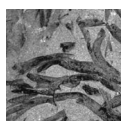


First record of the noncalcareous macroalga *Perissothallus* from shallow-water deposits (Pennsylvanian) in the Kladno-Rakovník Basin, Czech Republic

JOSEF PŠENÍČKA & MICHAEL KRINGS



The fossil genus *Perissothallus* is used for adpression fossils of late Palaeozoic noncalcareous freshwater algae consisting of erect, cylindrical branches that radiate from a central holdfast and dichotomize repeatedly. The taxon currently includes *P. versiformis* from the Upper Pennsylvanian of North America and *P. densus* from the Lower Permian of Germany. In this paper we describe a third species, *Perissothallus dekovensis* nov. sp., from the Gzhelian (Stephanian B; Upper Pennsylvanian) of the Kladno-Rakovník Basin, Czech Republic. The new species differs from the previously described forms with regard to thallus size and branching pattern of the erect parts. Sedimentological data and the fossils that co-occur with the algal thalli suggest that *P. dekovensis* lived in shallow-water areas of a lake or abandoned channel that was surrounded by tree ferns, cordaites (especially *Poacordaites*-type), and lycopsids. • Key words: Carboniferous, Kounov Member, palaeoecology, *Perissothallus densus*, *Schizopteris*, thallus.

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Algae today occur in a wide variety of environments, ranging from open oceans to desert sand (e.g. Andersen 1992, Norton *et al.* 1996); many forms thrive as epiphytes and endophytes on and in other organisms (Goff 1983, Chapman & Waters 1992). However, large algae with complex multicellular thalli (“macroalgae”) are typically restricted to aquatic habitats (Graham *et al.* 2009, Keith *et al.* 2014).

The fossil record of algae is extensive and ranges from the Mesoproterozoic (~1.2 Ga) (Butterfield 2000) to Quaternary (Garcia & Playford 2007, Taylor *et al.* 2009). Certain groups of unicellular algae, charophyte oogonia (gyrogonites), and the remains of calcareous macroalgae from marine and brackish water environments are abundant and diverse as fossils because their thick walls and/or calcium-based skeletons are readily preserved (e.g., Flügel 1977, Tappan 1980, Riding 1991). Conversely, noncalcareous macroalgae are rare as fossils. The fossil representatives reported to date for this group likely represent only an infinitesimal portion of the species diversity that

existed in various aquatic environments throughout geological time (Krings & Mayr 2004, Krings & Butzmann 2005). Nevertheless, noncalcareous macroalgae play important roles in the functioning of many aquatic ecosystems today (e.g., Round 1981), and likely were similarly important in the past. As a result, a detailed documentation of their past diversity and distribution is important in fully understanding the functioning and evolution of ancient aquatic ecosystems. Unfortunately, noncalcareous macroalgae become preserved only where the depositional environment provides ideal conditions for fossilization. Moreover, impression/compression fossils of these organisms may easily be confused with other plant remains such as bryophytes, aphanopetaloid foliage of several vascular plants, and roots, and thus are probably often overlooked or misinterpreted (Krings *et al.* 2007).

One excellent example is *Schizopteris* Brongniart, initially described for Carboniferous impression/compression fossils of aphanopetaloid foliage of uncertain affinity

