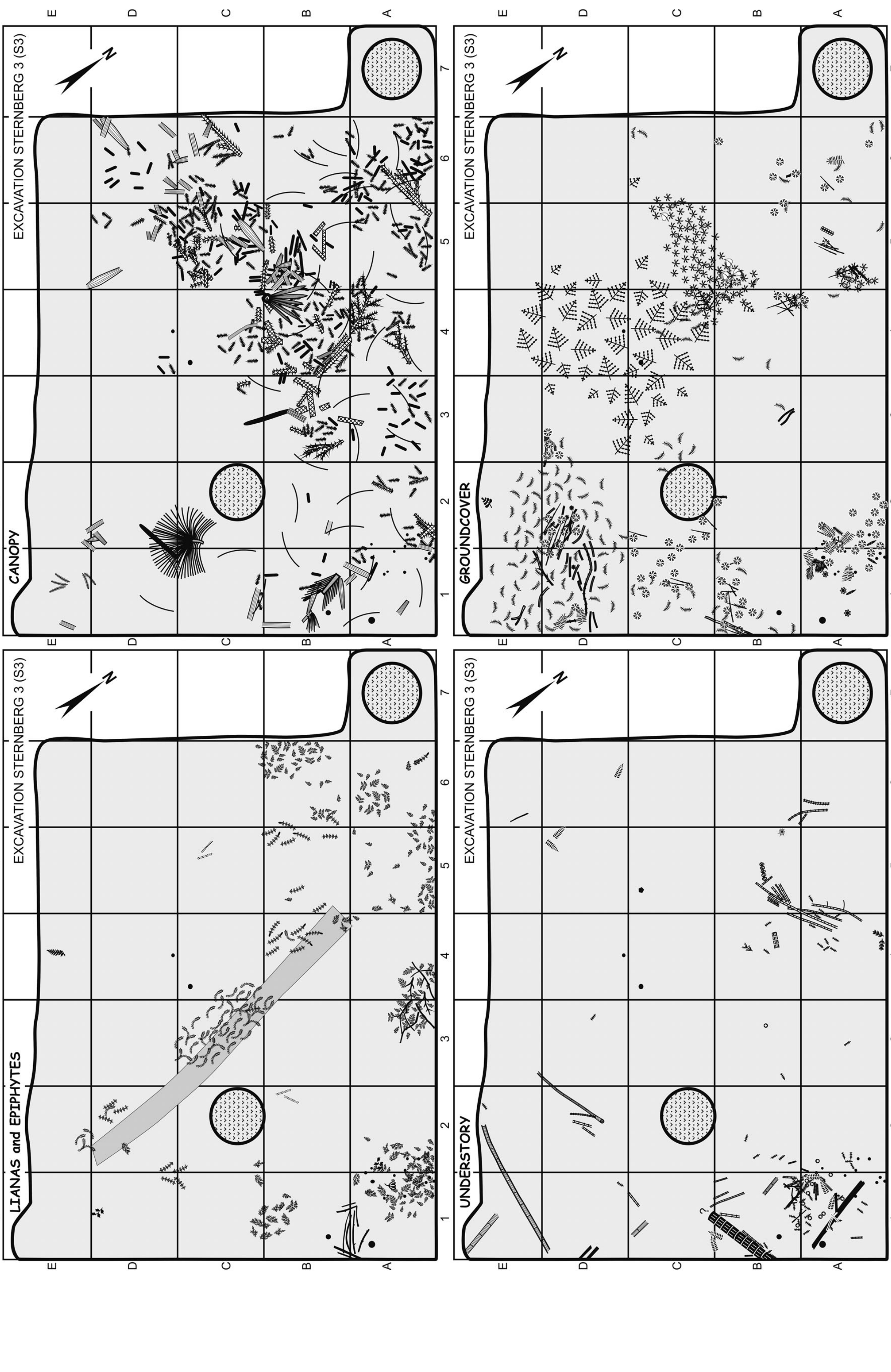


Figure 19. Density and distribution of remains in in each interpreted forest level over the excavated surface.

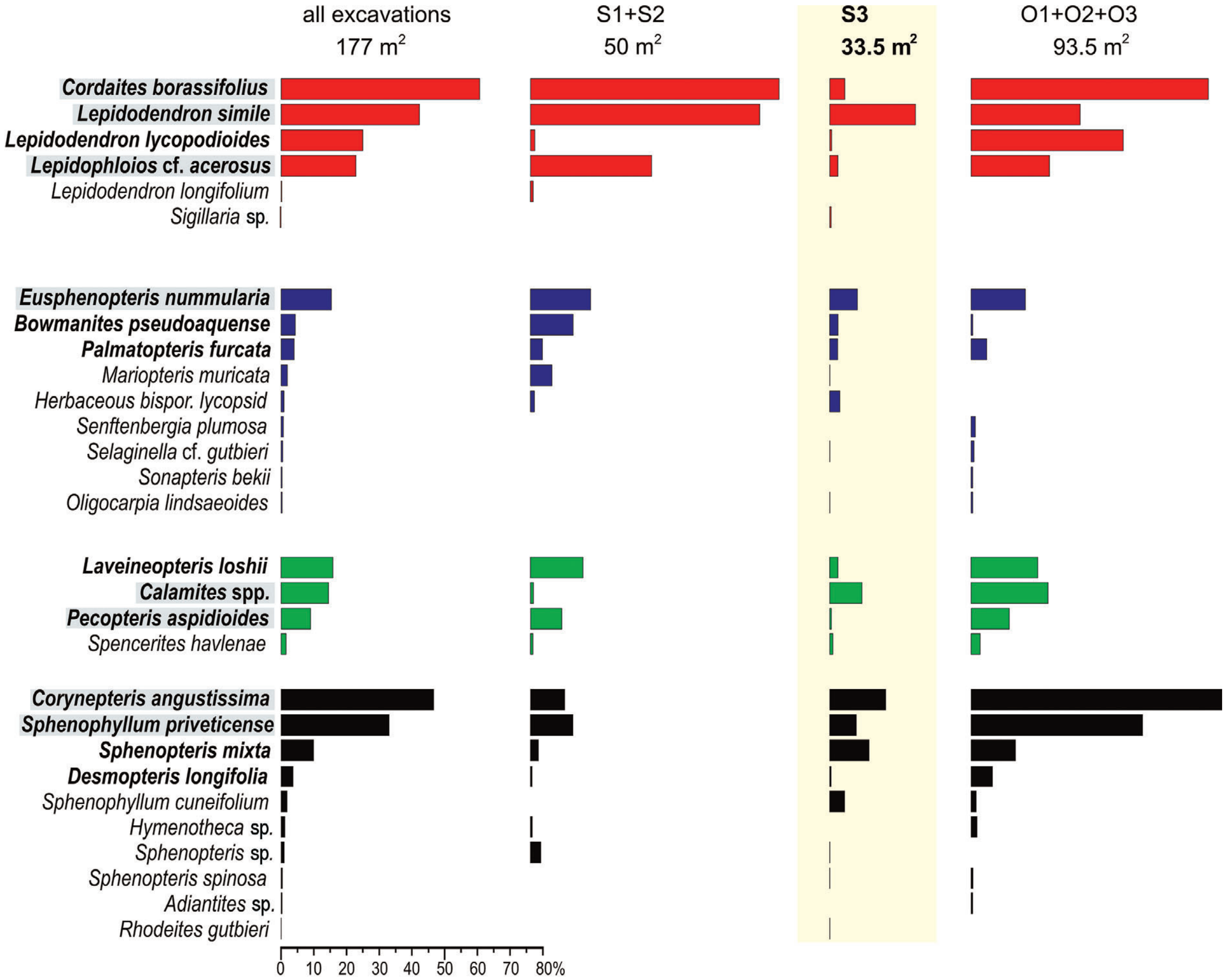


Figure 20. Percentage cover of individual taxa in the S3 excavation in comparison with previous excavations (Sternberg 1+2 and Ovčín 1+2+3 excavations) and all the excavations together. Area in each excavation group is indicated.

plant or complete fronds. No overlap with the canopy taxa and the presence of nearly complete fronds/plant 20–50 mm above the tuff base both suggest burial of the plants in early phase of the volcanic ash fall, which is typical for plants growing in groundcover. Less common within the ground cover are *Sphenophyllum priveticense* (Fig. 12A, B) and *S. cuneifolium* (Fig. 12D) covering 2.75 and 1.5 m^2 respectively (Table 3, Fig. 20). Both species are considered to represent dominantly ground cover taxa since we did not observe morphological adaptations such as climbing hooks on the leaves (Batenburg 1981). Remains of *Sphenophyllum priveticense*, which in previous papers on the Ovčín locality was identified as *S. majus* (Opluštil *et al.* 2007, 2009a, b), tend to form clusters scattered mostly near the northern and eastern excavation margins. In the NE corner the foliage is associated with several upright sphenophyll axes about 10 mm in diameter indicating the position where the individual plants were rooted. A compact area of leafy axes of *S. cuneifolium* occurred mostly near the middle of the excavation; a much smaller cluster was situated near the northern margin. Both probably represent individual plants.

