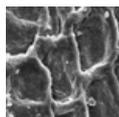# *Cordaites borassifolius* (Sternberg) Unger (Cordaitales) from the Radnice Basin (Bolsovian, Czech Republic)

ZBYNĚK ŠIMŮNEK, STANISLAV OPLUŠTIL & JANA DRÁBKOVÁ

The remains of cordaitalean plants are an important element in Bolsovian plant fossil assemblages from the Radnice Basin (Czech Republic). The study of historic collections and new excavations brings together new data on the *Cordaites* type species – *Cordaites borassifolius*. *Cordaites borassifolius* was probably quite a large tree of monopodial or even sympodial stature. Its trunk diameter was at a minimum 0.5 m. Branches were between 1.1 m and spaced less than 0.7 m appart. The bases of the branches usually attained about 2/3 to 1/2 of the trunk width. The abaxial cuticle has stomata arranged in multiplex stomatal rows that formed a wide stomatiferous band. A transverse crypt above the stoma is an important diagnostic feature. The cordaitalean leaves, twigs, pith casts, fertile organs and seeds found are referable to a single natural species. The associated fertile organs belong to two types: 1) male fertile organs *Florinanthus volkmannii* and 2) a more robust, probably female, form similar to *Cordaitanthus ovatus*. Cuticles from the scales and long bracts of *Florinanthus volkmannii* have been studied in detail. Most scale cuticles are astomatal, but stomata may occur very rarely on some parts of the abaxial cuticle. Small trichomes grew from the scale margins. The cuticle of the bract has elongate cells and stomata are arranged in single stomatal rows on the abaxial cuticle. Many bilateral monosaccate pollen grains [*Florinites ovalis*, *Florinites guttatus* and *Pseudoillinites*, with a central body bipolar attachment to the equatorial saccus were separated from scale surfaces of *Florinanthus volkmannii*. The pith cast belong to the species *Artisia approximata*. The seeds are small and of the "*Cardiocarpus*-type". *Cordaites borassifolius* grew in wet, peat-forming habitats and they were most likely trees of medium height. • Key words: Carboniferous, Radnice Basin, Cordaites, cuticles, cordaitalean fertile organs.

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Recent excavations of fossil-bearing tuff bed (called bělka) at the base of the Whetstone Horizon at the Ovčín locality in the Radnice Basin (Opluštil *et al.* 2009) has provided a collection of well preserved plant fossils representing a peat-forming vegetation buried in growth position by volcanic ash. Due to this unique burial history, different plant organs derived from the same plant are preserved in a natural association with the parent stem. These remains include cordaitalean leaves, pith casts, fertile organs such as cones and seeds, branches and several metre long stems. Cuticles isolated from 11 leaves found at the Ovčín locality are all conspecific with cuticles prepared from the holotype *Cordaites borassifolius* (Sternberg) Unger, described by Sternberg (1821) from the Radnice Basin as the remains of a palm – *Flabellaria borassifolia.* Since all the cordaitalean leaves found at the Ovčín locality appear to represent *Cordaites borassifolius* it seems that associated stems, branches and fertile or-

gans could also belong to this species. Therefore this contribution is focused on evaluating the potential of these new findings for the reconstruction of *Cordaites borassifolius*.

## Geological setting

Samples of *Cordaites borassifolius* discussed in this paper were recovered from the Radnice Basin, which represents only a small part of an extensive complex of late Palaeozoic continental basins in the Czech Republic (Fig. 1A). Sedimentary fill of these basins in Central and Western Bohemia ranges from the middle Westphalian (Bolsovian) through to late Stephanian (Pešek 1994) and it is divided into four formations (Fig. 2) based on the alternation of red beds and grey, coal-bearing strata (Weithofer 1902). However, in the Radnice Basin, only the lower part of the oldest
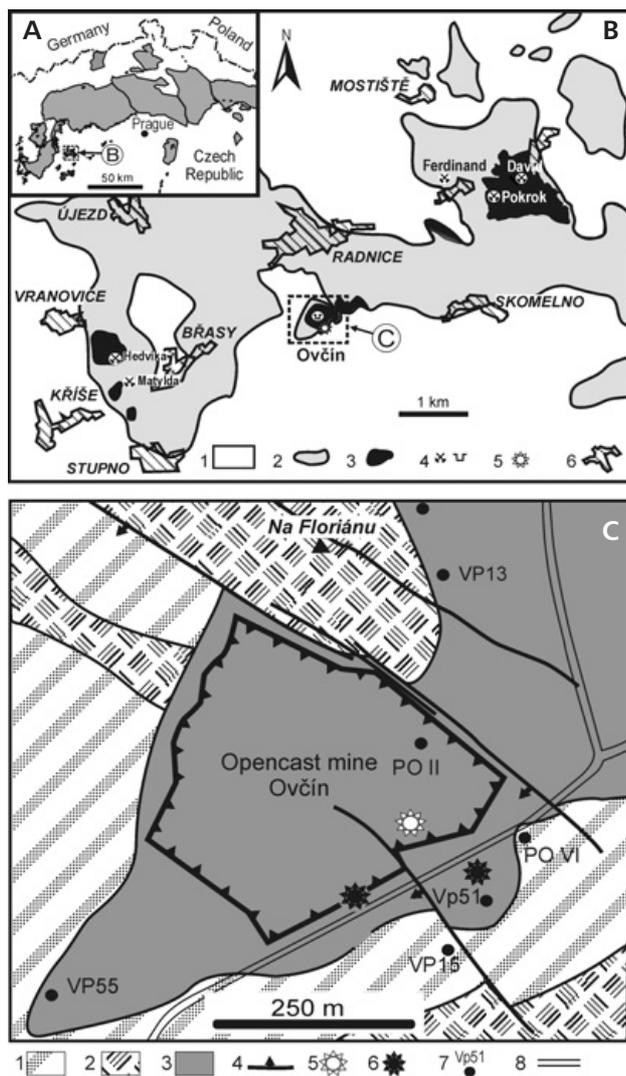
**Figure 1.** Location of the study area. A – Late Palaeozoic continental basis of the Czech Republic. Circled B shows the position of the Radnice Basin. B – Radnice Basin and adjacent relicts of Carboniferous sediments (1 – Pre-Carboniferous rocks, 2 – Carboniferous sediments, 3 – Lower Radnice Coal in workable thickness and quality, 4 – closed mines/opencast mines, 5 – excavation at the Ovčín locality, 6 – urbanised area). Circled C shows the position of the Ovčín locality. C – geological map of the Ovčín locality with the position of the Ovčín opencast mine and excavations. 1, 2 – Proterozoic basement (1 – shales, 2 – basic volcanites), 3 – Radnice Member, 4 – fault, 5 – site of cordaitalean remains collected in the opencast mine, 6 – excavations (OE – Ovčín Excavations, SE – Sternberg Excavations), 7 – borehole, 8 – road.



**Figure 2.** Lithostratigraphy of the Radnice Member (A) and architecture of the Whetstone Horizon at the Ovčín locality (B).

cally > 10 m thick. Both coal seams are separated by the Whetstone Horizon, which tends to be a few meters thick but locally can reach over 10 m in thickness. The Whetstone Horizon has a sharp contact with the underlying rock above which is a 0.6 m thick basal unit of pale yellow fossiliferous tuff (the "bělka"), overlain by up to 10 m of the "whetstone", poorly- to well-laminated tuffitic claystone and mudstone (Fig. 2). The bělka or tuff bed contains upright standing stems of peat-forming plants. Observation of the distribution of plant remains and their mode of occurrence indicates a simple burial history of the former peat-forming forest (Opluštil *et al.* 2007, 2009). In contrast, the overlying tuffitic mudstones (whetstone) contain only detrital plant remains concentrated on discrete bedding surfaces. The occasional larger plant fragments are randomly scattered within the unit. In the upper part of the whetstone, vertebrate and insect ichnofossils are frequently found (Turek 1989). Plant fossils of the Radnice Basin are mostly preserved in the Whetstone Horizon between the Lower and Upper Radnice Coals, and from the siliciclastic or volcanoclastic partings and roof shale of the Upper Radnice Coal.

## Material

Apart from Sternberg's holotype of *Cordaites borassifolius* (Sternberg) Unger and Corda's specimens from Svinná

unit, the Kladno Formation, is preserved. These sediments belong to the Radnice Member (Bolsovian), which is the most important coal-bearing unit of the basins in Central and Western Bohemia. In the Radnice Basin, coal seams are represented by the Lower and Upper Radnice Coals, which together comprise the Radnice group of seams. The Lower Radnice Coal is usually 1–4 m thick. The Upper Radnice Coal is the most important seam of the basin, lo-
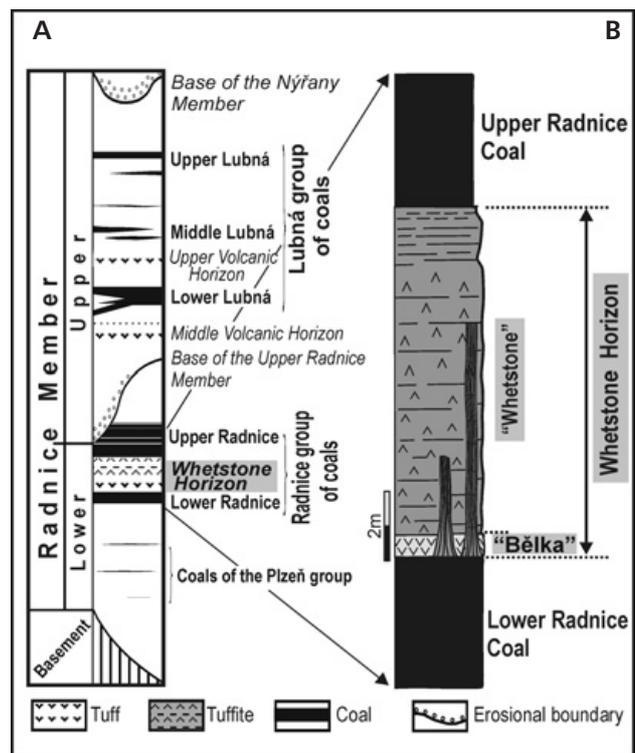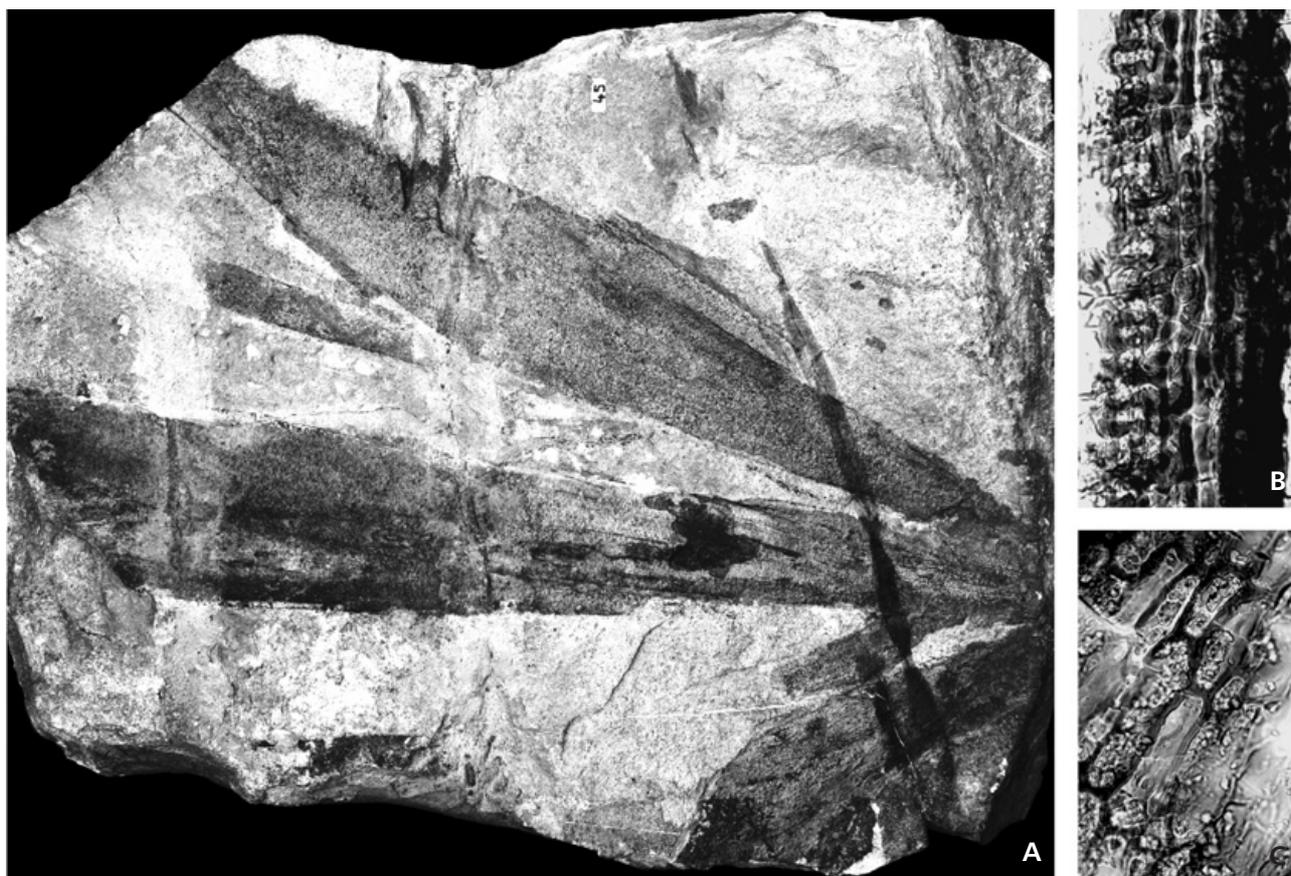
**Figure 3.** *Cordaites borassifolius* (Sternberg) Unger. • A – holotype, locality Svinná, Radnice Basin, Coll. Sternberg, National Museum Prague, No. E 5738, × 0.3. • B – abaxial cuticle with stomatal row isolated from the specimen on Fig 3A. Stomata have typical stomatal crypt. Slide No. 347/2, × 300. • C – adaxial cuticle isolated from the specimen on Fig 3A. Slide No. 347/2, × 300.