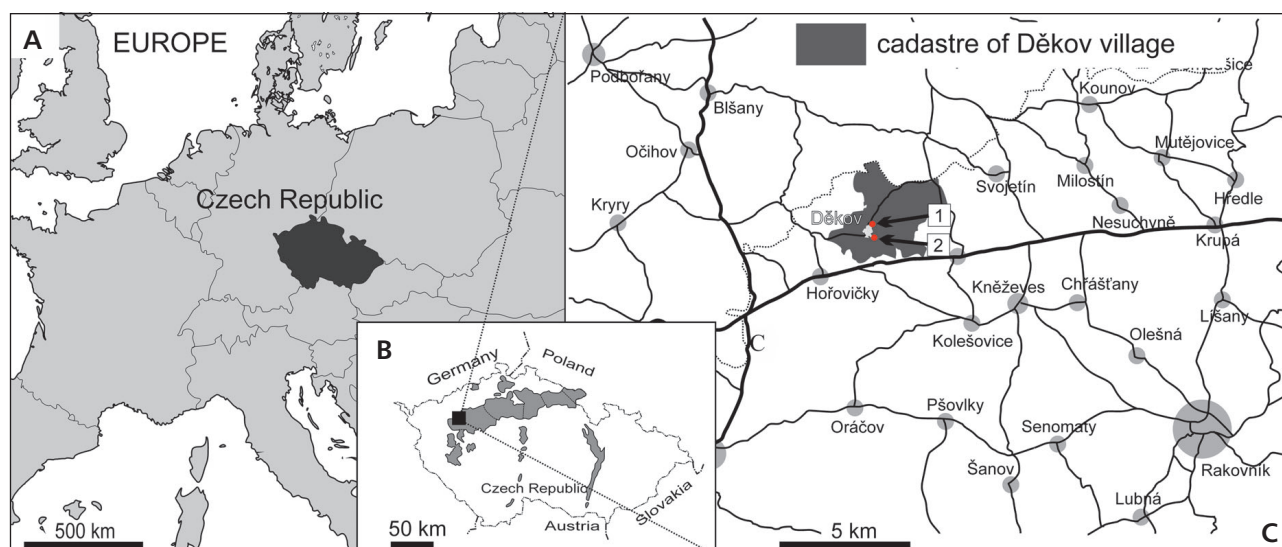


Figure 1. Geographic position of the Děkov locality. • A – location of Czech Republic in Europe. • B – late Palaeozoic continental basins in Czech Republic. • C – detail of the Rakovník area, showing Děkov village and the two localities mentioned in the text: 1 – abandoned quarry northeast of Děkov village, 2 – abandoned quarry southeast of Děkov village.

(Brongniart 1828–1837). Barthel (1982), Kerp & Fichter (1985), and Krings *et al.* (2007) suggested that some of the fossils conventionally assigned to *Schizopteris* do not represent aphleoid foliage, but rather thalli of noncalcareous algae similar in overall morphology to certain extant members of the Chlorophyta (green algae), Phaeophyceae (brown algae), and Rhodophyta (red algae). Krings *et al.* (2007) therefore formally excluded the algae from *Schizopteris* and introduced a new genus, *Perissothallus* Krings *et al.*, for these fossils, with two species, *P. versiformis* Krings *et al.* from the Upper Pennsylvanian of North America and *P. densus* Krings *et al.* from the Lower Permian of Germany. However, these authors acknowledged that many more specimens and forms need to be critically analyzed and formally described to complete the separation of the algae from *Schizopteris*, and to document the geographic distribution and stratigraphic range of these aquatic plants. For example, several impression/compression fossils of aphleoid foliage from the Carboniferous of the Czech Republic have been described under the name *Schizopteris* (e.g., Sternberg 1838, Němejc 1938). The paper presented here is the first record of *Perissothallus* from the Czech Republic based on specimens from the Slaný Formation (Gzhelian/Stephanian B) at Děkov, northwest of Rakovník. The thalli resemble *Perissothallus densus*, but are considerably smaller and display a different branching pattern of the erect parts. As a result, we have instituted a third species of *Perissothallus*, for which the name *P. dekovensis* nov. sp. is proposed. This discovery contributes to our understanding of the diversity, geographical distribution, and geological range of the late Palaeozoic algal genus *Perissothallus*.

Geological setting, material and methods

The specimens come from an abandoned quarry located near the village of Děkov, ~15 km northwest of Rakovník (Kladno-Rakovník Basin), Czech Republic (Fig. 1C – loc. 1). They were collected by J. Šetlík in the 1960s and are currently in the Czech Geological Survey, Prague, under numbers ZŠ 539 through 544. The fossil thalli are preserved as impressions/black compressions on an ochre-gray mudstone/siltstone matrix; co-occurring with the thalli on the same slabs are fragmented remains of plant roots and abundant detritus.