Remaining ground cover taxa (except the zygopterid ferns *Desmopteris longifolia* and *Rhodeites gutbieri*) include species of unknown habit (*Sphenopteris spinosa* and *Sphenopteris* sp.), which cover usually much less than 0.1 m^2 each. Remains of these species were found mostly in lower part of the tuff bed, which suggests they belong to ground cover taxa. However, we found only few tiny pinna fragments instead of complete plants buried by ash (as one could expect in the case of a small-sized ground cover plant), which does not exclude the possibility of a liana-like habit. This is further supported by overlap in areas of these species with canopy taxa. Since the habit of these species remains very uncertain, they are rather arbitrarily placed into ground cover. Probably three (or even more)

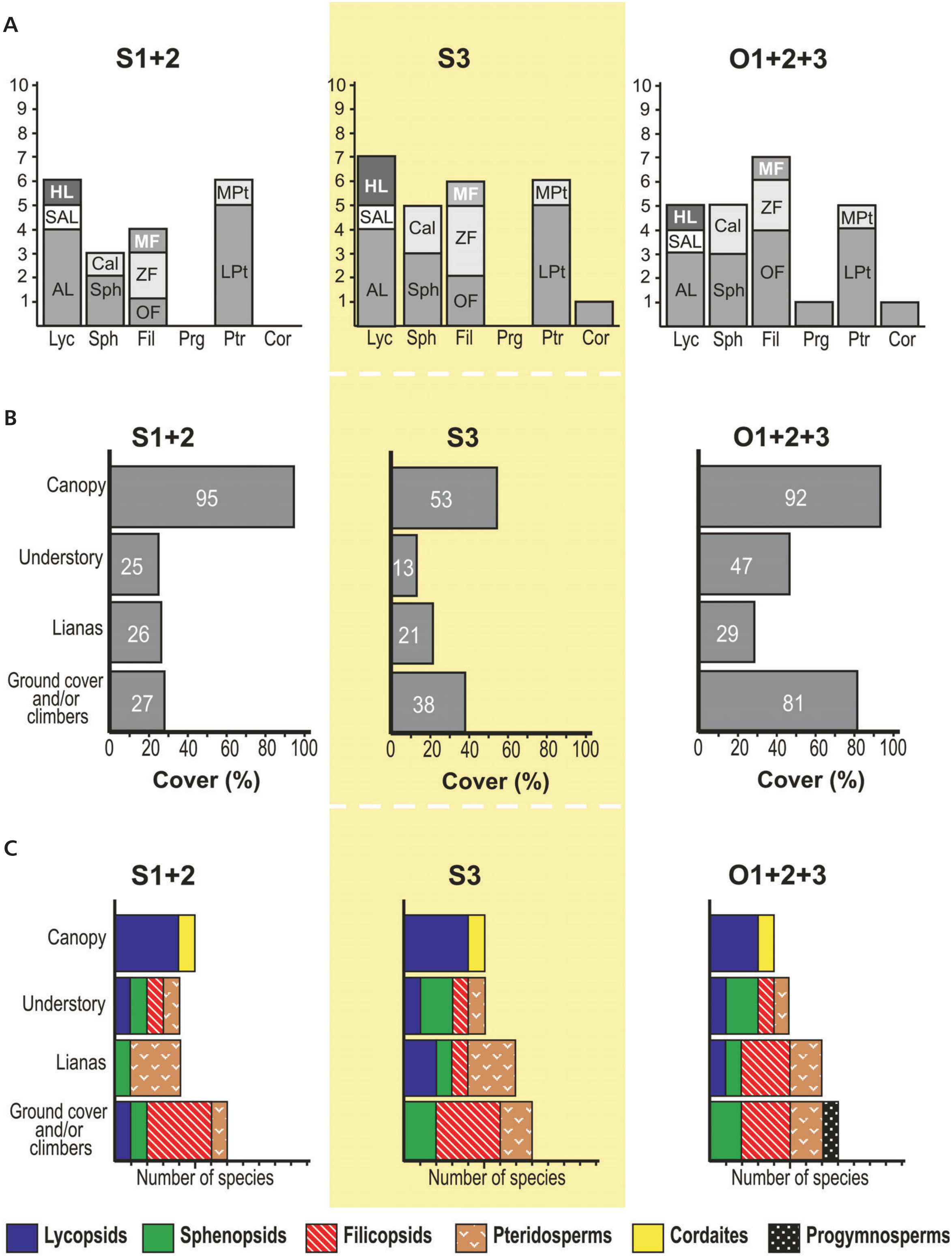


Figure 21. A – taxonomic composition of the plant assemblages discovered in particular excavation groups and the S3 excavation expressed by number of species in each plant group. Abbreviations: Lyc – lycopsids; Sph – sphenopsids; Fil – filicopsids; Prg – progymnosperms; Ptr pteridosperms; Cor – cordaites; AL – arborescent lycopsids; SAL – subarborescent; HL – herbaceous; Cal – calamiteans; MF – marattialean ferns; ZF – zygopterid ferns; OF – other ferns; LPt – lyginopterid pteridosperms; MPt – medullosan pteridosperms. • B – combined percentage cover of forest levels within the excavated area in the S3 excavation and other Sternberg and Ovčín excavations. • C – diversity of vegetation in excavations at the Ovčín locality expressed as number of taxa in individual storey.

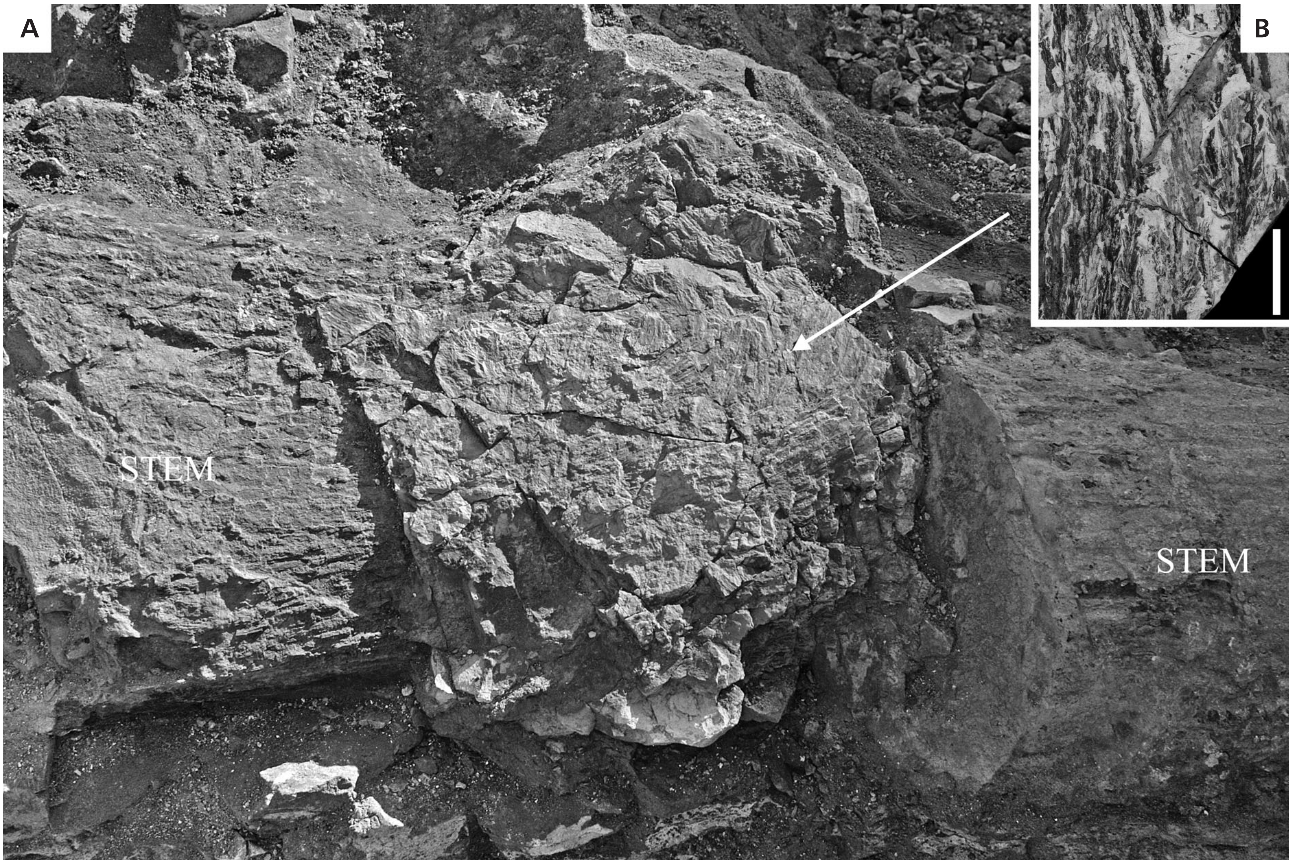


Figure 22. A – nearly a complete plant of bisporangiate herbaceous lycopsid (arrow) attached to a large lycopsid stem obliquely penetrating tuff bed up to the base of the overlying tuffite (Brousek). • B – detail of bisporangiate herbaceous lycopsid (scale bar 10 mm).

plants of *Desmopteris longifolia* grew in the study area whereas other species were represented probably only by one or two plants, as indicated by their distributional patterns.

The Minimal Area

Estimation of Minimal Area by counting of increments starting from the SW and NE corners (in steps 0.5, 1, 2, 4, 8, 16, 33 m^2) of the excavation produced essentially similar curves steepest up to the area of 8 or 16 m^2 and then irregularly decreasing in steepness (Fig. 23). Unfortunately the excavated area of about 33.5 m^2 is too small to be considered as the Minimum Area, *i.e.* to be a representative sample of the "Ovčín coal-forming forest" since the curves did not become nearly or completely flat. It is worth noting that arborescent plants were rooted outside the uncovered area, although they partly shaded the excavation by their crowns. Similar estimations from larger excavations in the same locality indicate that the curve becomes flat after the area increases to about double of the size of the S3 excavation.