in northern part of the Radnice Basin (Figs 3A, 7), the study material described herein was collected at the Ovčín locality near the town of Radnice in the southern part of the Radnice Basin (Fig. 1). At this locality plant remains were collected mostly in the 1980's during the operation of the opencast Ovčín Mine (formerly Pokrok Opencast Mine). Several tens of thousands of plant remains mostly from the bělka bed, forming the roof of the Lower Radnice Coal, with fewer specimens being from the associated siliciclastic sediments, were collected during the 8 years of the opencast operation (the mine was closed in 1986). All the fossils are now housed in the collections of the National Museum in Prague. This material includes cordaitalean leaves with excellently preserved cuticles from the bělka. Since the mine closed, additional specimens were collected during excavation of the fossiliferous bělka bed lateral to the extent of the opencast mine. In all, five excavations of the basal Whetstone Horizon between 2002 and 2006, have exposed a total area of about 150 m$^2$. Three excavations named Ovčín excavation 1, 2, and 3 (OE1, 2, and 3) are located just at the edge of the former Ovčín opencast mine (Fig. 1). They exposed a continuous area of about 100 m$^2$.

The other two excavations, Sternberg 1 (2005) and 2 (2006) (SE1, and 2) are located about 100 m east of the opencast mine margin and 200 m northeast of OE 1, 2, and 3 (Fig. 1). SE 1 and 2 exposed an area of about 50 m$^2$. The main purpose of these excavations was the study of species composition and structure of peat-forming forest. Therefore, the exposed surface was cleaned and grided by string into 1 m$^2$ units for precise location of the fossils. The tuff was then carefully removed in slabs and all the fossils were documented on a piece of graph paper unique to each grid unit. Such data provided detailed information about spatial distribution of species (Fig. 8D). The cordaitalean remains from the opencast mine and excavations include fragments of stems, branches, pith casts and leaves, some attached to branches, as well as reproductive organs including male and female cones and isolated seeds. The largest cordaitalean fragment was about 6 m long, a monopodially branched stem found in SE1 (Fig. 6). Although this stem was leafless, it was associated with shed leaves of *Cordaites borassifolius*. All these findings contributed significantly to the whole-plant reconstruction of the species. These large specimens are stored in the West Bohemian

Museum in Plzeň, where they are in the process of restoration and preparation. More than 30 fragments of *Cordaites borassifolius* leaves have been used in this study, and cuticular slides are stored in the Czech Geological Survey in Prague.

*Cordaites borassifolius* (Sternberg) Unger. – Material: About 100 specimens from the Přívětice – Ovčín locality, Pokrok Mine and new excavations OE1, 2, and 3, Radnice Basin, Radnice group of coals, Whetstone Horizon. The samples are stored in the National Museum, Prague (Nos. E 4749, E 4750, E 5738, E 5889–E 5892, E 5895–E 5898, E 6221–E 6223), Czech Geological Survey, Prague (No. ZŠ 301) and West Bohemian Museum, Plzeň (Nos. F 07705, F 07927, F 07931, F 07943, F 07952, F 07958, F 08044, F 08083, F 08084, F 08086, F 08132, F 08192, F 08197, F 08255, F 08333, F 08339, F 08414, F 08443, F 10578, FX 1, FX 3–5, FX 7–13). Cuticular slides: (Ovčín): 108/1–6; 120/1–3; 352/1–5; 353/1–2; 354/1–5; 355/1–5; 356/1–6; 357/1–3; 358/1–5; 416/1–23; 417/1–5; 468/1–8; (Svinná – holotype): 347/1–2 stored in the Czech Geological Survey in Prague.

*Cordaitanthus ovatus* (Lesquereux) Ignatiev & Meyen. – Material: West Bohemian Museum, Plzeň (Nos. F 02193, F 08058, FX 14–17).

*Cardiocarpus annularis* (Sternberg) Lesquereux. – Material: Sternberg's (1820) specimens are stored in the National Museum, Prague under the numbers E 1207 and E 1208. About 20 seeds from SE2 are stored in the West Bohemian Museum in Plzeň (Nos. F 07986A, B, F 08449A, B, C, FX 10–13); cuticular slides: 469/1–5 are stored in the Czech Geological Survey in Prague.

*Florinanthus volkmannii* (Ettingshausen) comb. nov. – Material: Several cones on one slab from the National Museum, Prague No. E 5896 (Pokrok opencast mine) and from the Ovčín excavation 2006 (SE) – West Bohemian Museum, Plzeň Nos. FX 6 and FX 9; cuticular slides: 416/1–23 stored in the Czech Geological Survey in Prague.

*Artisia approximata* Lindley & Hutton. – Material: West Bohemian Museum, Plzeň. Nos. F 08167, F 08168, F 08043, F 08045, F 08046, F 08059, F 08065, F 08074, F 08128, F 08129, F 08131, F 08139, F 08140, F 08142, F 08232, F 08331, F 08335, F 08389, F 08411, F 08426, F 08427, F 08442, F 08445, FX 2.

## Methods

Cuticles were prepared according to the method described by Kerp (1990). Coalified leafy fragments were separated from the rock by placing it in concentrated hydrofluoric acid (HF) for several hours. The isolated fragments were then bleached in Schulze's reagent (40% $HNO_3$ with crystals of $KClO_3$ according to Krings & Kerp 1997 and Kerp & Krings 1999), a procedure which lasted 20 to 73 hours depending on preservation. After treatment in Schulze's reagent, cuticles were washed in 10% potassium hydroxide (KOH) and finally rinsed in distilled water. Some cuticles were stained with safranin for several hours to accentuate anticlinal walls and stomata. Before embedding in glycerine gelatine, the cuticles were dehydrated in pure glycerine. The remaining cuticular fragments were affixed to film for observation under SEM.

## Systematic section

Division Gymnospermophyta ('seed plants')
Class Pinopsida
Order Cordaitanthales ('cordaites') Meyen, 1984

**Genus *Cordaites* Unger, 1850**

*Type species*. – *Cordaites borassifolius* (Sternberg) Unger

### *Cordaites borassifolius* (Sternberg) Unger
Figures 3, 7, 8

> 1821 *Flabellaria borassifolia* Sternberg; Sternberg, vol. I, 2: tent. 28, 32, pl. 18.
> 1825 *Flabellaria borassifolia* Sternberg; Sternberg, vol. I, 4: tent. 34, pl. 34, fig. 1.
> 1825 *Cycadites palmatus* Sternberg; Sternberg, vol. I, 4, p. 39, tent. 33, pl. 40.
> 1845 *Flabellaria borassifolia* Sternberg. – Corda, p. 44, pl. 24, figs 1–3, 8.
> 1850 *Cordaites borassifolia* Sternberg sp. – Unger, p. 227.
> 1852 *Cordaites borassifolia* Ung. – Ettingshausen, pp. 16, 17, pl. 5, fig. 5.
> 1968 *Cordaites borassifolius* Sternb. – Němejc, p. 219, pl. 26, fig. 1.
> 2000 *Cordaites borassifolius* (Sternberg) Unger. – Šimůnek, p. 29, figs 3–12.
> 2001 *Cordaites borassifolius* (Sternberg) Unger (morphotype 12 *sensu* Šimůnek 2000). – Šimůnek, fig. 35, pl. 1, figs 1, 2; pls 24–28.
> 2003 *Cordaites borassifolius* (Sternberg) Unger. – Zodrow, Mastalerz & Šimůnek, p. 97, figs 1A, B, D and 2.
> 2007 *Cordaites borassifolius* (Sternberg) Unger. – Šimůnek, pp. 131–133, fig. 29a–j, pl. 1, figs 1, 2, pls 24–28, figs .