The strata exposed at the Děkov locality have been assigned to the Kounov Member of the Slaný Formation (Pennsylvanian) based on the presence of thin, low grade coal layers intercalated with a whitish clay/sand layer (up to 7 mm thick) which has been interpreted as a so-called “Kamínek”, a volcanogenic sediment typical of the lower Kounov Coal (Němejc & Šetlík 1950). The Kounov Member is part of the Slaný Formation that extends from Pilsen to the Kladno-Rakovník and Mšeno-Roudnice basins (Pešek 2004). The formation represents a complex of fluvio-lacustrine deposits (30–50 m thick) composed of whitish-grey arkosic sandstone or arkoses that are locally rich in grey claystone and mudstone, and contains several coal seams of the Kounov Group (Pešek 1994). The Kounov Group is subdivided into a Lower and Upper Kounov Coal, the former characterized by the presence of a distinctive argillized volcanogenic “Kamínek” bed (Obrhel 1960; Pešek 1994, 2004). Kamínek is one of the most important correlation markers in basins of central and western Bohemia (Pešek 1994, 2004).

The geological setting at Děkov reflects the marginal development of the Lower Kounov Coal. The coal occurs in thin layers representing short episodes of water-table fluctuation. Precursor of the Kounov Coal probably was a planar peat swamp that experienced occasional flooding. The geological profile for the area was compiled by Němejc & Šetlík (1950) based on data obtained from the basal part of the upper dirty coal exposed in an abandoned quarry southeast of Děkov (Fig. 1C – loc. 2). The source locality of the fossils described here (Fig. 1C – loc. 1) is included in the same stratigraphic context. The sequence (Fig. 2) begins with massive arkoses deposited in a high-energy environment, possibly of fluvial origin. The arkoses are conformably overlain by grayish-green mudstones (*ca* 150 m thick) deposited in a low-energy environment, possibly lacustrine or an abandoned channel fill. This part of the profile consists of sediments indicative of a shallow-water environment. The overlying dirty coal (~70 mm thick) indicates formation via paludification. The horizon between the arkoses and dirty coal contains abundant roots and fragmentary remains of aerial plant parts. The algal thalli come from a thin layer of mudstone situated immediately below the lower dirty coal (see Fig. 2). Mudstone (~500 mm) lacking fossils occurs above this coal, at least according to Němejc & Šetlík (1950), however, these authors reported roots from the same stratigraphic interval exposed in the quarry southeast of Děkov (Fig. 1C – loc. 2). Both quarries are today closed and recultivated, which unfortunately precludes verification of Němejc & Šetlík's (1950) description of the geological sequence and a more precise sedimentological interpretation of the alga-bearing section.

Systematic palaeobotany

Algae incertae sedis

Fossil genus *Perissothallus* Krings *et al.*, 2007

Fossil species *Perissothallus dekovensis* sp. nov.

Holotype. – Specimen illustrated in Fig. 3A and B, housed in the collection of the Czech Geological Survey, Prague, Czech Republic (number ZŠ 593).

Etymology. – The epithet “*dekovensis*” refers to the provenance of the material.

Type locality. – Abandoned quarry southeast of the village of Děkov (50°10' 24.7" N; 13°33' 19.8" E).