Reconstruction of the vegetation cover in the S3 excavation

The uncovered taphocoenosis is a record of a mixed lycopsid-cordaites-dominated coal-forming forest. Although the excavated area represents only a very small segment of the former forest its species diversity is high, comprising about 25 biological species over 33.5 m^2. While the arborescent taxa were the major contributors to the biomass, the highest diversity was found within the ground cover and lianas comprising 16 species. The coal-forming forest had well-developed stories composed of plants of different growth habits.

The canopy story comprises three lepidodendrid species [*Lepidodendron* (*Paralycopodites*) *simile, L. lycopodioides, Lepidophloios acerosus*] and *Cordaites borassifolius* as a representative of gymnosperms, which together covered about 40% of the excavated area (Figs 19–21). The presence of *Sigillaria* in B3 square unit, another common Pennsylvanian arborescent lycopsid, is the first confirmation of the presence of this genus in any of our excavations, which suggests that sigillarian trees belonged to rare elements of the Ovčín coal forest. Although

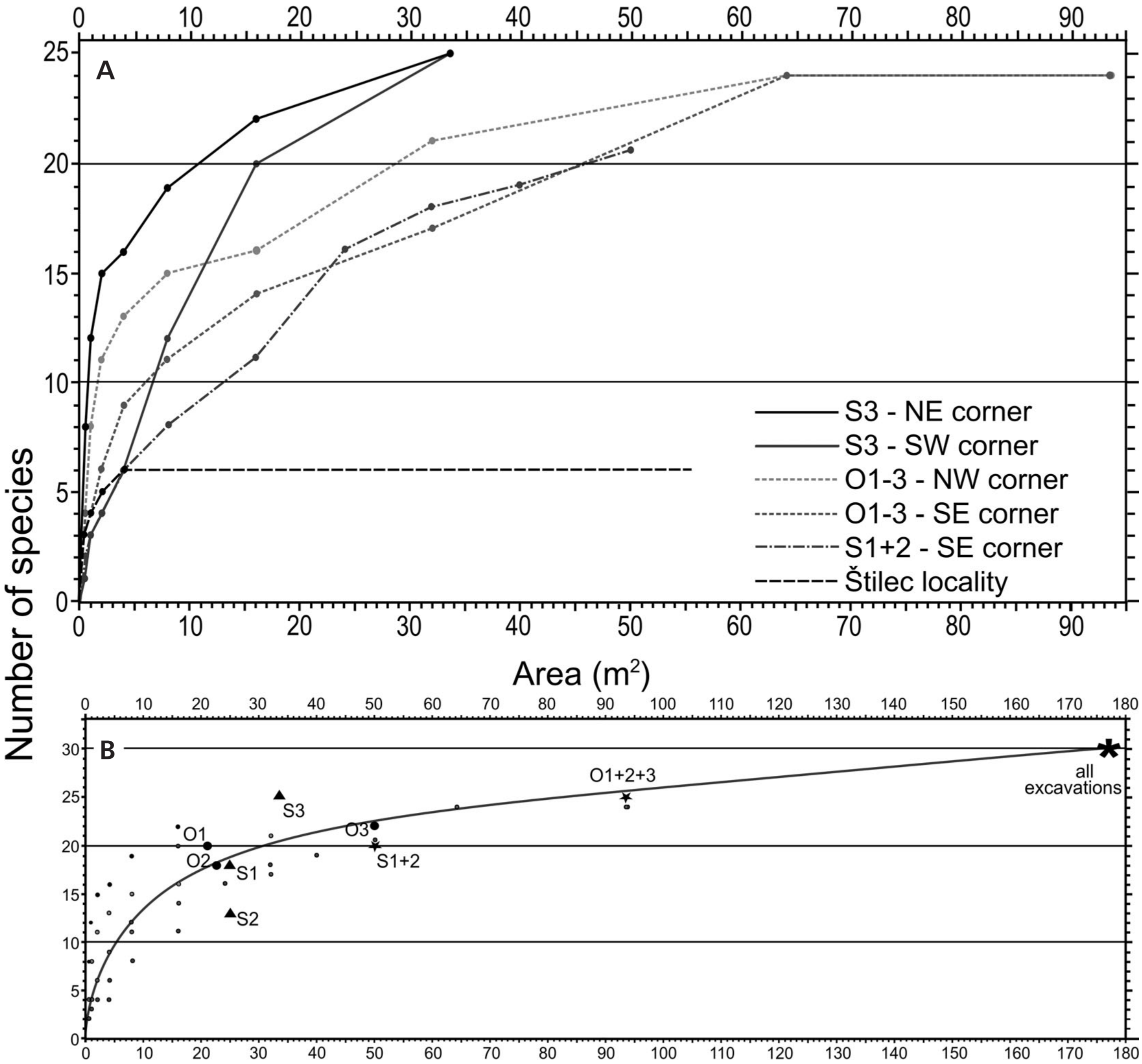


Figure 23. Increase in the number of new species with expanding area of the excavated area. • A – incremental curves of species as derived in individual excavations of the Ovčín locality and in the Štilec locality for comparison. • B – generalised trend of increasing diversity of the Ovčín coal forest for composite area including all the Ovčín and Sternberg excavations together. All the values from the diagramme in the Fig. 21A are indicated. See text for details.

none of the lycopsid trees were rooted in the excavated area, they overlapped the excavation by their crowns. Thus the crown diameter is estimated to reach about 5 to 6 m, whereas the height of trees could not be calculated. The common occurrence of remains of several canopy species in tuff indicates an overlap of their crowns probably due to different tree heights (Opluštil *et al.* 2009a). This resulted in locally dense canopy although uneven distribution of the remains of arborescent species across the excavation suggests that the canopy was not continuously compact and significant gaps disrupted it both vertically and laterally. These gaps (produced, for example, by fallen trees) allowed the "equatorial" sun to shed the light into deeper stories of the forest and thus promote the development of ground cover and understory plants.

The understory was the most poorly developed level, covering only about 13% of the excavation (Figs 19–21). It comprises few clusters of *Stylocalamites* and *Calamitina* stems with poorly developed foliage, and probably two scattered small medullosan pteridosperms, with *Laveineopteris loshii* foliage. Reed-like *Stylocalamites* grew both in the shadow of the canopy as well as in parts not directly overlapped by tree crowns, as indicated by comparison of the distribution of understory with canopy remains. Their height is estimated to vary mostly between 1 and 3 m. Absence of cones may suggest they were still immature. In one of the previous excavations (O1, Opluštil *et al.* 2009b), however, one of larger and naked *Stylocalamites* axes bore cones *Palaeostachya distachya*. Near the middle of the excavation grew a subarborescent lycopsid, *Spencerites havlenae*, which belongs to a common understory element of the Ovčín coal forest. On the opposite, a single fragment of *Psaronius* tree fern with *Pecopteris aspidioides* foliage in A–B1, a very common species in the Ovčín locality, suggests that the plant grew near but outside the S3 excavation.

The ground cover represents well-developed story spread over about 38% of the excavation mostly in areas of canopy gaps as suggested by only a narrow overlap of remains of both stories (Figs 19–21). The story comprises 8 species dominated by the zygopterid fern *Corynepteris angustissima*, the pteridosperm *Sphenopteris mixta* and two sphenophylls (*S. priveticense* and *S. cuneifolium*) whereas the remaining species are much less common.

An important component of the coal-forming forest covering 23% of the study area constitutes lianas and possibly epiphytic plants. Their remains are very often associated with canopy fragments derived from the supporting plants. These groups comprise 7 species, mostly lyginopterid pteridosperms (*Eusphenopteris nummularia*, *Palmatopteris furcata*, *Mariopteris muricata*), two species of herbaceous lycopsids (*Selaginella* cf. *gutbieri* and undescribed bisporangiate herbaceous lycopsid), *Bowmanites pseudoaquensis* and a fern *Oligocarpia* cf. *gutbieri*. Dominant are *Eusphenopteris nummularia* and *Palmatopteris furcata* whereas *Bowmanites pseudoaquensis* and an undescribed bisporangiate herbaceous lycopsid are co-dominant.

The animal remains and indications of plant/animal interaction

Animals play an important role in modern ecosystems and, we presume were equally, though perhaps differently, important in very ancient ecologial systems. Plant/animal interaction involves a number of different types of relationships. These include not only the use of plants as food for arthropods but also their use as protection (Scott & Taylor 1983). Animals also can assist plants in various phases of reproduction or propagule dispersal (Pšenička & Bek 2009). They are also an indirect effect on the decomposition of dead plant parts (Wootton 1976). Tokens of these interactions were observed in the Ovčín exacavations.

Palaeontological research at the Ovčín locality since the opencast mine was in operation has revealed several arthropod remains in the Bělka bed and the associated Brousek. Most of the body fossils are arachnids (*e.g.* trigonotarbids; Fig. 24B) but also discovered in one of the previous excavations were the remains of a giant meganeurid griffenfly *Bohemiatupus elegans* (Prokop & Nel 2010; Fig. 24A), reaching about 55 cm of wing-span. In the S3 exacavation a few fragments resembling body segments of an *Arthropleurid* arthropod were found (Fig. 24C–E), although the exact affiliation of these fossils remains unknown. No evidence of the presence of vertebrates has been found in the Bělka; in the upper part of the Brousek, however, Turek (1989, 1996) described a rich assemblage of ichnofossils indicating the presence of fish and tetrapods. Taphonomically, this fact can be explained by the high acidity of peat and volcanic ash, which redound to the dissolution of any vertebrate bones. In contrast, the invertebrates have chemically resistant cuticle, therefore they were not destroyed and could be found in the deposits.