*Holotype*. – Figured by Sternberg (1821), pl. 18, National Museum, Prague, No. Akc. 36675, E 5738.
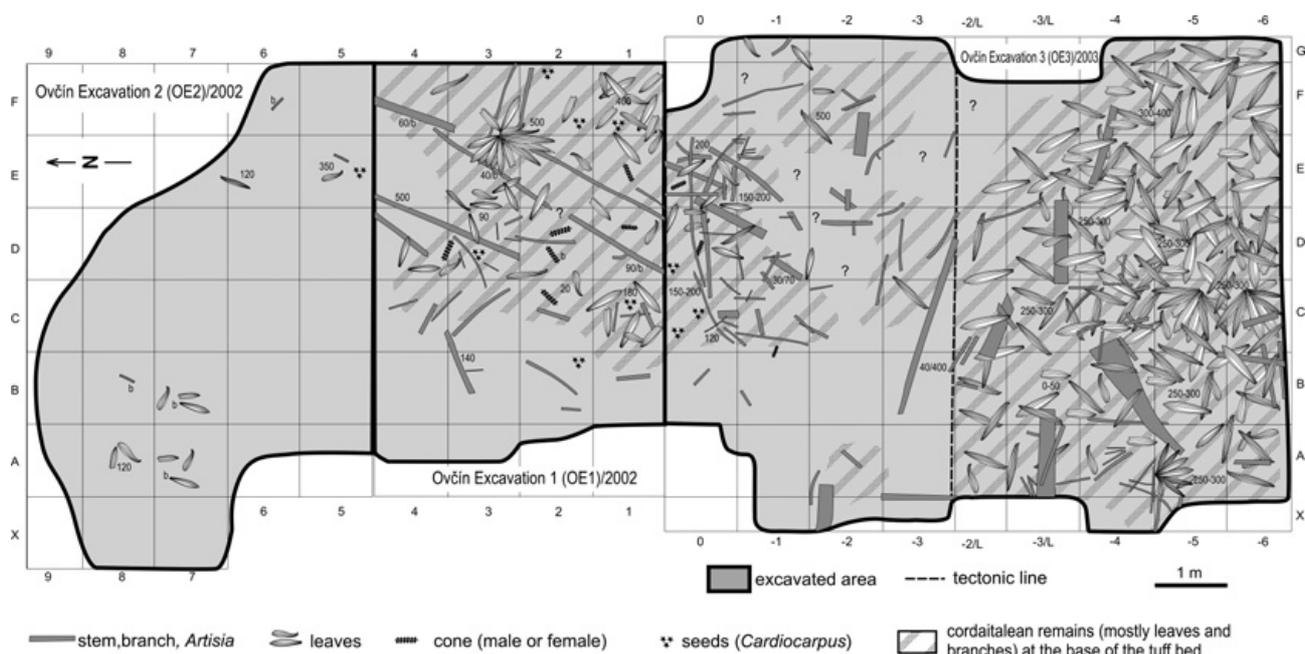
**Figure 4.** Distribution of remains of *Cordaites borassifolius* in the excavations Ovčín 1–3. Numerical values given in the format (*e.g.*, 30/150) correspond to diameter of branches or stems (*e.g.*, 30 mm) and height above the top of the Lower Radnice Coal at which the remains were found (*e.g.*, 150 mm). In this context, "b" means found at base of bělka tuff bed. If only a single value given, it relates to the distance above the roof of the Lower Radnice Coal.
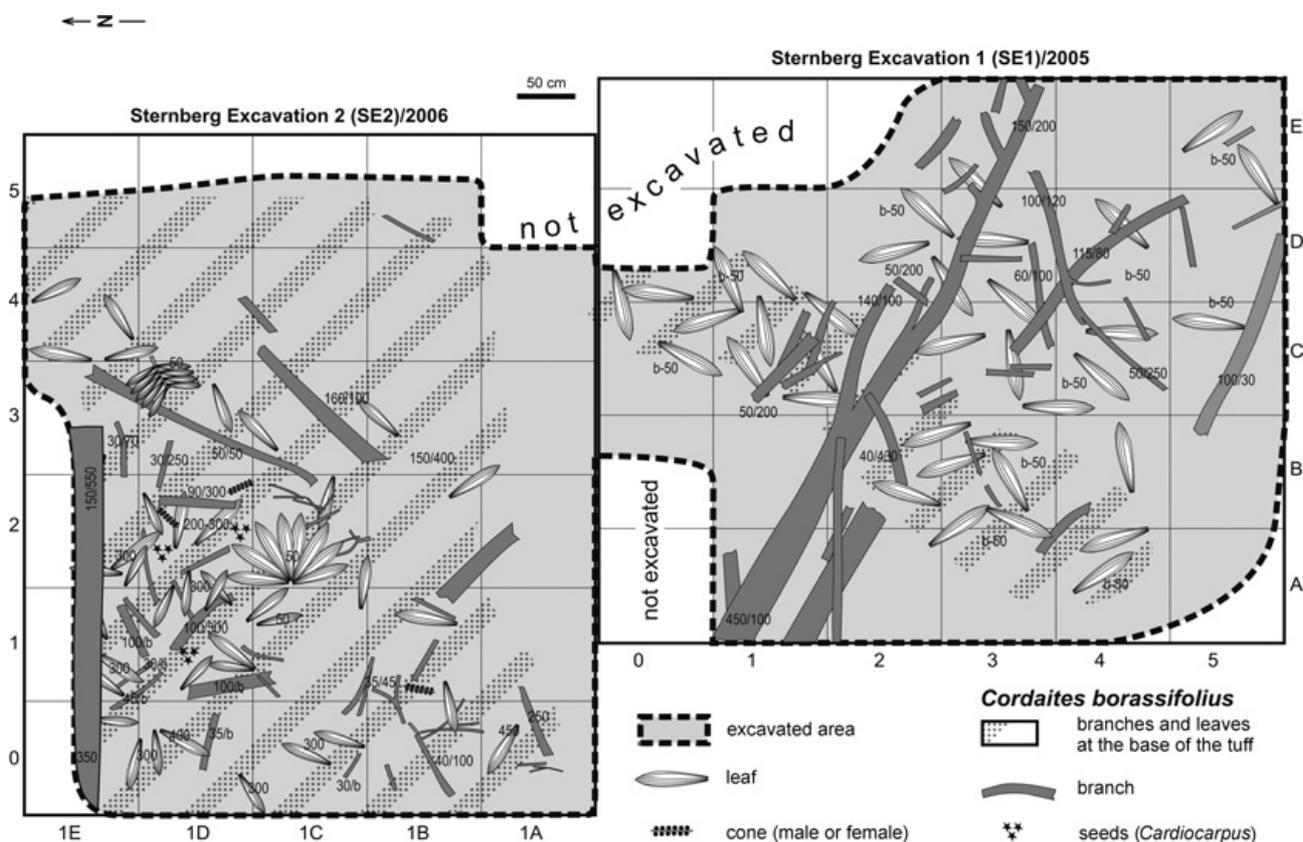


**Figure 5.** Distribution of remains of *Cordaites borassifolius* in the excavations Sternberg 1 and 2.
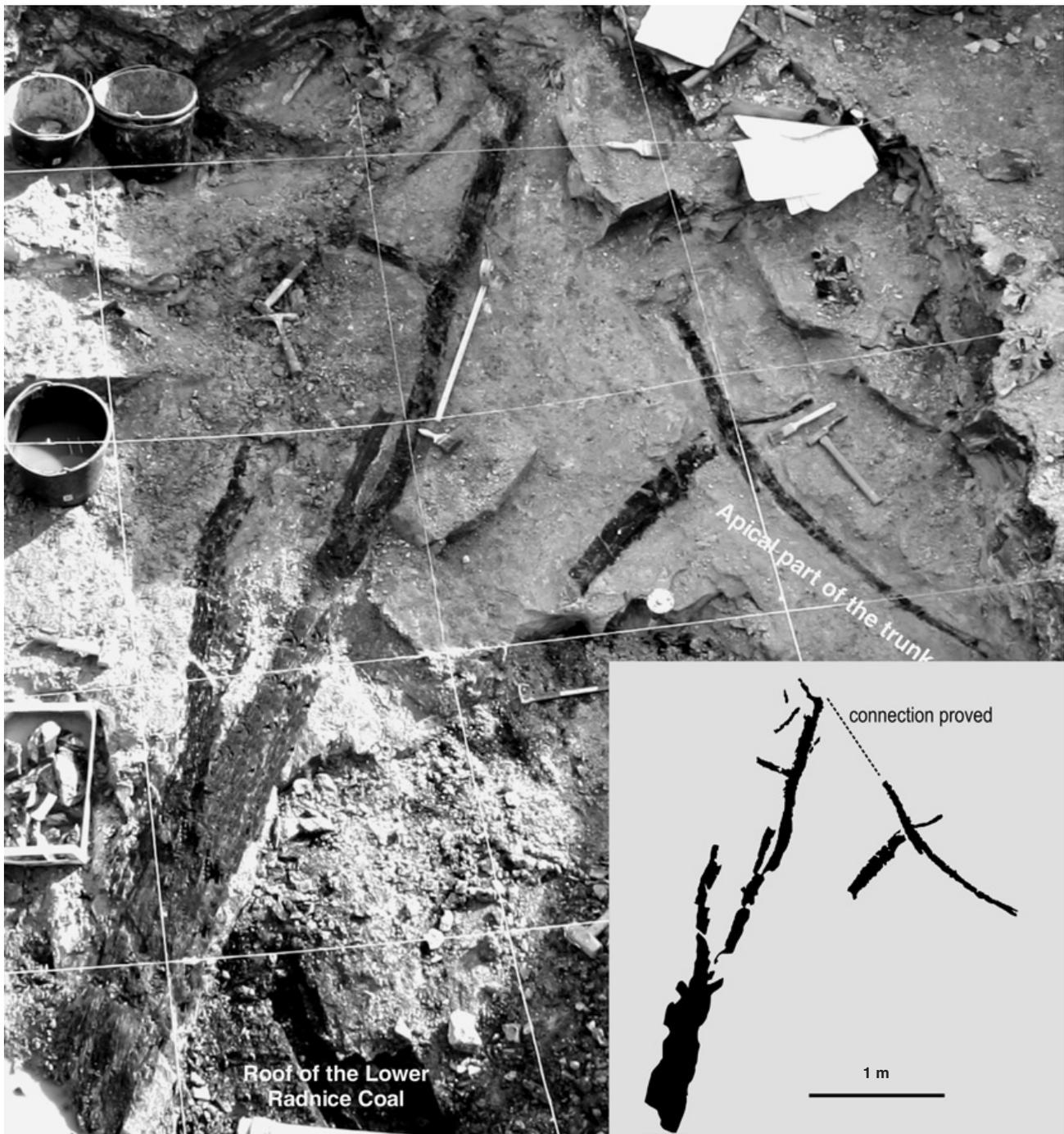
**Figure 6.** A trunk of *Cordaites borassifolius* (Sternberg) Unger in the excavation trench at the Ovčín locality (2005).

*Type locality*. – Svinná near Radnice, Radnice Basin.

*Type horizon*. – Kladno Formation, Radnice Member, Radnice group of seams, Whetstone Horizon, Carboniferous, Bolsovian.

*Emended diagnosis.* – Amphistomatic leaves large, entire, thick, ovate-lanceolate, apex bluntly pointed, occasionally deeply lacerated, veins medium-dense to dense. On adaxial side all veins approximately of the same thickness, on abaxial side 1 or 2 thin veins alternate with each thick vein. Abaxial cuticle with tetragonal, oblong square cells and irregularly dispersed stomata, abaxial cuticle with oblong cells and stomata arranged in stomatal rows forming stomatiferous bands. Polar cells rounded, lateral cells oblong to reniform. Tranverse oval crypt constricted in the center.

*Description of the holotype*. – The holotype is preserved as an imprint without coal matter on a 440 mm long and 350 mm wide (Fig. 3A) slab which is also without coal matter. It consists of two large leaf fragments and several small fragments. The largest fragment is in the middle of the leaf rosette. It is 425 mm long and 50 mm wide at its widest part in the middle. Another leaf is preserved behind this first one, as can be seen in Sternberg's (1821) figure. The leaf on the left is 390 mm long and 58 mm wide in its middle part. The leaf margins taper towards the base and towards the apex, which is not preserved in this slab. Another three narrow leaf fragments occur among the large, wide leaves. These smaller fragments were apparently enrolled before burial. There are another three smaller leaf fragments to the right from the middle of the large fragment, the largest of which is about 180 mm long and 40 mm wide. However, this cannot have been its full length, as the base and apex are not preserved. The base is also not preserved in these three leaves, and the smallest width represented is 18 mm. Due to the coarse nature of the rock, the venation is preserved in only a few parts. It is very dense and partly discontinuous. About 50 wide veins occur in 1 cm of leaf.

*External morphology*. – Trunk and branches: The ideas regarding whole-plant morphology are based on new material from SE1, a section of trunk about 5 m long with several articulated branches (Fig. 5) as well as several branches terminated with palm-like arranged leaves. The preserved length, however, exceeds the size of the excavation so that only the middle part of the trunk could be documented. The lower part of the exposed trunk, about 50 mm above the coal, is between 450 and 500 mm wide. The width of the opposite end of the stem is about 100 mm. The upper part of the trunk was, however, broken off and buried next to the main trunk (Figs 5, 6). It is approximately 2.7 m long and its apex is absent. The entire height of the tree was estimated based on Niklas (1994) formula [$\log_{10}H = 1.59 + 0.39(\log_{10}D) - 0.18(\log_{10}D)^2$, where H = tree height and D = base diameter of stem], which suggested a height between 28.1 and 28.6 m for the tree with a trunk diameter of 500 mm. However, such height seems unlikely because the main axis exposed in the excavation exhibits a rapid decrease in diameter distally (from 450 to 150 mm over a length of just 5.7 m) due to sympodial branching. Therefore, we believe that the tree was of the order of 15 to 20 m in height (Opluštil *et al.* 2009). The specimen displays monopodial to sympodial branching with four or five main lateral branches, of which only the basal parts are preserved. Some of them display the typical Artisia-type of pith cast (Fig. 20H). Monopodial branching is demonstrated in Fig. 20G. The branching apparently began only a few metres from the base of the tree, resulting in a plant that probably had a laterally and vertically wide crown. The dis-
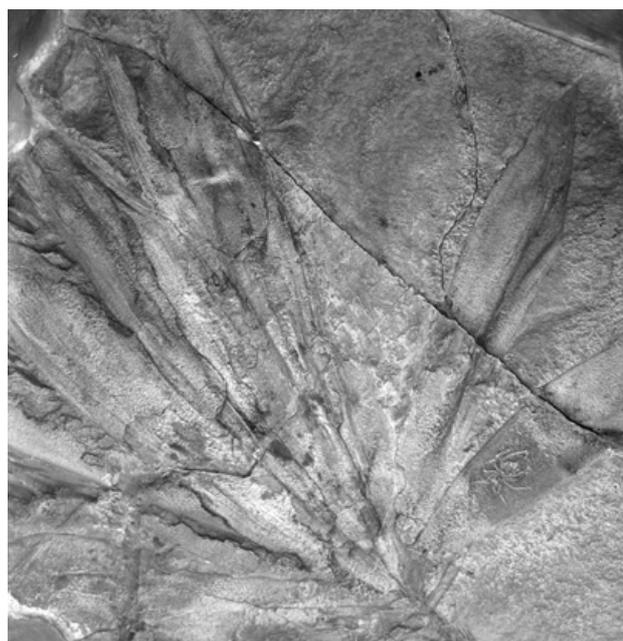


**Figure 7.** *Cordaites borassifolius* (Sternberg) Unger. Leafy apex of a twig. Counterpart of Corda's (1845) specimen figured on pl. XXIV, fig. 1; loc. Svinná, Radnice Basin, Bolsovian, Coll. National Museum, Prague, No. E 4270. × 0.2.

tance between neighbouring branches decreases upward, from about 1.1 m in the lower part of the trunk to about 0.7 m in its upper part. The existence of other branches on the opposite side of the trunk cannot be proved. The bases of the branches usually attain about 2/3 to 1/2 of the trunk width. The angle of branching of the two lowest branches is acute (10° and 30°), whereas that of the upper two branches is more obtuse (60° and 85°). However, it is possible that the preserved branching angles have been modified by volcanic ash load and post-sedimentary compaction, especially in the lower part of the trunk.