Type horizon. – Kounov Coals (layer directly below Lower

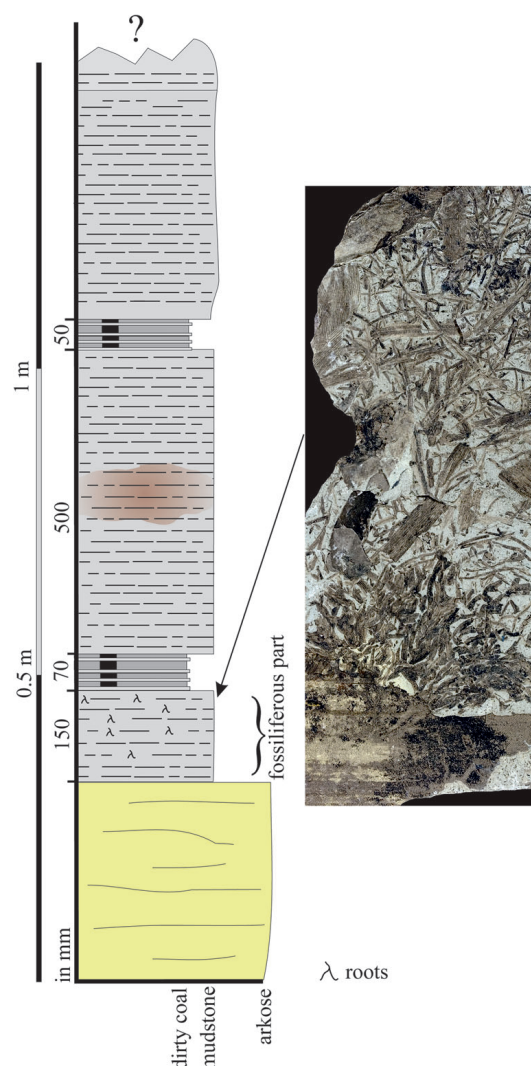


Figure 2. Sediment succession in quarry northeast of Děkov village according to Němejc & Šetlík (1950), showing dirty coals, mudstone deposits, and arkoses; photograph shows slab containing algal thalli, roots, and plant detritus.

Kounov Coal), Kounov Member, Slaný Formation, lowermost Gzhelian (Stephanian B), Upper Pennsylvanian.

Diagnosis. – Thallus small, sessile, solitary, relatively loosely organized; holdfast prominent, hemispherical; erect branches numerous, extending from entire surface of holdfast; branches cylindrical, usually up to 35 mm long and dichotomizing 5–6 times; branch segments (between two dichotomies) mostly between 3 and 10 mm long; ultimate segments short, often somewhat club-shaped, tips rounded or somewhat tapering.

Description. – The thallus of *Perissothallus dekovensis* (Fig. 3A–C) is relatively loosely organized and consists of numerous (>25) erect branches that extend from a prominent, more or less hemispherical or somewhat cylindrical

holdfast structure, which is 7.5 mm wide and 3.5 mm high in the specimen shown in Fig. 3A and B (arrow). The holdfast in this specimen is attached to what appears to be a segment of a large cordaitalean branch. We are unable to determine whether the two elongate structures that appear to extend from the holdfast into the cordaitalean branch belong to the algal thallus or represent preservation artifacts. The erect thallus branches measure 20–25(–35) mm long and 1–1.5 mm wide, and were probably more or less cylindrical in vivo. They dichotomize irregularly, usually 5–6 times (Figs 3E, 4). Branch segments between two dichotomies range from <3 to >10 mm long. Proximal branch segments often appear distinctly narrower than the distal ones (Figs 3E, 4). Ultimate branch segments are short and usually taper towards the tip or possess a rounded apex (Fig. 3D). Distal dichotomies sometimes show a faint constriction immediately below the dichotomy (arrow in Fig. 3E).

One specimen from the Šetlík collection is distinctly more compact in appearance than the others (Fig. 3F). Unfortunately, the number of dichotomies in this thallus cannot be determined because the branches are too densely compacted. This specimen is >60 mm in diameter, and thus exceeds the size of all other specimens of *Perissothallus dekovensis*.

Remark. – Features of the specimen illustrated in Fig. 3F are not included in the diagnosis because it is impossible to determine whether this specimen represents a large and unusually compact individual of *Perissothallus dekovensis* or belongs to a different species (see Discussion section below).