Although the macrofossil record suggests relatively low animal diversity, a fairly large number of different indices of animal activity provide an indirect evidence of their high diversity, especially among the invertebrates. These indicators include crypts in the plant tissues (wood) and coprolites, which are situated in crypts or were dispersed freely in plant litter on the peat swamp surface. As a result, most of the findings occurred in the basal part of the Bělka bed usually at the contact with the coal roof. The crytps are of different shapes, more or less oval (Fig. 25D) or tubular (Fig. 25A, B, E, F) suggesting they were inhabited by various invertebrates species. This is in agreement with the coprolites that also vary in size and shape. The oval or elongate, *ca* 1.2 mm long coprolites (Fig. 25C) resemble those produced by cockroaches (Orthoptera) (see Scott & Taylor 1983, table 5). Smaller, rounded, about 0.2 mm diameter coprolites may be assigned either to cockroaches or millipedes (Fig. 25D). The smallest coprolites found at the Ovčín locality are 50–100 μm long and could be produced by collembola or millipedes (Fig. 25B).

Comparisons

Comparison of the Bělka tuff and Brousek tuffite flora from the S3 excavation

The flora discovered in the Bělka bed is partially different in taxonomic composition from that in overlying whetstone (Brousek). The "Brousek flora" was collected within an interval of about two decimeters above its base. It consists of pteridosperm and fern foliage and lycopsid and sphenopsid leafy shoots/branches and naked unidentifiable axes (Figs 26, 27), including some diagonally disposed stems rooted in roof of the Lower Radnice Coal, continuing throughout the Bělka bed into the base of the Brousek.

Identifiable remains comprise the following species arranged approximately in decreasing abundance: *Eusphenopteris nummularia* (Fig. 27B), *Lepidodendron* (*Paralycopodites*) *simile* (Fig. 26F), *L. lycopodioides*, *Bowmanites pseudoaquensis* (Fig. 27E), *Sphenophyllum priveticense* (Fig. 27D), *Desmopteris longifolia* (Fig. 27F), *Rhodeites gutbieri* (Fig. 27C), *Saaropteris guthorli* (Fig. 27A), *Flemingites* sp. (Fig. 26B), *Lepidophloios acerosus*, *Spencerites havlenae* (Fig. 26C, E, G, H), herbaceous bisporangiate lycopsid (Fig. 26A), *Sphenopteris mixta* (Fig. 27G) or *S.* cf. *spinosa* and *Lepidocarpon majus* (Fig. 26D). The

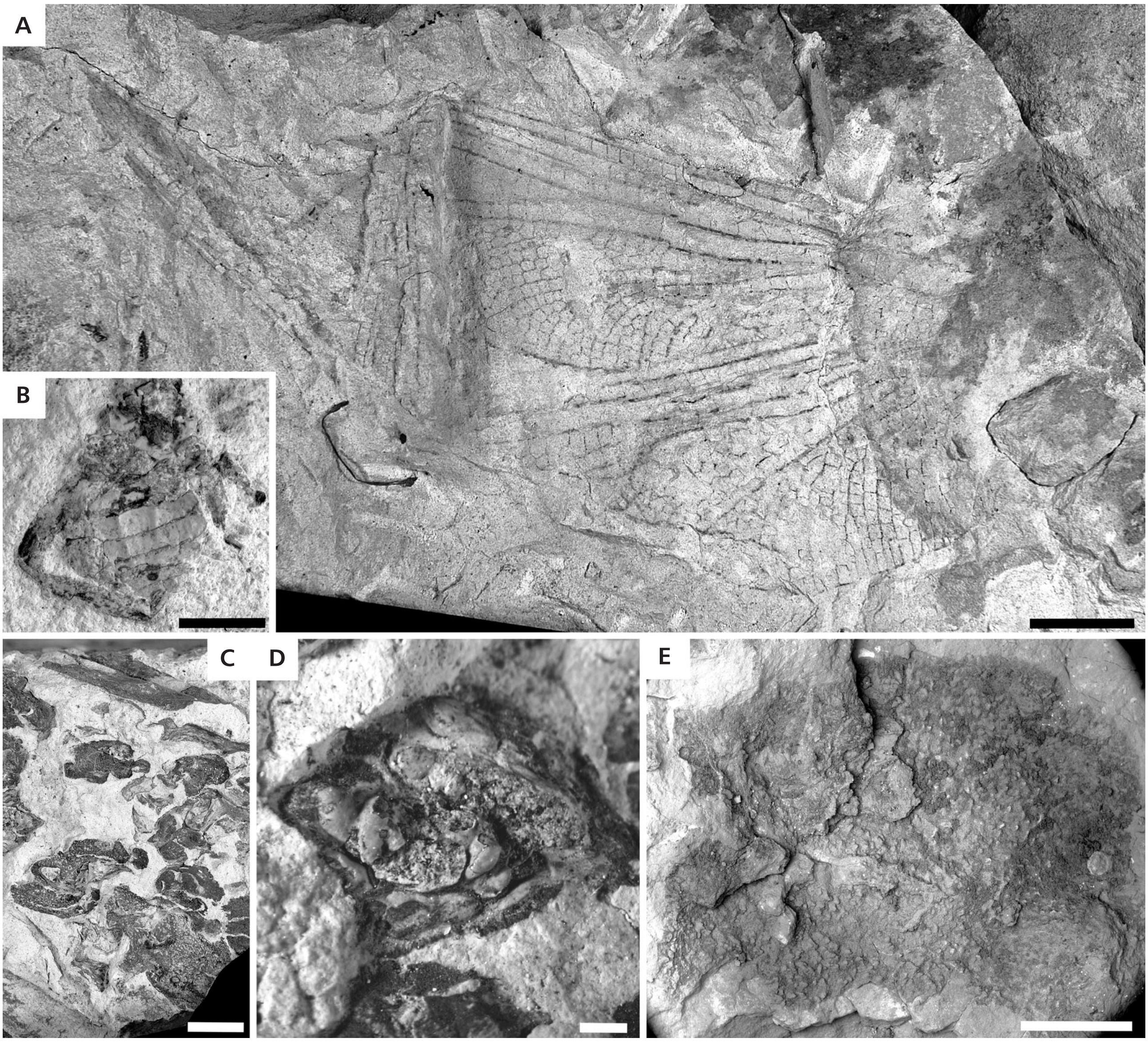


Figure 24. Faunal remains discovered in various excavations at the Ovčín coal deposit. • A – griffenfly *Bohemiatupus elegans*, excavation S1 (scale bar 20 mm). • B – trigonotarbid spider, excavation S3 (scale bar 5 mm). • C – probably an *Athropleura*-type body segments, excavation S3 (scale bar 5 mm). • D – detail of the specimen from the Fig. 22 (scale bar 1 mm). • E – detail of ?*Athropleura*-type body segment with well visible granulation; SEM (scale bar 2 mm).

position of the plants, just above the base, relatively large fragments and significant overlap with species discovered in the Bělka bed in this excavation indicate that these plant remains represent a parautochthonous association derived from peat swamp vegetation. Even absence of *Saaropteris guthorli* and *Rhodeites gutbieri* in the Bělka in this excavation does not affect this conclusion since these species are known from other Bělka excavations or localities, *i.e.* from peat swamp conditions (*e.g.* Opluštil *et al.* 2007, Pšenička & Schultka 2009).

When interpreting the origin of the "Brousek flora" in general, it is necessary to keep in mind that the peat swamp of the Lower Radnice Coal occupied a small, ~1–2 km wide river valley surrounded by tens (rarely over a hundred) of meters high ridges of the basement rocks (Opluštil *et al.* 2009a, fig. 2). Falling volcanic ash covered the whole landscape including the basement topography. Small plants were buried more or less completely while torsi of larger plants protruded above the buried landscape. Although mechanical properties of arborescent lycopsid and cordaites tissues are not known it is evident from the fossil record that their branches were not strong enough to resist excessive bending yet sufficiently flexible to dump part of the load and avoid damage. Trees thus suffered from heavy