Leaves: No leaves have been found attached to the trunk, but a few *C. borassifolius* leaves were found in close associatiation with the trunk or its branches. This observation, in combination with the fact that all of the branches were leafless, points to the conclusion that this tree had already fallen prior to the eruption. These leaves were probably derived from neighbouring cordaites trees standing only few metres away.

In other excavations (OE2, 3 and SE2), branches with spirally arranged organically attached leaves were found. Leaves are, entire, ovate-lanceolate, rarely obovate, maximum width 35–90 mm, length 400–700 mm. In the SE 2 and OE 1 and 3 excavations (Fig. 4, 8D), the leaf length was mostly between 450 and 550 mm being 493 mm on average. The terminal leaf rosette of Corda's specimen from the Svinná locality (Fig. 7, National Museum, No. E 4270) is preserved without leaf terminals, unfortunately. Leaf
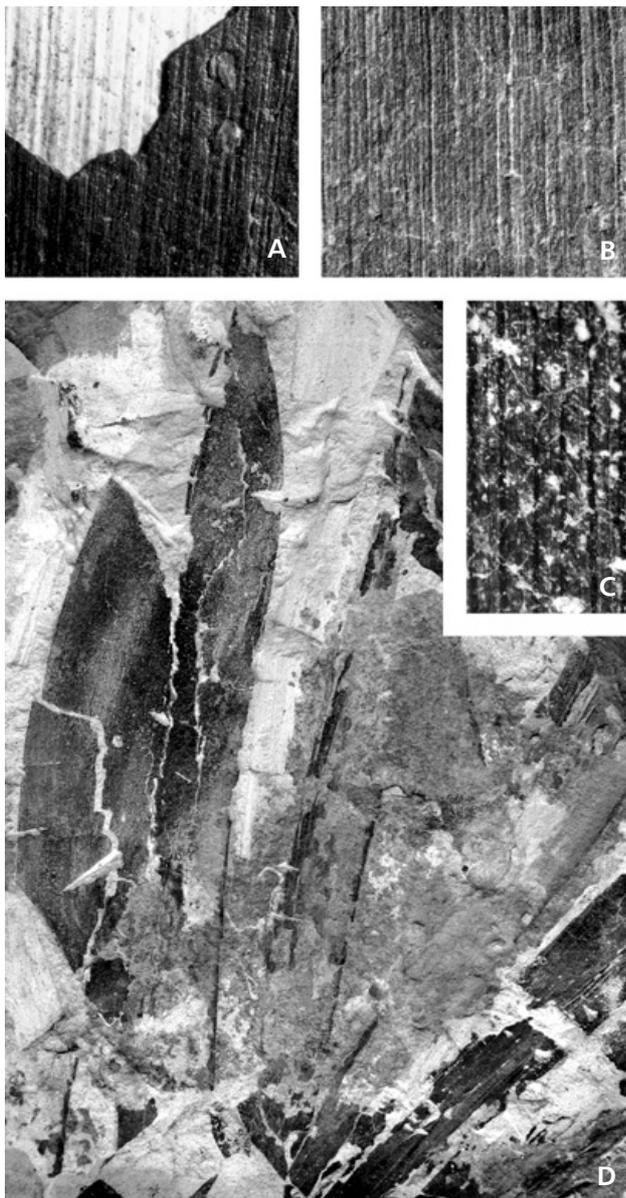
**Figure 8.** *Cordaites borassifolius* (Sternberg) Unger, locality Ovčín near Radnice, Pokrok Mine, Radnice Member, Bolsovian. • A – venation from a leaf, coll. National Museum, Prague, No.: E 5898; adaxial surface is white, abaxial surface is black. × 8. • B – venation with dense veins, probably of abaxial surface, coll. West Bohemian Museum, Plzeň, × 8. • C – venation with sparse veins alternating with very thin veins, probably of adaxial surface, coll. West Bohemian Museum, Plzeň, × 8. • D – several leaves from the terminal part of a twig,. West Bohemian Museum, Plzeň, × 0.4.

fragments are up to 500 mm in length. The leaf bases are 13–15 mm wide. Apices are bluntly pointed, but often apparently acute (because of the inrolling of the leaf margins). The leaves are seldom lacerated. Selected leaf specimens were used for statistical evaluation. The leaf length could only be measured on 13 specimens (Fig. 9), and therefore the histogram is biased. Most of the leaves from
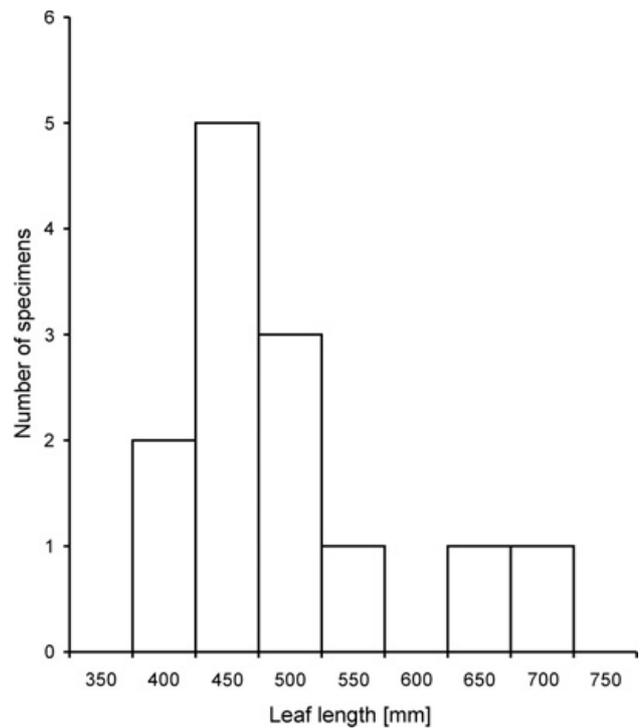


**Figure 9.** Histogram of relative frequencies of leaf length of *Cordaites borassifolius* (Sternberg) Unger plotted for 13 specimens.

Ovčín are 450 to 550 mm long. The longest specimen, 700 mm, is from Sternberg's holotype. The mean length is 493 mm. The leaves are often fragmentary thus width measurements do not usually represent the maximum, The measurement of 48 specimens produced highly variable results as the measurements were taken at different positions on the leaves relative to where the widest point would have been. The narrowest fragmentary leaves are only 15–20 mm wide (Fig. 10). They represent basal or apical parts of leaves. Most of the leaves are about 35 mm wide and many samples are in the interval from 45 to 60 mm. Several samples are up to 92 mm wide. The mean of this varied width is 45 mm. Fig. 11 shows the correlation between leaf length and width based on 13 complete leaves. If we use data from only these 13 specimens for calculation of the mean width, we find that 60 mm is the mean width. The symbols shown in Fig. 11 represent the maximum width of leaves.

Veins: The leaf veins are straight, parallel to the margins and to each other. The venation pattern depends on whether the adaxial or abaxial side is viewed, and on preservation. Usually one (or two) narrow veins alternate with one wide (or "true") vein. The number of veins per 1 cm ranges considerably, from 18–62. By means of the cuticles, it is possible to distinguish which parts represent the narrow and wide veins. The vein densities typically fall within a range from 24 to 26 veins per cm and 46 to 50 veins per cm. The
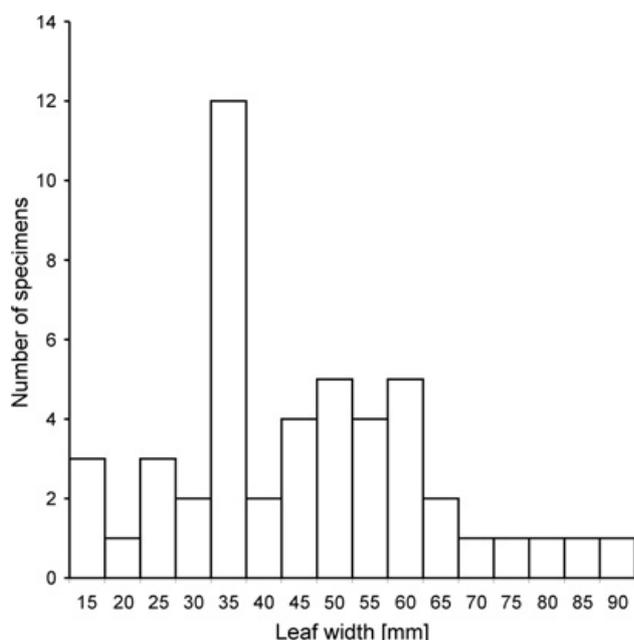
**Figure 10.** Histogram of relative frequencies of leaf width of *Cordaites borassifolius* (Sternberg) Unger plotted for 48 specimens.
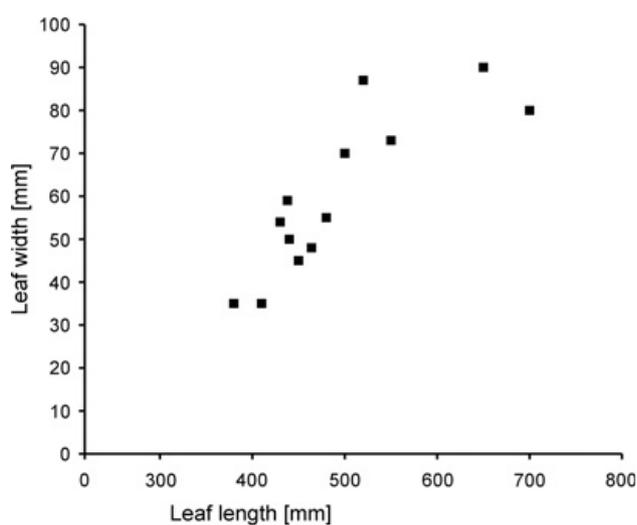


**Figure 11.** Graph showing the correlation between the length and width of *Cordaites borassifolius* (Sternberg) Unger leaves plotted for 13 specimens.



**Figure 12.** Histogram of relative frequencies of number of veins per 1 cm for *Cordaites borassifolius* (Sternberg) Unger leaves plotted for 34 specimens.