Discussion

Comparisons

The genus *Perissothallus* initially comprised two species, i.e. *Perissothallus versiformis* from the Upper Pennsylvanian of North America and *P. densus* from the Lower Permian of Germany (Krings *et al.* 2007). Krings *et al.* (2007) used three basic features to distinguish algae from *Schizopteris*-type aphlebooid foliage. These include (i) the overall appearance and morphology of the fossils with no consistent internal or surface structures (e.g., venation) visible, (ii) the presence of a basal holdfast, and (iii) variable morphologies suggestive of different developmental stages. *Perissothallus dekovensis* described in this paper is consistent with the first two of these features. However, the spe-

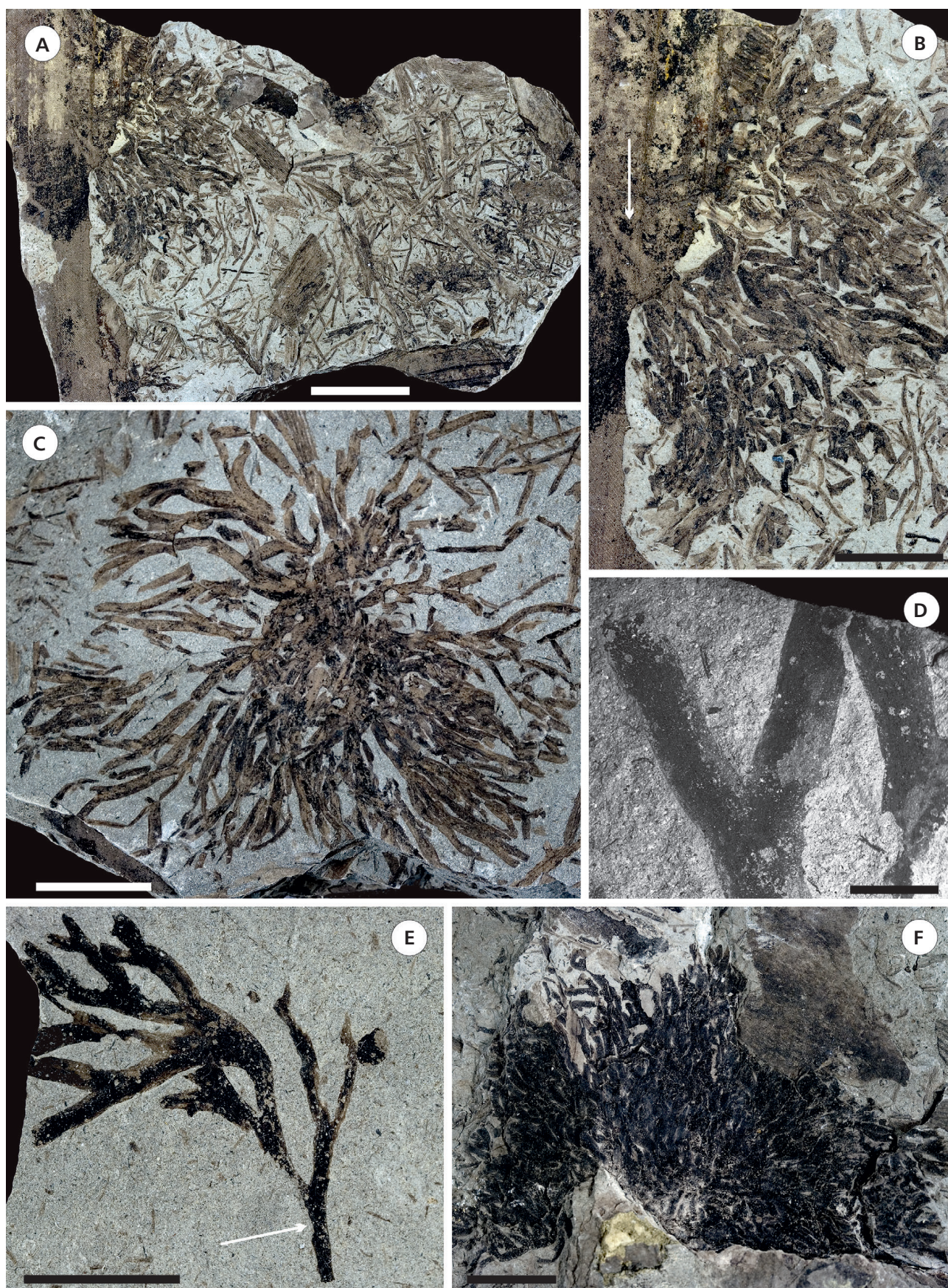
cies is represented by only two complete thalli (Fig. 3A, C) that are generally similar in morphology. Both thalli appear to be mature, based on the degree of differentiation of the erect branches, which is comparable to that seen in the mature specimens of *P. versiformis* and *P. densus* (Krings *et al.* 2007, figs 1, 8–10, 12, 13). Variable morphologies suggestive of developmental stages are not present in the material from the Czech Republic, with the possible exception of the specimen illustrated in Fig. 3F, which might be an old or exceptionally large of *P. dekovensis*, but also might represent a different species.