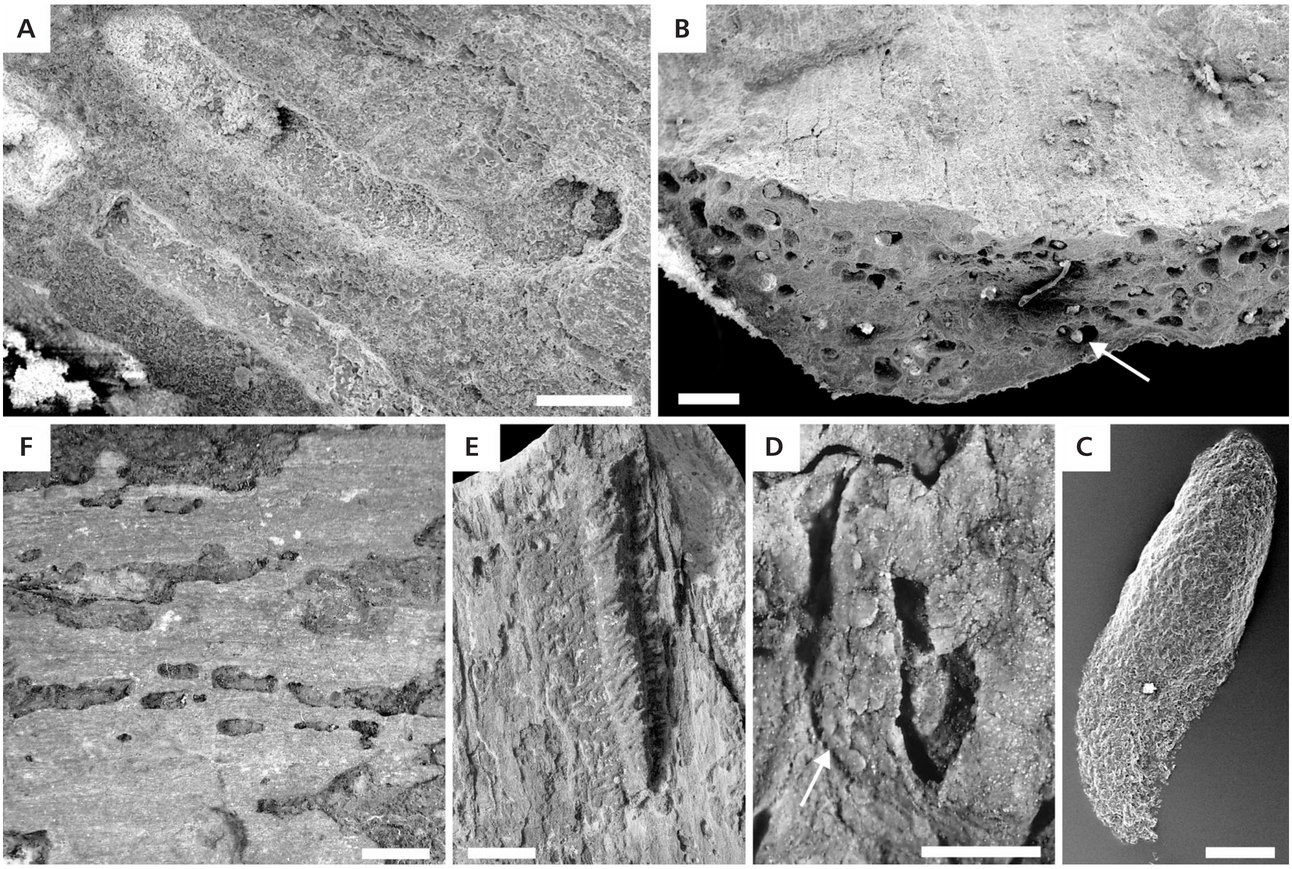


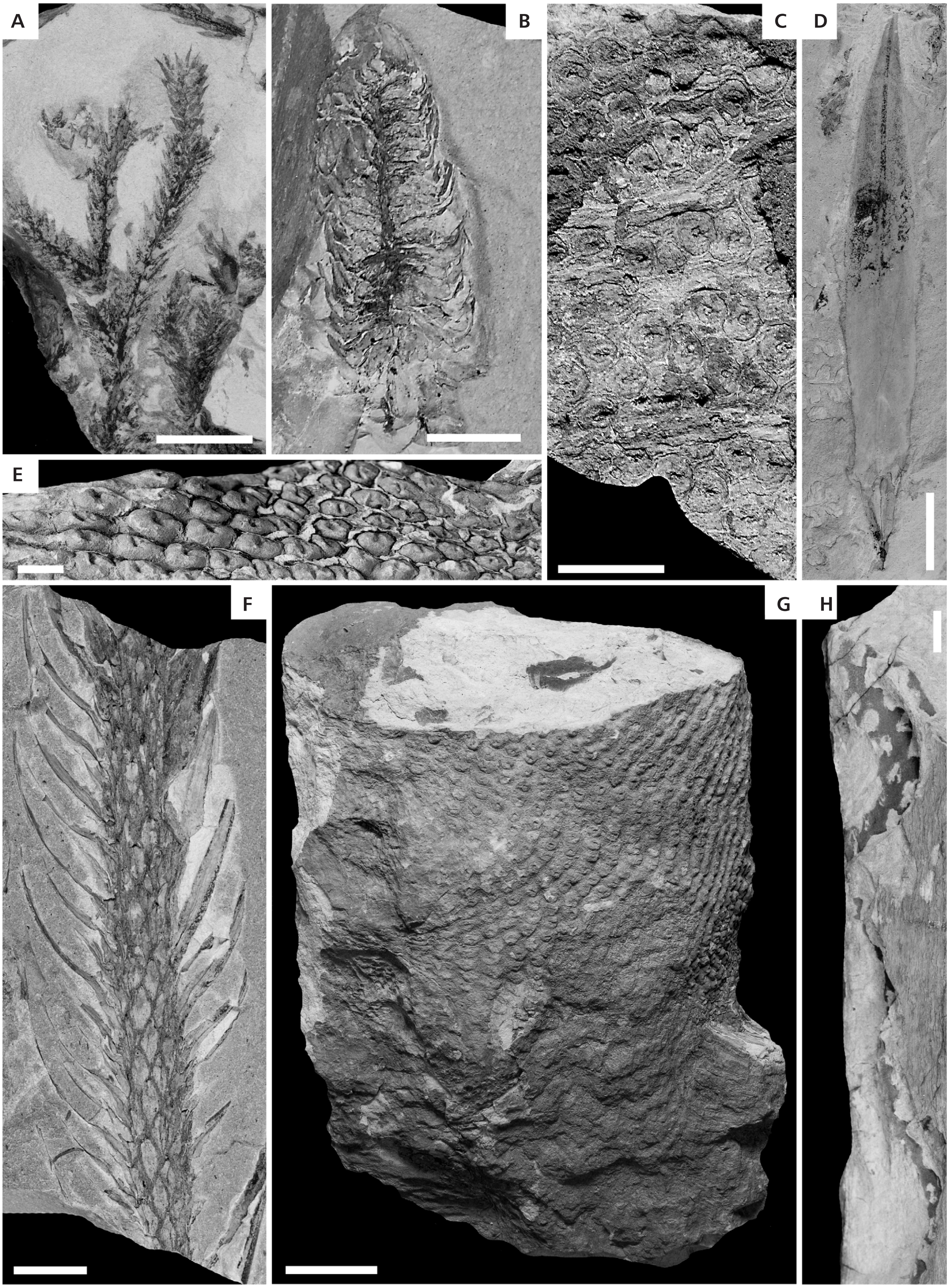
Figure 25. Insect crypts in plant tissues. S3 excavations. • A – a very small probably insect crypt going throughout the plant tissue; SEM (scale bar 0.1 mm). • B – probably insect crypt going throughout the plant tissue filled by coprolites (arrow); SEM (scale bar 0.2 mm). • C – dispersed 1.2 mm long coprolite from lowermost part of tuff; SEM (scale bar 0.2 mm). • D – probably insect crypt filled by small coprolites indicated by arrow (scale bar 1 mm). • E – conical crypts (scale bar 5 mm). • F – typical insect crypt in wood (scale bar 2 mm).

branch breakage and/or uprooting under the load of ash.

As a result most of the plants were killed directly and those surviving died soon after. Such a devastating effect (nearly total kill zone) on vegetation, as observed in modern volcanic areas (*e.g.* New Zealand; http://www.maf.govt.nz), results from 1.5 m (or more) of uncompacted tephra load. Following compaction, it is estimated (Bohor & Triplehorn 1993) this thickness can be reduced to about $^1/_2$ and even $^1/_3$, which fits well with the 50–60 cm of the present-day Bělka thickness. Brousek above the Bělka is a complex of re-deposited volcanic ash with a siliciclastic admixture in the upper part of its thickness (Drábková 1986). Its formation started with early rains following the deposition of tephra over the landscape. Unconsolidated ash was washed down the valley into a shallow lake produced by peat compaction resulting from the initial tephra fall. Re-deposited ash further enhanced the peat compaction producing new accommodation space. Vast amounts of unconsolidated tephra and siliciclastics on the landscape resulted in high sedimentation rates in the lake. It is estimated that upright stem >6 m tall were observed in the opencast mine (Drábková 1986). These trees had to be buried in a time frame of a few months, otherwise they would have completely decayed in a humid tropical climate (*e.g.* Gastaldo 1986, Gradziński & Doktor 1995, Gastaldo *et al.* 2004a, DiMichele & Falcon-Lang 2012).

The fossil record of the Brousek can be divided taphonomically into three basic groups, which all are believed to represent pre-eruption flora. The first group includes upright or inclined stems still rooted in the top of the coal bed and penetrating throughout the Bělka into the