**Figure 13.** Venation of *Cordaites borassifolius* (Sternberg) Unger. • a – adaxial side, • b – abaxial side with two different vein thicknesses, and fine transverse wrinkles in the place of stomatiferous bands.

former values probably represent the abaxial side, where the costal fields are prominent, whereas the latter values probably represent the adaxial side, where the wide veins are thinner and sometimes difficult to distinguish from the thin veins. The number of veins per 1 cm is shown on Fig. 12 based on 34 specimens. It was taken from the widest part of the studied leaf fragment. The veins terminate at the margin. Even though the mean is 34.3 veins per cm, the histogram has two peaks. The peak with a value of 26 veins per cm probably represents the adaxial side (Fig. 8A, C), where differences between the vascular bun-
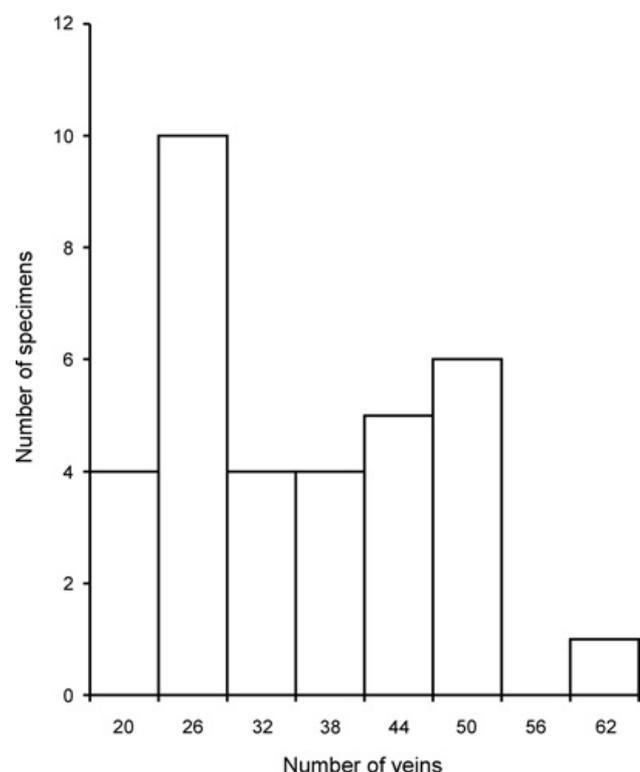
dles and sclerenchymatous tissue are prominent, whereas the peak with a value of 44–50 veins per cm probably represents the abaxial side (Fig. 8B). The strips of vascular bundles and sclerenchymatous tissue have approximately the same thickness, and they are usually considered as ordinary veins (Fig. 13). Even under magnification it is not possible to distinguish which veins belong to vascular bundles and which veins belong to sclerenchymatous tissue. The leaves are amphistomatic.

*Cuticles*. – Cuticle preparations make it possible to distinguish between narrow and wide veins.

**Figure 14.** Adaxial epidermis of *Cordaites borassifolius* (Sternberg) Unger, locality Ovčín near Radnice, Pokrok Mine, Radnice Member, Bolsovian. • A – adaxial epidermis with stomata, v, s – cells of "costal" fields: v – above the vascular bundles, s – above the sclerenchyma strands. Slide No. 35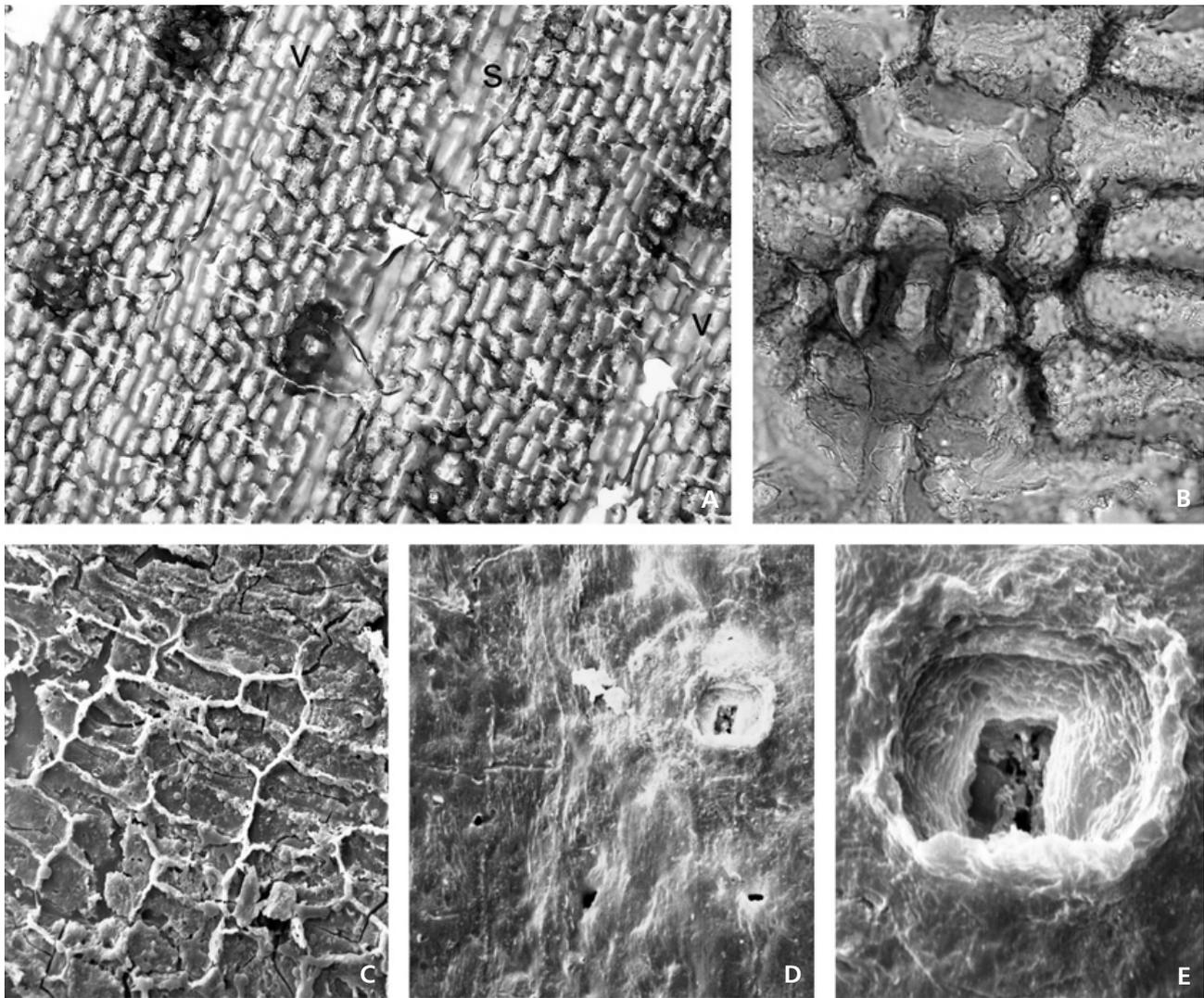3/2, × 100. • B – detail from Fig. 14A with a stoma, × 400. • C – SEM microphotograph No. 0754. View to inner side with prominent anticlinal cell walls, × 200. • D – SEM microphotograph No. 0758. View to outer surface with a small stoma, × 500. • E – SEM microphotograph No. 0759. Detail of a stoma from Fig. 14D, × 2000.

Adaxial cuticle (Fig. 14): Some adaxial cuticles have bands of cells that are slightly darker than others. The lighter cells are costal bands above vascular strands and are usually 80–160 μm wide. The darker intercostal bands are 240–490 μm wide with very rarely stomata. Occasionally, the costal band is only 50 μm wide and probably represents the epidermis above the sclerenchymatic tissue.

The adaxial cuticle is weakly cutinised, but more prominently than the abaxial cuticle. Cells are the same in both costal and intercostals areas. They are tetragonal and mostly oblong, and less often square or pentagonal to hexagonal in shape. The cells are 30–75 μm long and 20–35 μm wide. Anticlinal walls are slightly or strongly bent. The cells have rounded corners and are parallel to the veins. Stomata are at distances approximately 400 μm apart, but not in regular rows (Fig. 14A). The stomatal complex is formed by a pair of sunken elliptical guard cells, two polar subsidiary cells and two lateral subsidiary cells. Pairs of guard cells are 22–26 μm long and 13–16 μm wide. The complex is 60–80 μm long and 60–70 μm wide. Polar subsidiary cells are prominent, oval, and 20–30 μm in diameter (Fig. 14B). Lateral subsidiary cells are prominent, oblong, with bulging anticlinal walls, 34–50 μm long and 16–25 μm wide. A square to round outer stomatal cavity is developed above the stomatal pore. The stomatal density is very low, ranging from 6–9 stomata per 1 mm$^2$. The value of the stomatal index varies from 0.7 to 0.9 (Table 1).
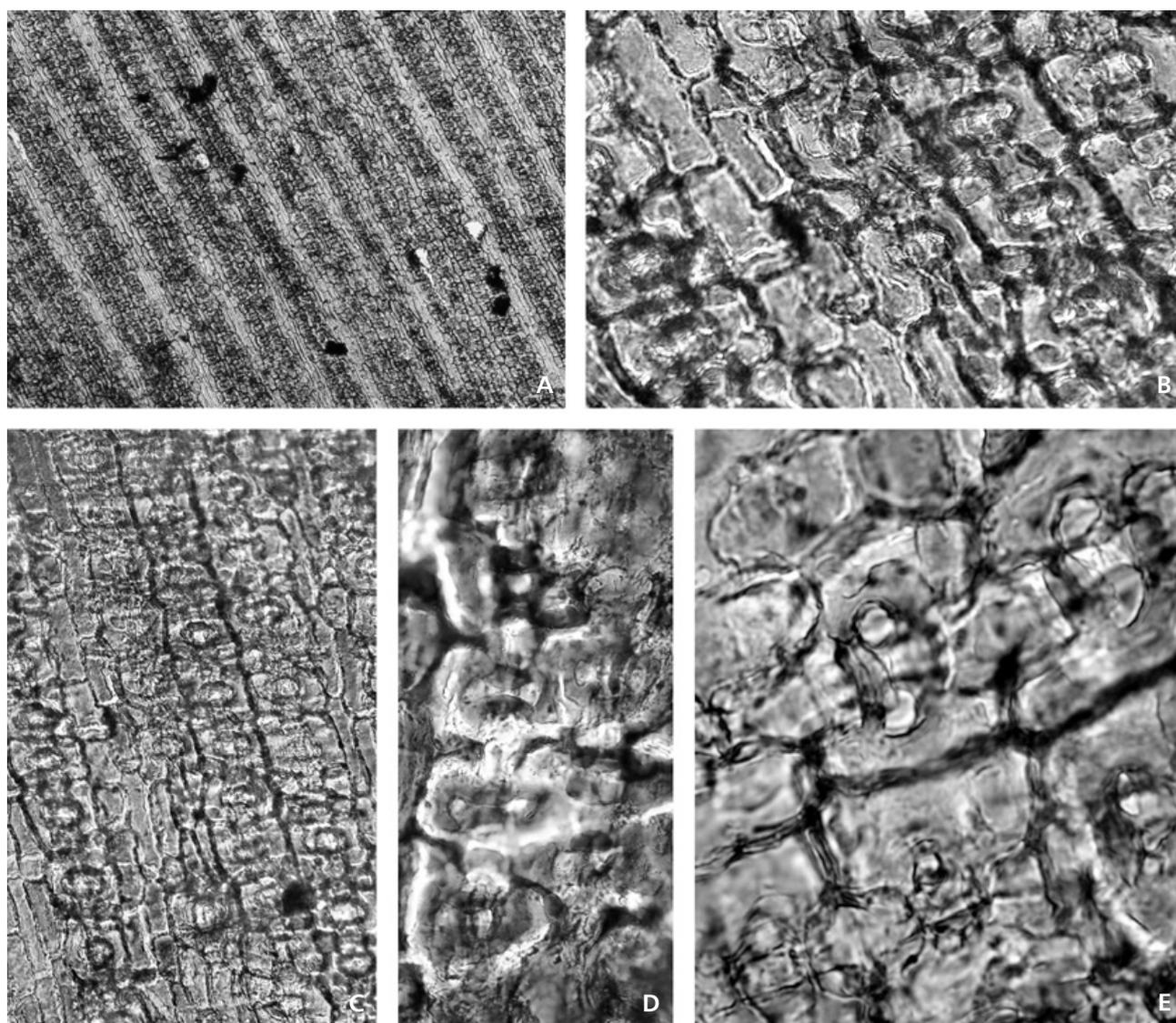
**Figure 15.** Abaxial epidermis of *Cordaites borassifolius* (Sternberg) Unger in optical microscopy, locality Ovčín near Radnice, Pokrok Mine, Radnice Member, Bolsovian. • A – cuticle with many stomatiferous and non-stomatiferous bands. It is difficult to judge which non-stomatiferous bands are below the vascular bundles and which are below the sclerenchyma strands. Slide No. 356/3, × 50. • B – detail of a stomatiferous band from Fig. 15C, × 400. • C – cuticle with stomatal and non-stomatiferous bands. Slide No. 356/3, × 200. • D – stomata with very well preserved crypt viewed under Nomarski interference contrast. Slide No. 355/2, × 400. • E – detail of stomata from stomatiferous band from Fig. 15B, × 800.