If our interpretation of the specimens illustrated in Fig. 3A and C as mature thalli is correct, then *Perissothallus dekovensis* differs from both previously described taxa primarily with regard to size. *Perissothallus versiformis* and *P. densus* are considerably larger than *P. dekovensis* (e.g., branches are up to 70 mm long in *P. densus* vs 35 mm in *P. dekovensis*). Moreover, *P. dekovensis* differs from *P. versiformis* in the branching pattern of the erect parts, which uniformly dichotomize in the former but demonstrate a more irregularly monopodial branching pattern in the latter species. In addition, the spacing of the erect branches in *P. densus* is more dense than in *P. dekovensis*. Finally, thalli extending from elongate prostrate axes, a typical feature of *P. densus* (see Krings *et al.* 2007, figs 6, 10, 11), have not been observed in *P. dekovensis*. However, the latter difference might also represent a small sample size for *P. dekovensis*. The possibility also exists that some or all of the features used to delimit *P. dekovensis* from *P. versiformis* and *P. densus* are not diagnostic, but rather represent patterns of intraspecific variability. However, since our analysis is restricted to the morphology of sterile thalli, we are confident in interpreting the specimens illustrated in Fig. 3A–C as a separate fossil species.

Palaeoenvironment

The fossils described in this paper come from sediments deposited in an intramontane basin that, together with several other basins, developed in central and western Bohemia (henceforth abbreviated CWB) during the Pennsylvanian as a result of the Variscan Orogeny (Krs & Pruner 1995; Pešek 1994, 2004; Opluštil & Pešek 1998). The basin fills consist of up to 1400 m of Moscovian/Gzhelian sediments, which have been subdivided and formally described as Kladno (humid phase), Týnec (arid phase), Slaný

Figure 3. *Perissothallus dekovensis* nov. sp. • A – holotype. Mature thallus attached to cordaitale branch co-occurring with abundant roots and plant detritus; specimen ZŠ 539; scale bar = 20 mm. • B – detail of Fig. 3A, showing system of erect branches emerging from holdfast (arrow); scale bar = 10 mm. • C – second specimen of complete mature thallus; specimen ZŠ 540; scale bar = 10 mm. • D – slightly widened distal (ultimate) units of erect branches; specimen ZŠ 540; SEM; scale bar = 2 mm. • E – branch of mature thallus; note that proximal branch segments (arrow) appear narrower than the distal ones; specimen ZŠ 541; scale bar = 10 mm. • F – large compact thallus; specimen ZŠ 543; scale bar = 10 mm.