Figure 26. Plant remains preserved in the Brousek (Whetstone) tuffite bed of the S3 excavation. • A – bisporangiate herbaceous lycopsid; B – *Flemingites* sp.; C – *Spencerites* cf. *havlenae* (scale bar 10 mm); D – *Lepidocarpon majus*; E – *Spencerites* cf. *havlenae* (scale bar 2 mm); F – *Lepidodendron simile* (scale bar 5 mm); G – main stem of *Spencerites* cf. *havlenae* preserved in upright position; H – *Spencerites* cf. *havlenae*.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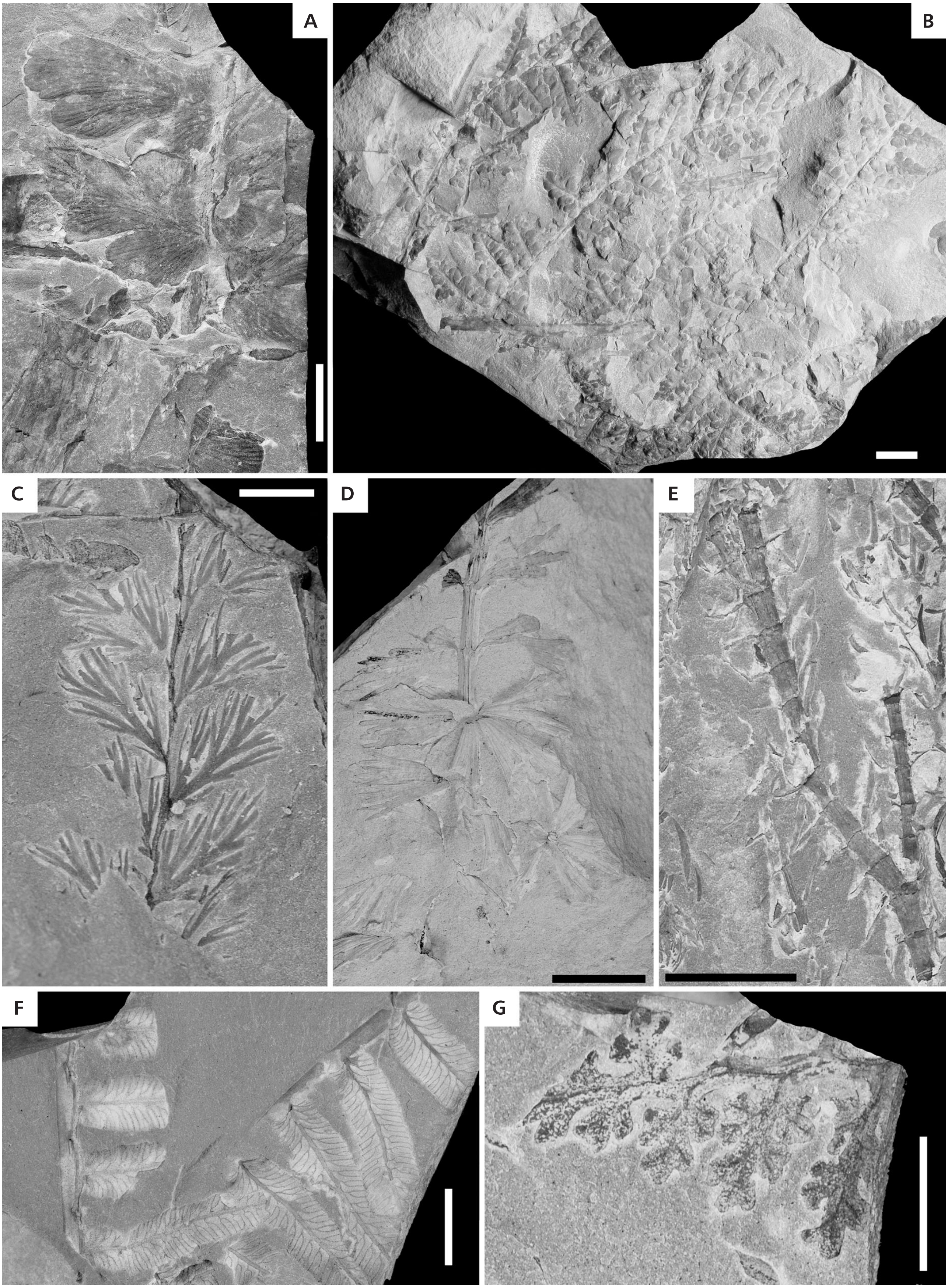
Brousek. This group evidently represents plant remains buried *in situ*. The second group involves parautochthonous (Gastaldo *et al.* 1996) plant fossils encountered in the Bělka overlying the Lower Radnice Coal, transported over a short distance within the former peat swamp and therefore composed of peat-forming species. In the Brousek fossil assemblage, coal-forming species occur as relatively large foliage fragments and prostrate branches and stems not in contact with the coal seam and either concentrated on discrete bedding planes or randomly scattered. These remains were probably derived from plants killed by the ash fall but not completely buried by ash, mostly larger shrubs, trees, but also epiphytes and climbing plants (Opluštil *et al.* 2009a, b). The remaining elements of the third group, preserved in the Brousek, are derived from areas outside the former peat swamp, *i.e.* along valley margins, foothills or even valley slopes, which also are assumed to have been vegetated (Falcon-Lang & Bashforth 2005; DiMichele *et al.* 2009, 2010; DiMichele 2014). Here the unconsolidated tephra and buried plant remains were exposed to erosion and washed down the slope into the lake formed in the valley soon after the peat swamp was buried by ash. The fossil record typically includes unidentifiable comminuted plant remains with scattered identifiable plant fragments concentrated mostly into thin beds or even bedding planes up to several meters above the Brousek base. Besides the remains derived from plants growing outside the peat swamp, there additionally are fragments derived from decaying torsi of dead trees protruding through the volcaniclastics above lake level.

Comparison with roof shale and coal ball floras

Pennsylvanian roof shale and coal ball floras are among the best-studied and known fossil floras. Roof shale floras preserved as adpressions are probably the most common type of plant fossil record of Pennsylvanian times providing mostly outer anatomical (morphological) information. The ecological significance of these floras has been thoroughly discussed for a long time (for an overview see Gastaldo *et al.* 1995). Most of them are parautochthonous and allochthonous (drifted) in origin, although a number of *in situ* preserved drowned coal-forming forests (Type A assemblage of Gastaldo *et al.* 1995), described in literature as T^0 assemblages, is reasonably high and sufficient for comparison with our data (*e.g.* DiMichele *et al.* 1996, 2007; Gastaldo *et al.* 2004a, b; DiMichele & Falcon-Lang 2011). Since such comparison was already made in the case of previous Ovčín excavations, we kindly refer readers to our corresponding papers (Opluštil *et al.* 2009a, b).

Coal balls are carbonate concretions formed during early diagenesis (Scott & Rex 1985) which contain anatomically preserved remains of purely coal-forming vegetation, basically preserved *in situ* as a consequence of a low dynamic peat-swamp environment. Coal balls thus have provided important data not only on plant anatomy but also on composition of peat-forming vegetation (*e.g.* Phillips 1981, Phillips *et al.* 1985, Galtier 1997). Comparison of the peat-forming Ovčín-type of forest described herein with those from middle Pennsylvanian coal balls of Euramerica is therefore a logical test of the reliability with which two independent fossil records capture the composition of peat-forming vegetation. Such comparison was made when analysing data from previous excavations (Opluštil *et al.* 2009a, b) and readers are again kindly referred to these papers for details. Here only the basic outlines are mentioned. Euramerican Duckmantian to Bolsovian coal-ball floras are dominantly composed of arborescent lycopsids, which makes 44–74% of the biomass volume (Phillips 1981, Phillips & DiMichele 1990) and whole plant species diversity of particular coal seams from this time interval varies between 40 and 50 species (DiMichele & Phillips 1996, Galtier 1997). Both parameters are in agreement with data from the Ovčín locality although the diversity of plant assemblage is seemingly higher in coal balls. However, we have to realise that coal ball analyses are based on large and statistically relevant amounts of data collected from larger study areas and across the whole coal seam thickness. They, thus, represent many generations of hydroseral succession. This is evident also in the scale of the Ovčín locality when comparing number of species from any individual excavation with that from all excavations or even with that known from the former opencast mine (see below). Assuming that this is only a single generation preserved as T^0 assemblage, it is reasonable to assume that the number of species of the whole Lower Radnice Coal at the Ovčín locality would fall within the that determined from coal ball data. Similarly, if data from all the Bělka localities (material mostly collected from coal mine dumps) in central and western Bohemia are involved then the number of species increases to 95, averaging 21 species per locality (Opluštil *et al.* 2007). The assemblage described from the Ovčín excavations seems to be most similar to the *Medullosa* spp. – polycarpic lycopsid (*Paralycopodites* spp.) assemblages from Desmoinesian coals of the North America (DiMichele & Phillips 1996).

Figure 27. Plant remains preserved in the Brousek (Whetstone) tuffite bed of the S3 excavation. • A – *Saaropteris guthorli* (scale bar 10 mm). • B – *Eusphenopteris nummularia* (scale bar 10 mm). • C – *Rhodeites gutbieri* (scale bar 5 mm). • D – *Sphenophyllum priveticense* (scale bar 10 mm). • E – *Bowmanites pseudoaquense* (scale bar 10 mm). • F – *Desmopteris longifolia* (scale bar 10 mm). • G – *Sphenopteris mixta* (scale bar 5 mm).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Conclusion: general characteristics of the "Ovčín coal forest"

In this chapter we focus on comparison of data from all the 6 excavations and from the former opencast mine with the aim to better understand lateral heterogeneity of the Ovčín coal forest over a larger area and to describe its general characteristics.

The Ovčín coal deposit represents about 12 hectares of a tectonically and erosionally semi-isolated protrusion of coal-bearing strata in the southern edge of the Radnice Basin (Fig. 1D). Of this area, about 8 hectares were mined out between 1979 and 1986 in the former opencast mine Ovčín. During its operation systematic but non-localised sampling of fossils was done by K. Drábek, a palaeobotanist from the National Museum in Prague, with the help of students, some of them now being members of this author's team (JD, SO, ZŠ). Unpublished data from the former opencast mine (*e.g.* Drábková 1986) and a plant fossil collection stored in the National Museum were explored to complete the list of flora from the Ovčín coal deposit. The bulk of the data for general characterisation of the Lower Radnice Coal phytocoenoses of the Ovčín coal deposit, however, comes from six excavations made near the eastern edge of the former opencast between 2002 and 2009 (for details see the chapter Material and methods).