Abaxial cuticle (Figs 15, 16): The abaxial epidermis is quite different. Stomatiferous bands 75–270 µm wide are separated by narrow, non-stomatiferous (lighter) bands only 30–75 µm wide. The wider ones, 45–75 µm wide, probably represent the tissue above (or below) the vascular bundles, whereas the thinner ones, 30–45 µm wide, represent the bundles below the sclerenchymatic tissue.

The abaxial cuticle is weakly cutinised compared to the adaxial one. It consists of stomatiferous intercostal bands that are 200–300 µm wide and costal bands that are 60 µm wide and formed by three rows of cells (Fig. 15A). All intercostal cells are incorporated into stomatal complexes (Fig. 15B, C). Cells of costal bands are tetragonal, mostly

elongate, oblong, 35–110 µm long, and 15–30 µm wide and orientated parallel to the veins. Anticlinal walls are straight or slightly bent. Stomatal complexes comprise a pair of sunken elliptical guard cells, two polar subsidiary cells and two lateral subsidiary cells (Fig. 15D, E). Stomata are orientated parallel to the veins and occur in rows. Pairs of guard cells are 22–26 µm long and 12–16 µm wide (Fig. 16A, B). The stomatal complex is 40–60 µm long and 40–60 µm wide. Polar cells are rounded and 15–20 µm in diameter and are often shared by adjacent stomata. The lateral subsidiary cells are oblong to kidney-shaped, 40–50 µm long, and 20–28 µm wide and about the adjacent lateral cell of the neighbouring stomata in the row. The

**Table 1.** Morphological features of cuticles of leaves *Cordaites borassifolius* and scales and bracts *Florinites volkmannii*.

| Species | | | *Cordaites borassifolius* | *Florinanthus volkmannii* | |
|---|---|---|---|---|---|
| Organ | | | Leaf | Sterile scale | Bract |
| **Adaxial cuticle** | | Difference between stomatiferous and non-stomatiferous bands | – | – | – |
| | | Cell shape of stomatiferous bands | Tetragonal - oblong, square | – | – |
| | | Size of stomatiferous cells (μm) | (30–75) x (20–35) | – | – |
| | | Cell shape of non-stomatiferous bands | Tetragonal - oblong | Longitudinally tetragonal (oblong, trapezoidal), pentagonal; base: isodiametric | Oblong |
| | | Size of non-stomatiferous cells (μm) | (30–75) x (20–35) | (45–75) x (12–20); base: 30–50 in diameter | (50–110) x (10–20) |
| | **Stomata** | Distribution | Irregularly dispersed | – | – |
| | | Density per 1 mm² | 6–9 | – | – |
| | | Stomatal index | 0,7–0,9 | – | – |
| | | length and width of guard cells (μm) | (22–26) x (13–16) | – | – |
| | **Subsidiary cells** Polar | Number and shape | 2; prominent, oval | – | – |
| | | Size (μm) | 20–30 in diameter | – | – |
| | Lateral | Number and shape | 2; prominent, oblong | – | – |
| | | Size (μm) | (34–50) x (16–25) | – | – |
| **Abaxial cuticle** | | Difference between stomatiferous and non-stomatiferous bands | + | – | + |
| | | Cell shape of stomatiferous bands | Only stomatal complexes | – | Oblong |
| | | Size of stomatiferous cells (μm) | - | – | (40–85) x (10–20) |
| | | Cell shape of non-stomatiferous bands | Longitudinally oblong (tetragonal) | Longitudinally tetragonal (oblong, trapezoidal), pentagonal; base: isodiametric | Oblong |
| | | Size of non-stomatiferous cells (μm) | (35–110) x (15–30) | (45–75) x (12–20); base: 30–50 in diameter | (50–110) x (10–20) |
| | **Stomata** | Distribution | Stomatiferous bands | irregularly, only in parts | Single stomatal row s |
| | | Density per 1 mm² | 350–370 | 0–40 | about 300 |
| | | Stomatal index | 16–20 | <1 | 4.2–5 |
| | | Shape of guard cells | Elliptical | ± Oblong | Elliptical |
| | | length and width of guard cells (μm) | (22–26) x (12–16) | (22–28) x (10–15) | (25–30) x 22 |
| | **Subsidiary cells** Polar | Number and shape | 2; rounded | 2–3; as ordinary cells | 2; oblong |
| | | Size (μm) | 15–20 in diameter | | (25–60) x (12–18) |
| | Lateral | Number and shape | 2; oblong to reniform | 2–3; as ordinary cells | 2; oblong |
| | | Size (μm) | (40–50) x (20–28) | | (40–50) x (15–22) |
| | | Shape of crypt | Transverse oval, constricted in the centre | – | Round, of Florin ring shape |
| **Trichomes on the margin** | | | – | Uniseriate; 100–150 μm long | – |

outer stomatal cavity is developed transversely across the lateral subsidiary cells. It is elongate and constricted in the central part (Fig. 15D, E, 16C–F). Stomatal complexes are arranged in rows; with three to six rows forming a band. The stomatal density is 350–370 per 1 mm². The value of the stomatal index varies from 16 to 20 (Table 1).

*Remarks.* – A detailed description of material later assigned to *C. borassifolius* by Unger 1850 was made by Corda (1845), who described large specimens from Svinná in the Radnice Basin (Fig. 7) under the name *Flabelaria borassifolia*. He also studied the anatomy of partly carbonised stems and cuticles of leaves. Corda (1845) described the typical *Cordaites borassifolius* venation as narrow and wide alternating veins. A few years later, Unger (1850) erected the name *Cordaites*, and the species *Cordaites borassifolius* was selected as the type of this genus. Unger's definition was based on both leaf form and stem anatomy.

Zeiller (1886, p. 628) excluded from *Cordaites borassifolius* leaves figured by Ettingshausen (1852, pl. 5, fig. 5). According to Zeiller (1886), the veins are varied and he

suggested that Ettinghausen's material instead belonged to *Cordaites principalis* (Germar) Geinitz. This opinion was also accepted by Crookall (1970). However, Ettingshausen's (1852) specimen comes from Stradonice (Hýskov relict), which is relatively close to Svinná, the type area of *C. borassifolius*. In fact, the horizon is practically the same as the unit from which the holotype of *C. borassifolius* was collected. The venation pattern can vary, as we know from the *C. borassifolius* sample population from the Ovčín locality. Unfortunately, some cuticles prepared from a *C. borassifolius* specimen from Stradonice (Naturhistorisches Museum, Wien) are strongly corroded, which does not allow comparison with the holotype of *C. borassifolius*. The cellular structures of the adaxial epidermis of *C. borassifolius* were already studied by Corda (1845, pl. 24, figs 2, 3). He observed leaves without maceration and correctly interpreted the alternating thin and thick veins, cellular shape and orientation and also the stomata distribution. However, he was unable to observe details of the stomatal structure.

Florin (1931, p. 499, fig. 105a) figured abaxial cuticles from a specimen determined as *Cordaites* sp. 1, which origi-
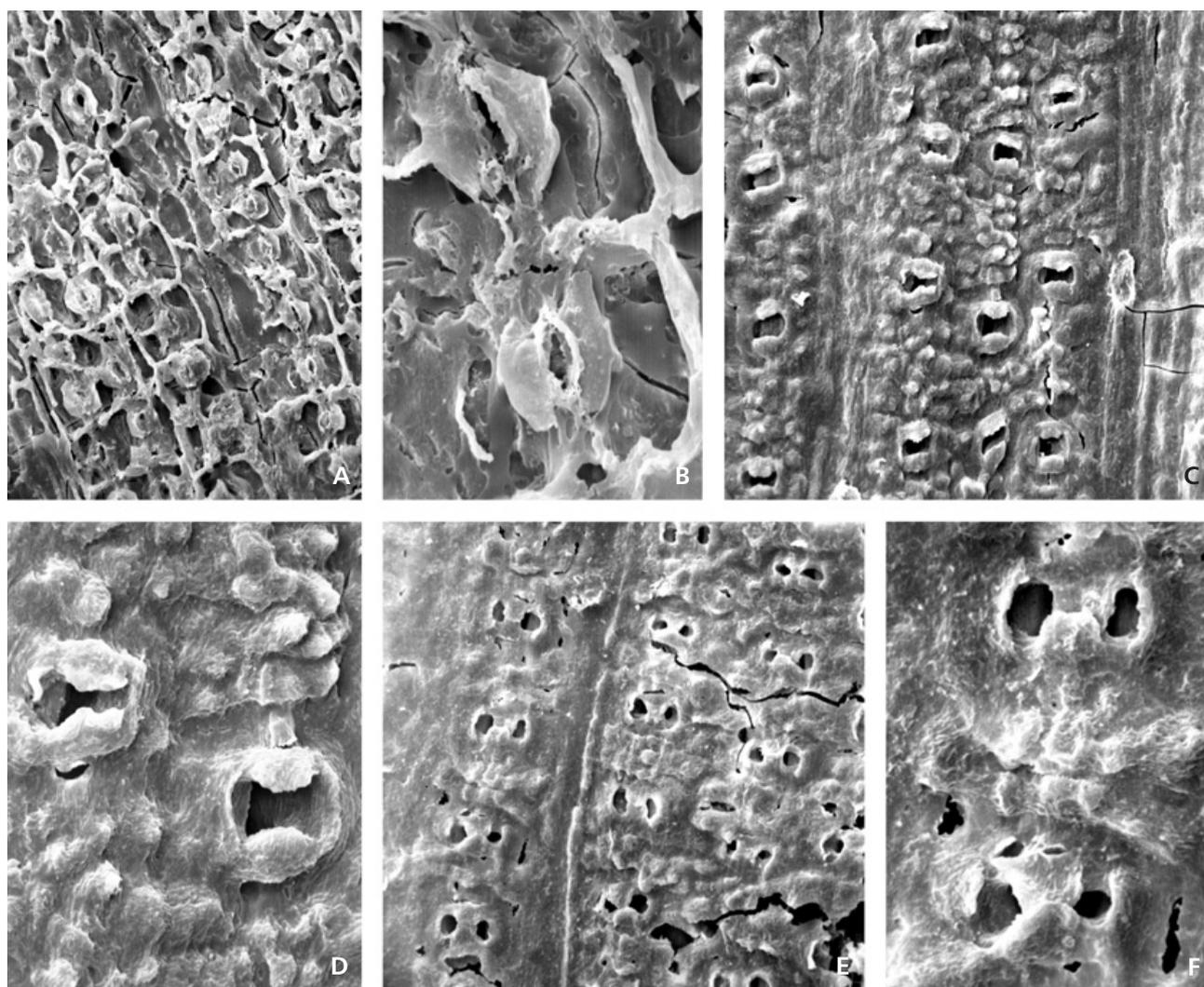
**Figure 16.** Abaxial epidermis of *Cordaites borassifolius* (Sternberg) Unger under SEM, locality Ovčín near Radnice, Pokrok Mine, Radnice Member, Bolsovian. • A – view to inner surface with stomatal and non-stomatiferous bands. SEM microphotograph No. 0749, × 200. • B – detail from Fig. 16A with two stomata. The guard cells are well visible. SEM microphotograph No. 0751, × 1000. • C – view of outer surface with stomata. Note that the crypt is not fully developed, and only two papillae projections per stoma are developed. SEM microphotograph No. 0761, × 400. • D – detail from Fig. 16C with two stomata. SEM microphotograph No. 0762, × 1000. • E – view of outer surface with stomata. The crypt is well developed. SEM microphotograph No. 0752, × 400. • F – detail from Fig. E with two stomata. SEM microphotograph No. 0753, × 1000.

nated from the Radnice Member (Bolsovian) of the Rakovník locality, Czech Republic, and from another specimen he referred to as *Cordaites* sp. 2 from New Brunswick (Westphalian D), Canada. The stomatal complexes of both specimens are structurally similar; two large lateral subsidiary cells and two small polar subsidiary cells. They only differ in the shape of these cells. Both species have a crypt across the guard cells as in *C. borassifolius*. However, they differ in the shape of the subsidiary cells and therefore their mutual identity is questionable. These samples differ from our material in the shape of the subsidiary cells and the distribution of stomata. Stomata of Florin's (1931) *Cordaites* sp. 1 are arranged in simple stomatal rows, whereas stomata of *Cordaites borassifolius* are in multiple rows in bands.