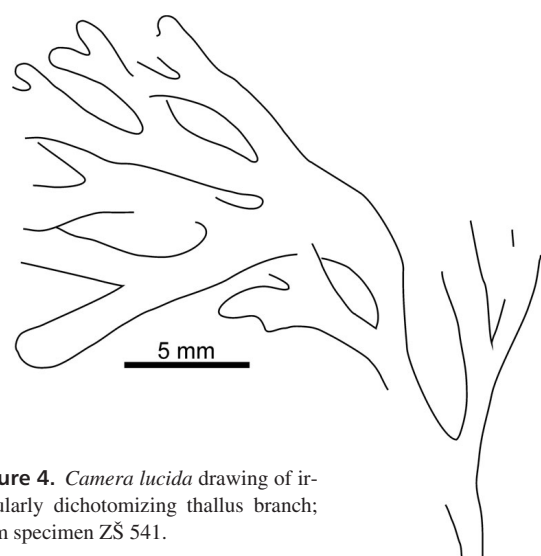


Figure 4. Camera lucida drawing of irregularly dichotomizing thallus branch; from specimen ZŠ 541.

(humid phase), and Líně (arid phase) formations (Pešek 1994, 2004; Opluštil & Cleal 2007). The *Perissothallus* specimens come from the Slaný Formation, which is Gzhelian (Stephanian B) in age (Němejc & Šetlík 1950; Obrhel 1960; Havlena 1961; Pešek 1994, 2004). During this period, an extensive freshwater lake was present in the north-eastern part of CWB (Lojka *et al.* 2010). The sedimentary record indicates that the region was governed by wet and dry seasonality (Lojka *et al.* 2010). Moreover, the sediment sequence contains alginite layers that formed during the phase when the lake was deepest and had its largest geographical extent; Lojka *et al.* (2010) report on the presence of unicellular and colonial algae such as *Botryococcus* Kützing and *Tasmanites* Newton, as well as certain thin-walled benthic algae in these layers. However, the alginite was deposited earlier (*i.e.* Mšenec Member) than the source sediments of the *Perissothallus* specimens.

The *Perissothallus* fossils come from the marginal development of the Lower Kounov Coal, with short episodes of water table fluctuations reflected in the alternation of mudstone and dirty coal layers. All specimens are preserved in the mudstone occurring between the arkoses at the bottom of the profile and the dirty coal (Fig. 2), and were recovered from the layer situated immediately below the lowermost dirty coal layer. Coal is visible on virtually all slabs, suggesting that the fossils comprising the assemblage all reflect the same general taphonomic history. The fossil assemblage is composed of highly fragmented remains of vascular plants, including pinnules, roots, large cordaitalean leaves, and unidentified axes. Many pinnules show evidence of early stages in the disintegration along the veins and partial skeletonization (*i.e.* only the venation is preserved) probably due to catabolic processes or microbial decay prior to embedding. Among the highly fragmented plant fragments are *Annularia spicata* (Gutbier) Schimper, *A. spinulosa* Sternberg, *Diplazites unitus*