All the available data show that the pre-eruption peat swamp was colonized by a mixed lepidodendrid-cordaitalean forest (here called the "Ovčín coal forest" for simplicity) with well-developed understory and ground cover, the density and species composition of which display a certain degree of variability (Fig. 29). At the scale of the whole Ovčín coal deposit (*i.e.* including the opencast mine and our excavations), 35 species have been identified from the Bělka bed of which 30 species occurred in at least one of the six excavations, the pooled area of which is 177 m^2. Of these species, *Lepidodendron simile*, *Lepidophloios acerosus*, *Stylocalamites* sp., *Sphenophyllum priveticense*, *Corynepteris angustissima*, *Pecopteris aspidioides*, *Eusphenopteris nummularia* and *Cordaites borassifolius* remains occurred in each individual excavation. Together with other 7 species (*Lepidodendron lycopodioides*, *Calamitina* cf. *goepperti*, *Laveineopteris loshii*, *Bowmanites pseudoaquensis*, *Desmopteris longifolia*, *Sphenopteris mixta* and *Palmatopteris furcata*), which were absent only in one of the excavations, these 15 species are considered as typical elements of the lepidodendrid-cordaitalean Ovčín coal forest. This forest phytocoenosis consists of plants of different growth forms ranging from canopy to groundcover.

Canopy taxa, a dominant component of the phytocoenosis and the main contributor to the biomass, comprise four lepidodendrid species and *Cordaites borassifolius* (Fig. 19). Three of the lepidodendrids (*Lepidodendron simile*, *L. lycopodioides*, *Lepidophloios acerosus*) were present in all the 6 excavations and *L. lycopodioides* was absent only in one of them. Because of the small size of individual excavations (30 m^2 in average), absence of one arborescent species does not necessarily mean variability in density of its population. The density of the canopy is expressed here as a percentage of the area covered by the remains of canopy taxa within the whole excavated area Figs 20, 21). This parameter varies between the excavation groups from 40 to 95% and indicates significant gaps in an otherwise relatively continuous and compact canopy (Opluštil *et al.* 2009a, b). The common presence of remains of several arborescent species in the same area further suggests overlap of tree crowns probably at various heights and points to the existence of a vertically structured canopy.

The density of the population of particular canopy species, deduced from the ratio between the area covered by remains of a particular taxon and the whole excavated area (expressed in percentage), also varies. The most common arborescent species is *Cordaites borassifolius*, which covers between 4 and 73% of the area of any particular excavation and accounts for 61% in weighted average for all excavations (Fig. 20). This taxon is also the most widespread of all the species found in the excavations. The second most common canopy species is *Lepidodendron* (*Paralycopodites*) *simile*, which covers 26–70% of any particular excavation (42% of weight average). Still lower coverage is displayed by *Lepidodendron lycopodioides* (0.4–47%; weight average 25%) and *Lepidophloios acerosus* (2.4–37%; weight average 23%), which, nonetheless, still belong among the typical elements of the Ovčín coal forest. Remaining canopy species, *Lepidodendron longifolium* and *Sigillaria* sp. are very rare elements known only from a single excavation (S2 and S3 respectively) and therefore are not included among the typical species of the Ovčín coal forest.

Differences in coverage of individual canopy species mentioned above cannot be, however, directly interpreted in terms of variability in the density of their populations. This is because of small sizes of individual excavations, which are individually comparable to the area covered by a tree having a crown about 6 m in diameter. Any shift of the excavated area by a few meters could therefore have significantly changed the coverage of individual canopy species, but also that of species in other stories. Reliability of this parameter for estimation of variability in population density increases when comparing excavation groups (Sternberg and Ovčín, Fig. 1) or all our excavations with the opencast mine. Available (unpublished) data from the opencast mine indicate a higher density of arborescent lycopsids (especially *Lepidodendron lycopodioides*) at the expense of *Cordaites borassifolius* in the central part of the opencast mine compared to its margin and to our excavations. Thus the center of the opencast mine was characterised by a lepidodendrid forest with sub-dominant *Cordaites*. A stem diameter-derived calculation of tree

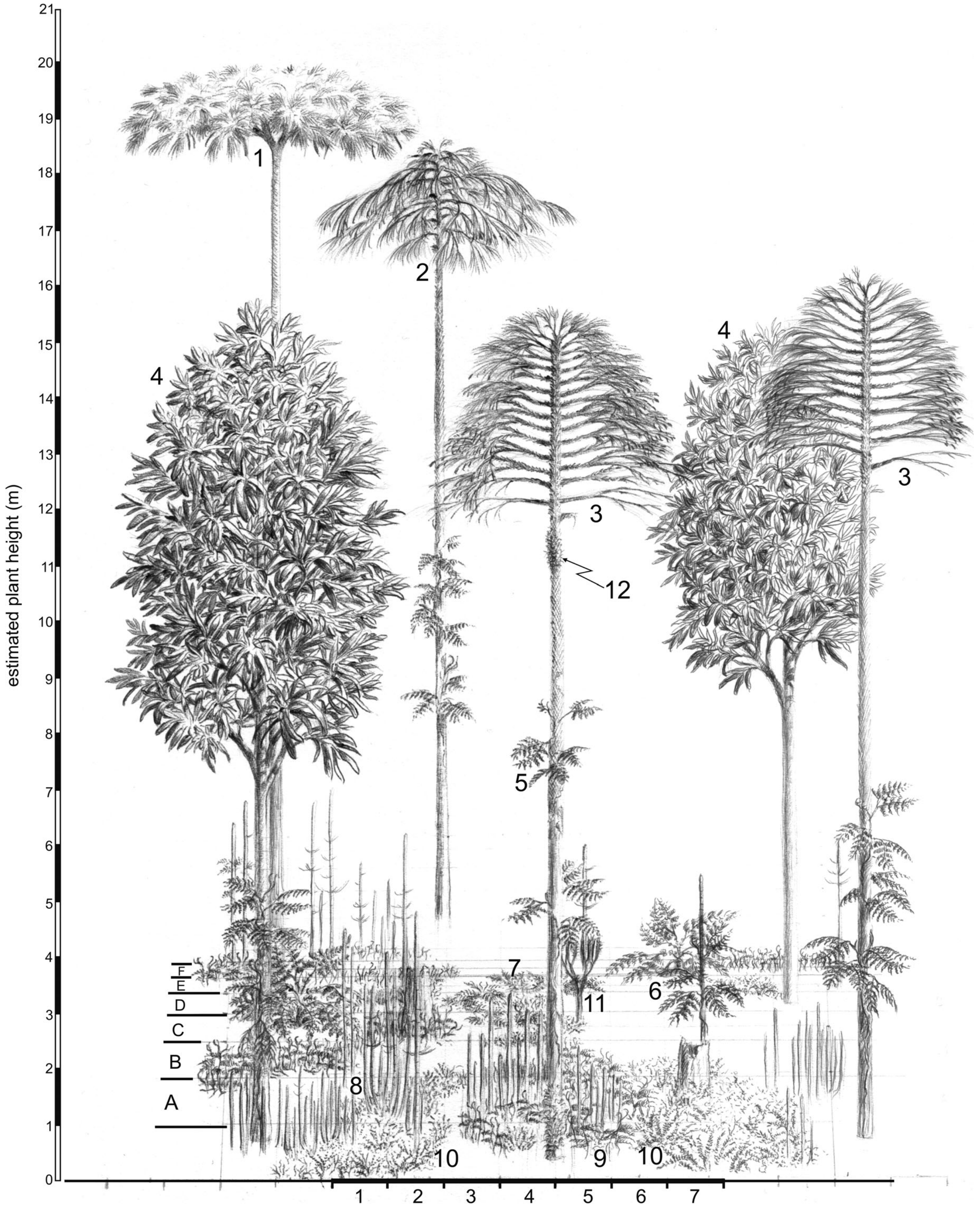

Figure 28. Reconstruction of the peat-forming forest of the Lower Radnice Coal in the S3 excavation and their immediate proximity. 1 – *Lepidophloios acerosus*; 2 – *Lepidodendron lycopodioides*; 3 – *L. (Paralycopodites) simile*; 4 – *Cordaites borassifolius*; 5 – *Eusphenopteris nummularia*; 6 – *Laveineopteris loshii*; 7 – *Sphenopteris mixta*; 8 – *Calamites* spp.; 9 – *Corynepteris angustissima*; 10 – *Sphenophyllum priveticense*; 11 – *Spencerites havlenae*; 12 – herbaceous bisporangiate lycopsid. Letters on left side and numbers across bottom correspond to square units in the S3 excavation as indicated in Fig. 5 *etc*. Drawn by Jiří Svoboda.

heights using the formula of Niklas (1994) indicates that most trees were probably between 18 and 23 m high (Opluštil *et al.* 2009a, b).

Lianas and epiphytes are plants that occupied the canopy level but in comparison with arborescent taxa are more diverse, being represented by 9 species in the Ovčín coal forest. Their distribution pattern corresponds significantly to that of arborescent plants presumably because the latter provided support. Nevertheless the coverage of liana/epiphyte species is lower in comparison to canopy taxa and varies between 21 and 29% in any particular excavation (Fig. 21). The most common species of this growth form are *Eusphenopteris nummularia* (15.5%), *Bowmanites pseudoaquensis* (4.4%) and *Palmatopteris furcata* (4.0%), which all belong among typical taxa of the Ovčín forest, present in all or most excavations. Subdominant are *Mariopteris muricata*, herbaceous bisporangiate lycopsid and, locally, also *Senftenbergia plumosa*. The remaining, mostly fern species, covered much smaller areas, although some of them occurred in several excavations (*e.g. Oligocarpia lindsaeoides*).