Barthel (1964) described *Cordaites* cuticular morphotype 6 from the Autunian of the Döhlen Basin as having a transverse crypt across the guard cells, which is very similar to the Bohemian species *Cordaites borossifolius* (Sternberg) Unger from the Radnice Member. Barthel compared this species with Florin's (1931) *Cordaites* sp. 1 from the Bolsovian of Rakovník.

*Fertile organ of indeterminate sex (possibly female).* – Two types of strobili were found at the Ovčín localities. We consider the more robust form to be the female fertile organ even though seeds have not yet been found in connection with it [determined as *Cordaitanthus ovatus* (Lesquereux) Ignatiev & Meyen], and the smaller form as the
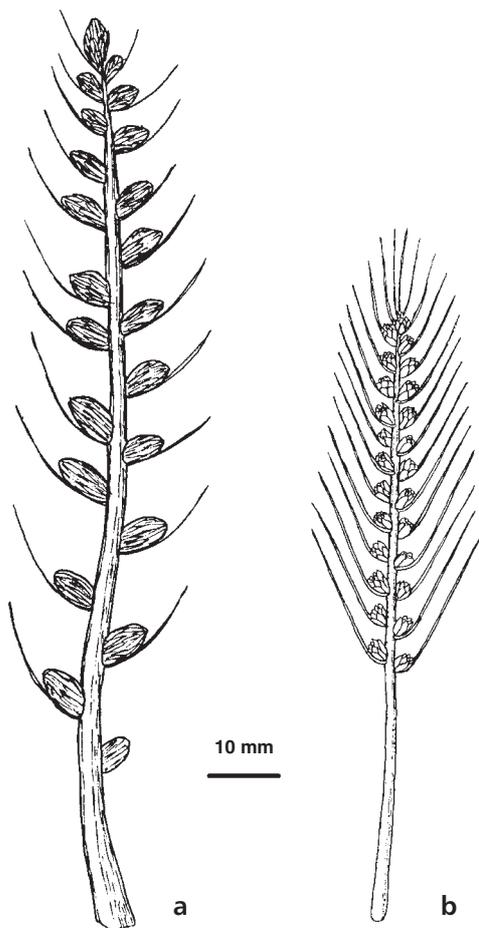
**Figure 17.** Fertile organs of *Cordaites borassifolius* (Sternberg) Unger, • a – probably female cone *Cordaitanthus ovatus* (Lesquereux) Ignatiev & Meyen, • b – male cone *Florinanthus volkmannii* (Ettingshausen) comb. nov. Scale bar = 10 mm.

male fertile organ of the form refereable to as *Florinanthus volkmannii* (Ettingshausen) Šimůnek, Opluštil & Drábková comb. nov.

**Genus *Cordaitanthus* Feistmantel, 1876**

*Type species.* – *Cordaitanthus communis* Feistmantel, 1876

*Basionym.* – *Antholithes triticum* Andrae, 1864, pp. 174, 175, pl. 4, fig. 6.

*Proposed lectotype.* – *Cordaitanthus communis* Feistmantel, 1876, pl. 12, fig. 4.

*Remark.* – Feistmantel (1876) on pl. 12, figs 1–4, figured 4 syntypes of his *Cordaitanthus communis.* They come from different localities (Stradonice, Kralupy nad Vltavou, Ný-řany) and evidently they belong to different species. We propose to choose Feistmantel's (1876) specimen figured in his pl. 12, fig. 4, as a lectotype of the genus *Cordaitanthus.* Feistmantel (1876) refigured Andrae's (1864) *Antholithes triticum* from pl. 4, fig 6. *Antholithes triticum* is an earlier nomenclatural synonym of *Cordaitanthus communis* and takes priority over *Cordaitanthus communis.* Therefore *Cordaitanthus triticus* becomes the effective type species of *Cordaitanthus.*

*Diagnosis of the genus Cordaitanthus.* – Original diagnosis of Ignatiev & Meyen, 1989. Primary axis elongate, up to 300 mm long, and 15 mm wide. Axillary bract complexes borne on both sides of the axis, arranged in juxtaposition or alternate, and composed of helically arranged scaly appendages. Bracts ranging from scaly to needle-shaped, up to 33 mm long. The bracts frequently have become turned down and the fertile organ looks as if it lacks bracts.

**Cordaitanthus ovatus (Lesquereux) Ignatiev & Meyen, 1989**
Figures 17a, 18A–F

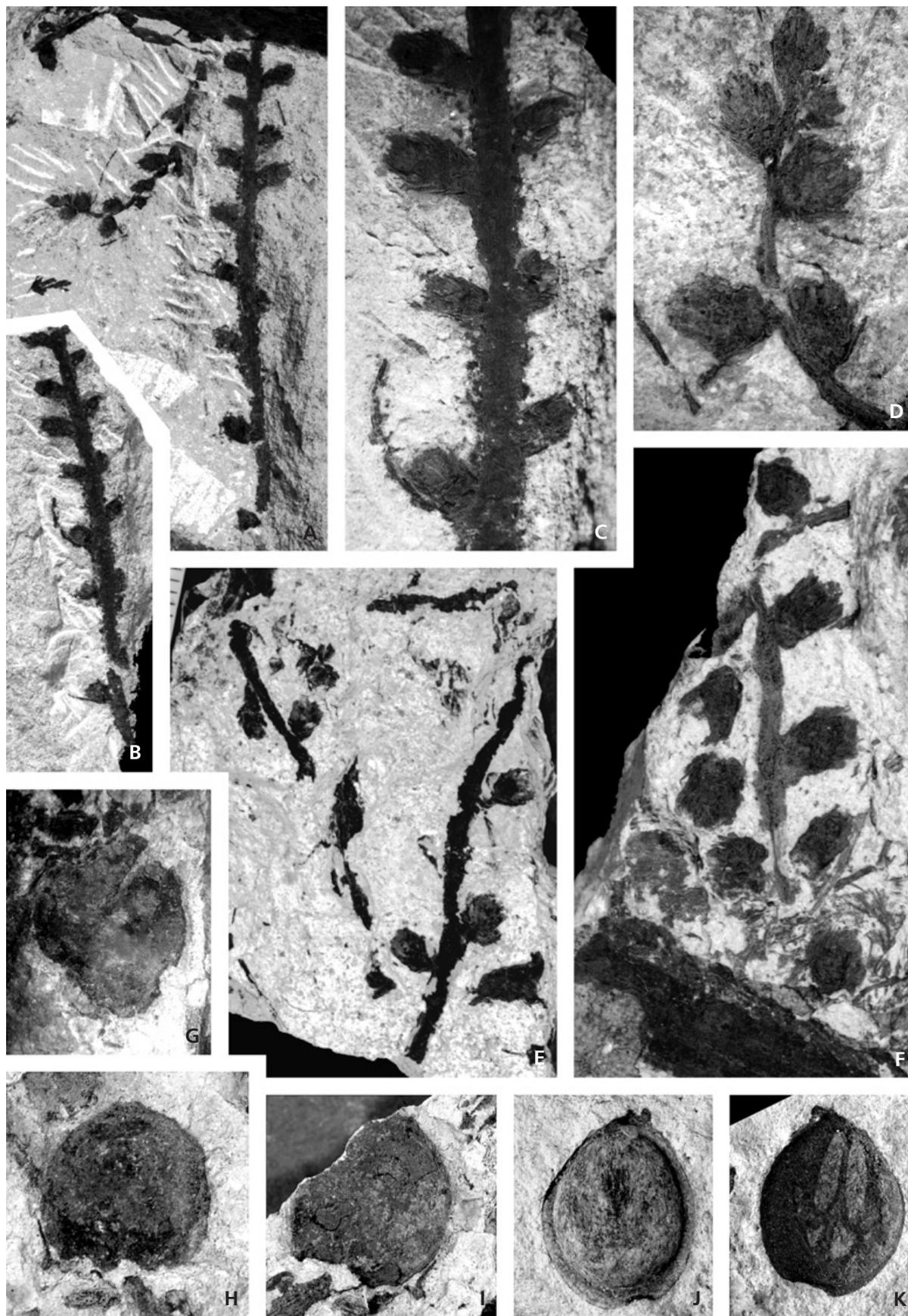1880 *Cordaianthus ovatus* Lesquereux, p. 545, pl. 76, fig. 5, 5a.
1989 *Cordaitanthus ovatus* Lesquereux. – Ignatiev & Meyen, p. 335.

*Type locality.* – Cannelton, Pennsylvania, U.S.A.

*Type horizon.* – Westphalian D.

*Description.* – Based on material from OE1, 2, and 3, West Bohemian Museum, No. F 08054 and F 07986A. Fragments of primary axes up to 90 mm long (Fig. 18A) and typically 3 mm wide. The axillary complexes are borne on both sides of the axis somewhat irregularly and alternately. They are closely arranged in the terminal part and sparsely

**Figure 18.** A–F – *Cordaitanthus* cf. *ovatus* (Lesquereux) Ignatiev & Meyen. Probably the female fertile organ of *Cordaites borassifolius.* Locality Ovčín near Radnice, Radnice Member, Bolsovian. Coll. West Bohemian Museum, Plzeň, × 1. C – detail from Fig. 18B, × 3. D – detail from Fig. 18A, × 5. E, F – cone fragments, E – locality Ovčín, D1; 100 mm above coal, No. F 08054, × 2; F – locality Ovčín, No. F 02193, × 3. • G–K – seeds *Cardiocarpus annulatus* (Sternberg) Lesquereux that probably belong to *Cordaites borassifolius*; coll. West Bohemian Museum, Plzeň. G – locality Ovčín, D3 base, No. F 08045, × 3; H – locality Ovčín, D 2 base, No. F 07986B, × 3; I – locality Ovčín, D 2 base, No. F 07986A, × 3. J, K – imprint and counterpart of Sternberg's type specimens of *Cardiocarpus* "*Carpolites*" *annulatus* Sternberg, possible seed of *Cordaites borassifolius.* Locality Radnice, coll. National Museum, Prague, Nos. E 1207 and 1208, × 3.

in the basal part of the fertile organ. Axillary buds are formed by a small secondary axis and helically arranged scales. The shape, dimension and number of scales per bud are usually difficult to determine due to poor preservation. The buds are 6–9 mm long and 4–6 mm wide. Their apex is conical (Fig. 18D). The shape of the scales is probably lanceolate. The bracts are 0.4 to 1 mm wide, 10–15 mm long, and turned upwards (Fig. 18C).

*Remarks.* – The specimens found at Ovčín OE1, 2, and 3 fit Lesquereux's description of *Cordaitanthus ovatus.* It is more robust than the male fertile organ *Florinanthus volkmannii* (Fig. 17B), and for this reason we consider it to be the female fertile organ of *Cordaites borassifolius*, although direct evidence is lacking. The buds of *Cordaitanthus ovatus* are 6–9 mm long and 4–6 mm wide, whereas those of *Florinanthus volkmannii* are 2–4 mm long and only 1.5–3 mm wide. The sterile scales of *C. ovatus* are lanceolate, whereas those of *F. volkmannii* are spatulate. Only the small inner scales of *F. volkmannii* are lanceolate.

**Seeds**
(Figs 18G–K, 19, 20A–F)

Sternberg (1820) figured 12 seeds of the genus "*Carpolites*" from Radnice, and some of them could belong to cordaitalean plants. Of these seeds, *Carpolites (Cardiocarpus) annularis* Sternberg, 1820 (Lesquereux, 1884), *Carpolites (Cardiocarpus) regularis* Sternberg, 1820 (Lesquereux, 1880), and perhaps *Carpolites (Cardiocarpus) retusum* Sternberg, 1820 (Newberry, 1873) are most similar to the seeds found at Ovčín. Because Sternberg (1820) did not describe them, all of these names are invalid as *nomina nuda*. We believe that the shape and dimensions of material from Ovčín fit best to the name *Carpolites (Cardiocarpus) annularis* and therefore we add its description and diagnosis to validate this name.

***Cardiocarpus annularis*** **(Sternberg) Lesquereux, 1880**
Figures 18G–K, 19, 20A–F

1820 *Carpolites annularis* Sternberg, pl. 7, fig. 15.
1825 *Carpholites annularis* Sternberg, tent. 40.
1884 *Cardiocarpus annularis* (Sternberg). – Lesquereux, p. 814, pl. 110, figs 28–30.

*Holotype*. – National Museum, Prague, No. E 1207, Stern-

berg, pl. 7, fig. 15, refigured here on Fig. 18J; counterpart E 1208 is figured here on Fig. 18K.