(Brongniart) Wagner, *Acitheca polymorpha* Schimper, *Nemejcopteris feminaeformis* (Schlotheim) Barthel, *Neurodontopteris neuropteroides* (Göppert) Cleal, *Pseudomariopteris cf. cordato-ovata* (Weiss) Gillespie, *Linopteris neuropteroides* (Gutbier) Potonie, *Callipteridium trigonum* Franke, *Taeniopteris* sp., *Dolerotherca* sp. and *Artisia* sp., *Annularia sphenophylloides* (Zenker) Gutbier, *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, and *S. longifolium* (Germar) Gutbier. Based on the level of degradation, these fossils probably represent a portion of the vegetation that grew some distance from the site of sedimentation. On the other hand, large cordaitalean leaves (*Poacordaites* sp., *Cordaites* sp.) and two different *Samaropsis*-type seeds are quite common. These forms are characterized by thick, leathery leaves, which likely were more resistant to mechanical degradation than the leaves of sphenophytes, ferns, and pteridosperms, and thus transported farther without significant destruction. As a result, it is impossible to determine whether the cordaitalean leaves stem from plants growing in close proximity to or further away from the place of sedimentation. In addition, several representatives of the pollen genus *Florinites* [*i.e.* *F. antiquus* Schopf, *F. circularis* Bharadwaj, *F. junior* Potonié & Kremp, *F. mediapudens* (Loose) Potonié & Kremp, *F. minutus* Bharadwaj, *F. ovalis* Bharadwaj, and *F. pumicosus* (Ibrahim) Schopf *et al.*] have been recorded for the Lower Kounov Coal (Kalibová 1960). *Florinites* is attributed to the Cordaitales based on in situ occurrences in *Cordaitanthus* Feistmantel (Brush & Barghoorn 1962) and *Florinanthus* Ignatiev & Meyen (Šimůnek *et al.* 2009). Unfortunately, the pollen record does not aid in determining the exact site of growth of the cordaitalean plants because *Florinites* can be transported over long distances by wind. Nevertheless, the overall high frequency of cordaitalean macroremains, along with the abundance of *Florinites* in the palynomorph assemblage, suggest that cordaitaleans constituted a significant component of the vegetation. Kalibová (1960) also found abundant spores attributable to the marattialean ferns. In addition, one lycopsid, *Polysporia* sp., which is regarded as a peat-forming element (Bek *et al.* 2008), has been reported from the mudstone layer immediately below the thin coal bed. The Lower Kounov Coal contains dispersed miospores of the *Endosporites*-type [*E. formosus* Kosanke and *E. globiformis* (Ibrahim) Schopf *et al.*] (Pešek 2004) and megaspores of *Valvisporites auritus* (Zerndt) Gastaldo (Kalibová, 1959) that are all believed to have been produced by *Polysporia* Newberry (Bek *et al.* 2008). Since only a single macrofossil of *Polysporia* sp. has been discovered, we are unable to determine how abundant this plant was and what role it may have played in the physiognomy of the vegetation.

The abundance of large root fragments is significant with regard to assessing the palaeoenvironment at Děkov. Root fragments are variable in size (Fig. 3A); they occur in

Figure 5. Suggested reconstruction of *Perissothallus dekovensis* growing on a submerged cordaitalean axis.



horizontal position in the sediment layers below the lower coal bed. Evidence of rhizoturbation is lacking. It appears that the assemblage consists of two morphologically different types of roots, one of which is a *Pinnularia*-like form attributable to sphenophytes (Jongmans 1911), which represent common elements of the flora at this locality (see above). The frequent presence of roots assignable to these plants adds support to the suggestion that sphenophytes grew close to the place of sedimentation. A second type of root may have been produced by some type of gymnosperm based on structural similarities to material described by Krings (2003).

It is especially interesting to note that one of the *Perissothallus dekovensis* specimens occurs attached to a relatively large plant part, probably a cordaitalean branch (Fig. 3B). This is consistent with the observations of Barthel *et al.* (1998) and Krings *et al.* (2007), who described the occurrence of *P. densus* from the Lower Permian of southwestern Germany on roots of the enigmatic gymnosperm *Dicranophyllum hallei* Remy & Remy. These authors hypothesized that plants growing near or perhaps in the water may have produced roots directly into the water, or soil roots were washed free by the water, and that these roots were subsequently colonized by *Perissothallus*. The colonization of roots and other submerged plant parts by *Perissothallus* seems a plausible hypothesis (Fig. 5) because the bottoms of lakes and streams were largely composed of loose sediment and organic debris, and thus offered no secure growth sites for macroalgae that attach to the substrate by a holdfast (Krings *et al.* 2007).

In conclusion, the nearshore shallow-water areas of a lake or an abandoned channel that in turn was surrounded by a forest dominated by tree ferns, cordaitaleans, and lycopsids based on frequency of plant remains in combination with palynological evidence, probably represents the environment in which *Perissothallus dekovensis* lived. Sphenophytes including several *Sphenophyllum* species also grew in these areas or around the trunks of various trees. Although the Pennsylvanian coal swamp forests of Europe and North America

represent the most intensively studied late Palaeozoic ecosystems, (re-)analysis of hitherto neglected or overlooked specimens and collections from historically important but no longer available localities continues to broaden our understanding of the vegetation that grew in these ancient landscapes.

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