Understory, the medium-tall level of the Ovčín coal forest, has relatively low α-diversity comprising about 5 species (Fig. 20). In comparison with the canopy, it shows a patchier distribution, probably as a consequence of a relatively dense forest canopy. Coverage of the story varied between 13 and 47% among individual excavations. The story was dominated by medullosan pteridosperm with *Laveineopteris loshii* foliage, the coverage of which varied between 2.4 and 20.3% (weighted average 15.7%), and *Calamites* spp. (~ two species), with coverage 0.8–23.5% (14.5% weighted average). *Psaronius* is a sub-dominant but still typical species of the Ovčín coal forest, represented by *Pecopteris aspidioides* foliage (0–11.8%; 8.9% weighted average). *Spencerites havlenae*, a sub-arborescent lycopsid, was rare. The opencast mine collections revealed an additional medullosan species, *Alethopteris distantinervosa* foliage.

The lowest story of the Ovčín coal forest is groundcover, which yielded the highest α-diversity of all the stories and is, together with the lianas, responsible for generally high diversity of the forest over a small area (Table 3, Figs 20, 21). The ground cover consists of 10 species identified in excavations, although growth habit of some of them is not well constrained and they were assigned to this story based on the vertical distribution of their remains in the Bělka bed, which is indicative of plant habit (see the chapter Ground cover and occasional climbers). The story also includes plants that normally grew as groundcover (*e.g. Corynepteris angustissima*) but they were able to climb if they found a supporting plant. Coverage of this story is patchy and varied among the groups of excavations from 27–81% (Table 3). The dominant ground cover species, *Corynepteris angustissima*, is also one of the most common species of the forest, having coverage of 10.6–76.5% (46.6% weighted average) in any particular excavation group. The co-dominant species, *Sphenophyllum priveticense*, covered 13–52.4% (32.9% weighted average). This association is often accompanied by the ?lyginopterid pteridosperm *Sphenopteris mixta*, another typical element of the Ovčín coal forest. This latter species occupied 2.3–13.4% (10.0% weighted average). Sub-dominant groundcover taxa include *Desmopteris longifolia*, *Sphenophyllum cuneifolium* and locally also *Hymenotheca* sp., *Desmopteris longifolia*, with 3.6% (weighted average), is among the typical species of the Ovčín coal forest. Remaining, mostly fern taxa, are rare.

Although the vegetation in the Bělka tuff bed is preserved *in situ* in extraordinary detail, there are only few parameters used by botanists for description of modern phytocoenoses, which can be applied to characterise the extinct Ovčín coal forest. This is because most of them require knowledge of number of the individual plants, which is, however, usually not exactly known for fossil deposits, even those of T^0 character. Therefore we could adopt only few parameters including estimation of the Minimal Area, which statistically represents that area necessary to encompass the composition and diversity of the phytocoenosis. Such an area in the case of modern forest phytocoenoses varies usually between 200 and 500 m^2 (*e.g.* Meuller-Dombois & Ellenberg 1974, Moravec *et al.* 1994), which is twice as large as our maximum continuously excavated area (the Ovčín group of excavations (O1–3, 93.5 m^2) and still larger than the size of the composite area of all the excavations together (177 m^2). Therefore we can assume that our excavations represent only fragments of the Ovčín lepidodendrid-cordaitalean coal forest. This is evidently true in the case of the S3 excavation analysed here (33.5 m^2), which, although providing remains of 25 biological species, none of the five canopy taxa were among those rooted in the study area (Fig. 28). Instead their crowns partially overlapped the excavation and the α-diversity of the S3 excavation is in reality "only" 20 non-arborescent species rooted in the excavated area.

Even the largest continuously exposed area (excavations Ovčín 1–3, 93.5 m^2) does not reach the full diversity of the Ovčín coal forest, although its steeply rising curve becomes flat between 64 and 93.5 m^2 (Fig. 23). The absence of several species known from the Sternberg excavations and the opencast mine only suggests that there would be another gentle rise in the curve were area to be increased. This can be tested when examining α-diversity across a composite area of all the excavations, where 29 biological species have been identified within 177 m^2 (Fig. 23). This diversity is already close to the approximately 35 species found in the 120,000 m^2 of the Ovčín coal deposit. Therefore we estimate that ~200 m^2 can be considered as a sufficiently representative area (*i.e.* the Minimal Area) of the Ovčín Lower Radnice Coal forest

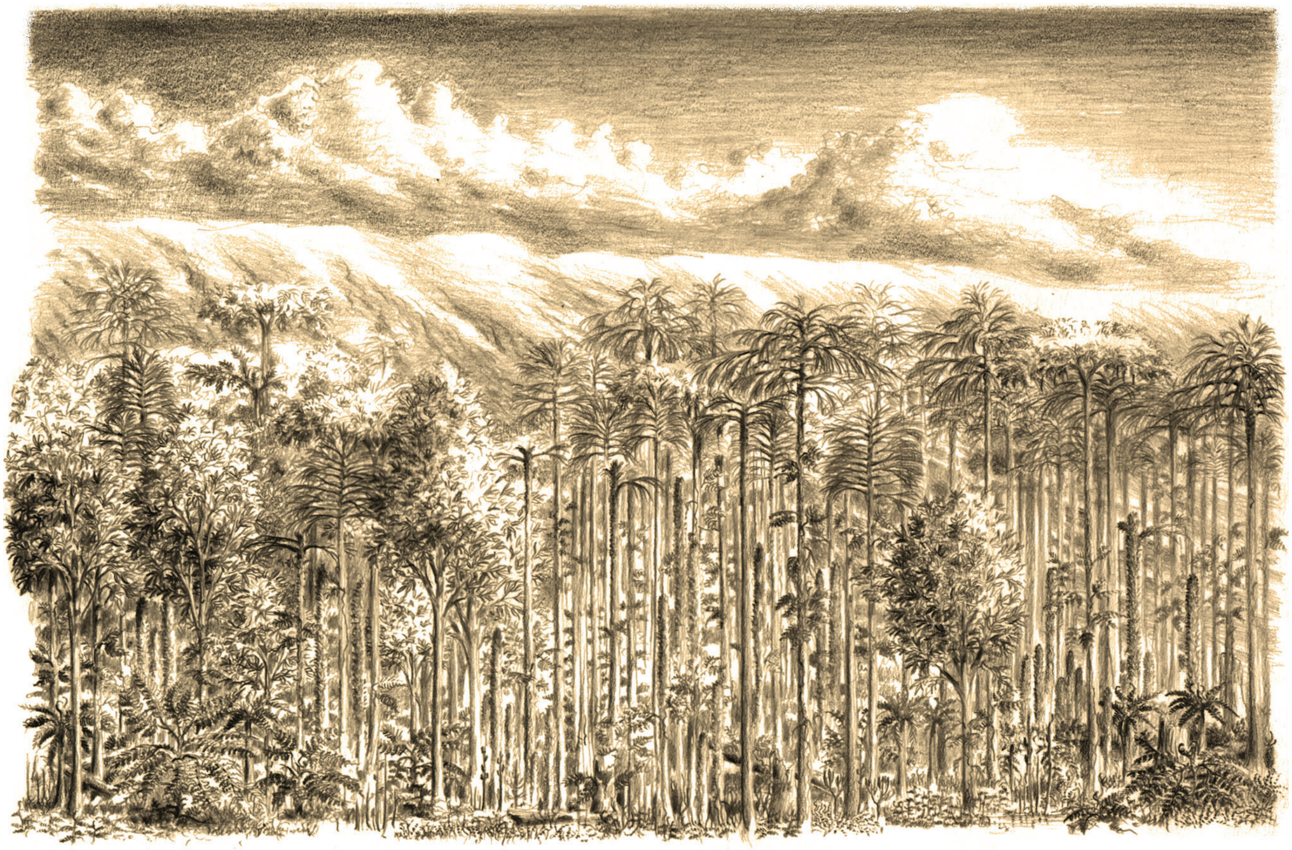

Figure 29. Reconstruction of a mixed lepidodendrid-cordaites coal forest of the Ovčín coal deposit bordered by basement palaeohighs. Drawn by Jiří Svoboda.

phytocoenosis prior to the volcanic eruption. The high diversity over a relatively small area is reached mainly due to groundcover and liana-like plants.

A notable characteristic of the Bělka and Brousek fossil record at the Ovčín coal deposit, revealed by our excavations and the Ovčín opencast mine, is that large tree stumps, having 50–90 cm in diameter, end either in the Bělka or basal part of the Brousek and are filled by the Bělka tuff. This suggests that they were stumps (*i.e.* torsi of dead trees) already prior the eruption and therefore represent an earlier generation of the Ovčín coal forest preceeding that one killed by volcanic ash fall and recorded in the Bělka. Stumps of this later generation are often much taller and slimmer stems filled by the Brousek, which indicates that they were trees, alive-and-well prior to the eruption. Diameter of these upright stems is only about 30 cm maximum. The absence of large trees in the later Ovčín coal forest buried by volcanic ash thus indicates that the previous (earlier) Ovčín coal forest was destroyed by some catastrophical event (*e.g.* long-lasting flooding, strong wind, *etc.*), which interrupted progress of the hydroseral succession of the peat swamp. Once the site again became suitable for plant colonisation, a new succession started to evolve. This could explain why the largest trees of the younger Ovčín coal forest are all roughly of the same size. Events like catastrophic floods were probably a common part of the Pennsylvanian tropical forest dynamics as documented at the Štilec locality, 20 km from the Ovčín site. Here in the Bělka, a dwarf calamites-fern-dominated, low-diversity, pioneer assemblage, described by Libertín *et al.* (2009), colonised the previously drowned mire.

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