*Diagnosis.* – Seeds small, round to oval, surrounded by narrow rim (sarcotesta), surface of sclerotesta smooth (occasionally crumpled). Epidermis composed of polygonal cells.

*Description of the holotype* (Fig. 18J). – The seed is oval, 13 mm long and 11 mm wide, the sarcotesta rim is widest near the base > 1 mm and tapers near the apex to 0.7 mm.
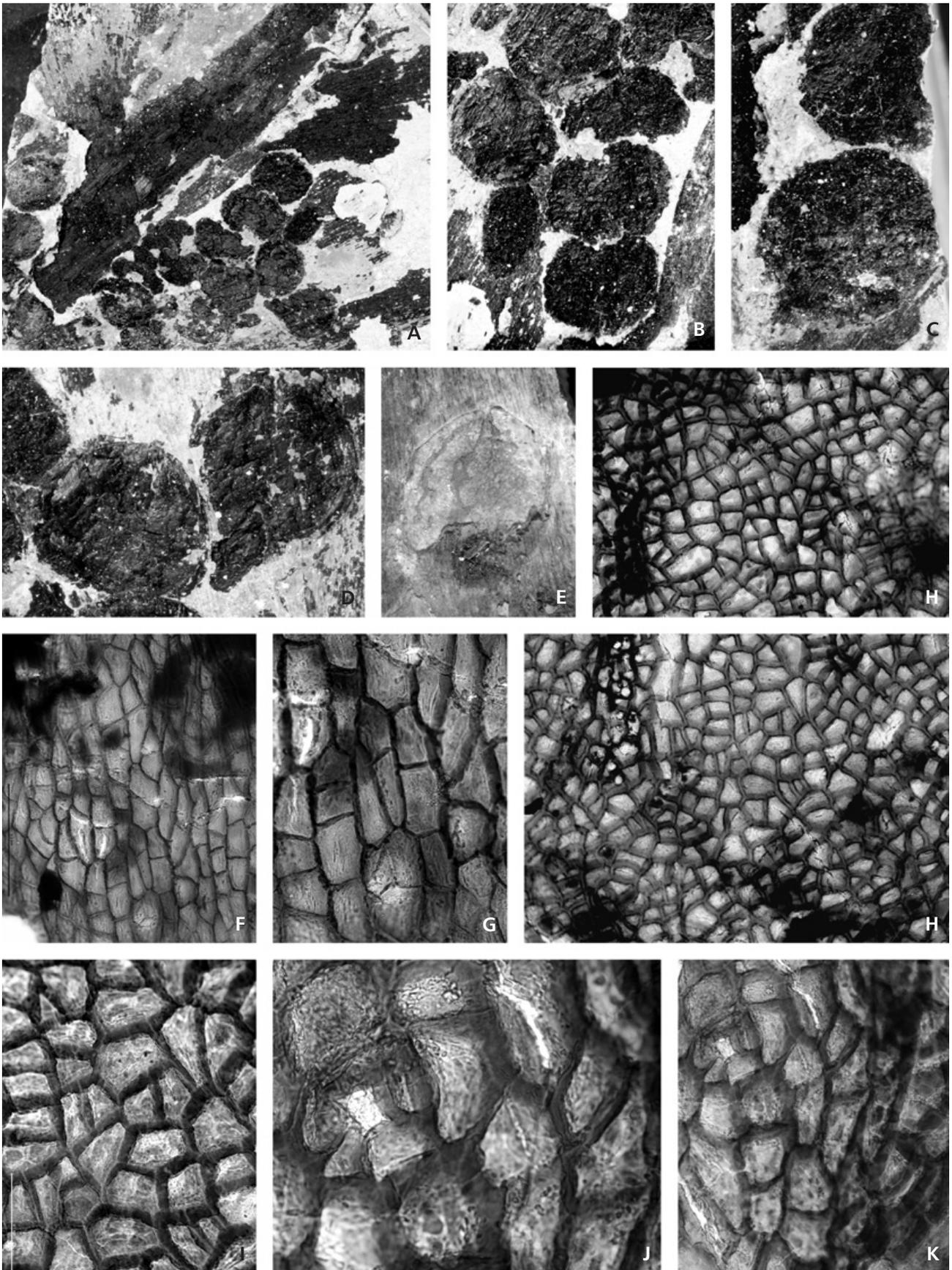
*Description.* – Seeds are small wingless, platyspermic, round or oval, and in their terminal parts a little tapered. The inner sclerotesta layer and outer sarcotesta layer are preserved (Fig. 18I–K, 19D, E). The sclerotesta consists of thick-walled sclerotic cells and the sarcotesta of fleshy cells. The seeds are 10–11 mm long and 9–11 mm wide. Most of the seed area is occupied by sclerotesta, while the sarcotesta forms a narrow rim less than 0.7 mm thick.

*Cuticles.* – Two types of cuticles have been recovered from the SE material. The most common is a thick-walled cuticle with randomly orientated polygonal cells, 40–90 μm long and 30–50 μm wide (Fig. 19H, I). The anticlinal walls are very thick and prominent (Fig. 20B). In some parts, the cells tend to be elongated, tetragonal, parallel orientated (Fig. 19F, G), 40–110 μm long and 20–40 μm wide. Only one stomata-like oblong aperture (Fig. 19J, K), 17 μm long and 12 μm wide, surrounded by 5 very small subsidiary cells was observed. Guard cells are not present.

The second type consists of two thin-walled layers of cells (Fig. 20D–F). The cells are polygonal, 35–100 μm long and 35–50 μm wide. The anticlinal walls are very thin (Fig. 20F).

*Remark.* – It is not exactly known from which part of the seed a particular cuticular type came from, however, we presume that the thick-walled cuticle covered the sclerotesta and the thin-walled cuticle covered the sarcotesta, because this layer is fleshy and its cuticle is usually thinner than cuticle of the sclerotesta. Dispersal of these wingless seeds was limited and resulted in them being clustered on the ground at the base of the tree as they were found in Ovčín locality.

**Figure 19.** Seeds of *Cordaites borassifolius* comparable to *Cardiocarpus* "*Carpolites*" *annulatus* (Sternberg) Lesquereux. Locality Excavation Ovčín 2006, base 1D–2. • A – accumulation of seeds together with *Cordaites borassifolius* leaves, × 1. • B – detail from Fig. 19A, × 2. • C, D – detail from Fig. 19A. Most of the seed body encompass sclerotesta and only a thin rim sarcotesta. × 3. • E – a seed adpression from excavation "Ovčín", × 3. • F–K – seed cuticle probably from the sclerotesta layer from seeds on Fig. 19A. F, G –cuticle with longitudinally oriented cells, slide No. 469/2, F × 100, G × 200; J, I – cuticle with randomly oriented cells, slide No. 469/1, H × 100, I × 200; J, K – stomata-like structure, slide No. 469/3. J × 400, K × 200.

**Male fertile organ**

**Genus *Florinanthus* Ignatiev & Meyen, 1989**

*Type species*. – *Florinanthus concinnus* (Delevoryas) Ignatiev & Meyen, 1989.

*General characteristics.* – The primary axis arising from the axil of a leaf is more or less bilaterally symmetrical. The medullated stele of the primary axis gives off traces to four rows of secondary shoots and their subtending bracts. Auxillary bract complexes (secondary shoots) are arranged in a compact helix and consist of a short axis on which there are numerous (up to 100) scaly appendages. Up to 40 terminal scales are fertile. Sporangiophores are unbranched or apically forked once. Each sporangiophore (fertile scale) is terminated by a maximum of 6 microsporangia (pollen sacs), which are fused at the base. They are elongate with a longitudinal dehiscent slit and contain monosaccate pollen of the *Florinites*-type (Ignatiev & Meyen 1989).

*Florinanthus volkmannii* (Ettingshausen) comb. nov.
Figures 17b, 21–29

 1852 *Calamites Volkmanni*, Ettingshausen, pp. 5, 6, pl. 5, figs 1–3 (non fig. 4, non pl. 6, figs 1 and 2).
 1911 *Cordaianthus Volkmanni* Ettingshausen. – Kidston, p. 236.
 1968 *Cordaianthus* sp., Němejc, pl. 24, fig. 3.
 1970 *Cordaitanthus volkmanni* Ettingshausen. – Crookall, p. 828, text-fig. 239 (syntypes) (non pl. 158, fig. 4).

*Specimina excludenda*. –
 1886 *Cordaianthus Volkmanni* Ettingshausen. – Zeiller, p. 637, pl. 94, fig. 6.
 1917 Cordaianthus Volkmanni Ettingshausen. – Seward, p. 267, fig. 480B.
 1963 *Cordaianthus volkmani* (Ettingshausen) Zeiller. – Lee, p. 160, pl. 13, fig. 7.
 1970 *Cordaitanthus volkmanni* Ettingshausen. – Crookall, p. 828, pl. 158, fig. 4.

*Syntypes*. – *Calamites Volkmanni*, Ettingshausen (1852), pl. 5, figs 1–3.

*Type locality*. – Stradonice near Beroun (Hýskov relict).

*Type horizon*. – Kladno Formation, Radnice Member, Radnice group of seams, Whetstone Horizon, Carboniferous, Bolsovian.

*Description.* – Primary axis elongate, up to 100 mm long, and about 1 to 1.5 mm wide (Fig. 17b). It bears 4 rows of axillary secondary shoots that are subtended by very long, narrow bracts, arching more or less towards the axial tip. Axillary bract complexes in two paired rows (Fig. 21) seem to be only in two rows in the impression/compression state (Fig. 23B). The flattened axis could be taphonomic. The two buds on the right side are bent towards the axis and their ramification is not clear, whereas the ramification on the left side is clearly visible. The lower and upper buds arise from the upper side of the axis, whereas the middle bud arises from the lower side. The divergent angle of each pair of rows of axillary bract complexes (orthostichies) is estimated to be 30–40°. The bracts are usually 0.5 mm wide and up to 25 mm long. Their apex is sharp. The buds (Fig. 22A) are relatively small and wide, usually 2.8–3.5 mm long and 2–3 mm wide (Ovčín – Přívětice, mine Pokrok). The sterile and fertile scales are of different shapes and sizes. There are only a few scales per bud, usually 20–30. The outer scales (Fig. 22c, 24D) are spatulate up to 3 mm long and 1.8 mm wide. The scales near the centre (Fig. 22B, 24B) are smaller, lanceolate, with a round apex 2–2.5 mm long and up to 1.4 mm wide. The third type of scale (Fig. 22D, 24C) is small and lanceolate with a sharp apex, 1.5 to 2 mm long and 0.8 to 1.1 mm wide. These scales are situated in the very centre of the bud and were probably fertile. The schematic cross section of a bud is illustrated in Fig. 22B. However, pollen sacs have not yet been found, but accumulations of prepollen grains have been discovered stuck to such scales (National Museum, E 5896). Small trichomes, 100–150 µm long, grow out of the scale margins in their terminal parts.

*Cuticle of the scale* (Figs 25, 26). – The adaxial and abaxial cuticles are very similar and the epidermis shows an elongate cellular structure (Figs 25B, C, 26E, G). Individual cells are oblong, trapezoidal or elongate pentagonal and are 45–75 µm long, and 12–20 µm wide. Near the base of the scale (Fig. 25E), the cells are more or less isodiametric in

**Figure 20.** Seed cuticles of *Cardiocarpus* "*Carpolites*" *annulatus* (Sternberg) Lesquereux belonging probably to *Cordaites borassifolius.* Loc. Excavation Ovčín 2006, base 1D–2. A. – C. Cuticle of sclerotesta in SEM. • A – longitudinally oriented cells, × 100, • B, C – inner view to sclerotesta cuticle with randomly oriented cells. Note the prominent thick anticlinal cell walls. B × 400, C × 100. • D, E – cuticle of sarcotesta. It is formed by two layers of cells. Note the very thin-walled, randomly oriented polygonal cells. Slide No. 469/5, D × 150, E × 300. • F – inner view to the sarcotesta cuticle in SEM. Note the very thin anticlinal walls of polygonal cells, × 250. • G, H – trunk or twig surfaces of *Cordaites borassifolius,* coll. West Bohemian Museum, Plzeň. G – A fragment of trunk with a twig, loc. Ovčín A1; base, × 1; H – a fragment of a twig with transition between surface and "*Artisia*" type preservation. Locality Ovčín (Sternberg) C3, × 0.5.
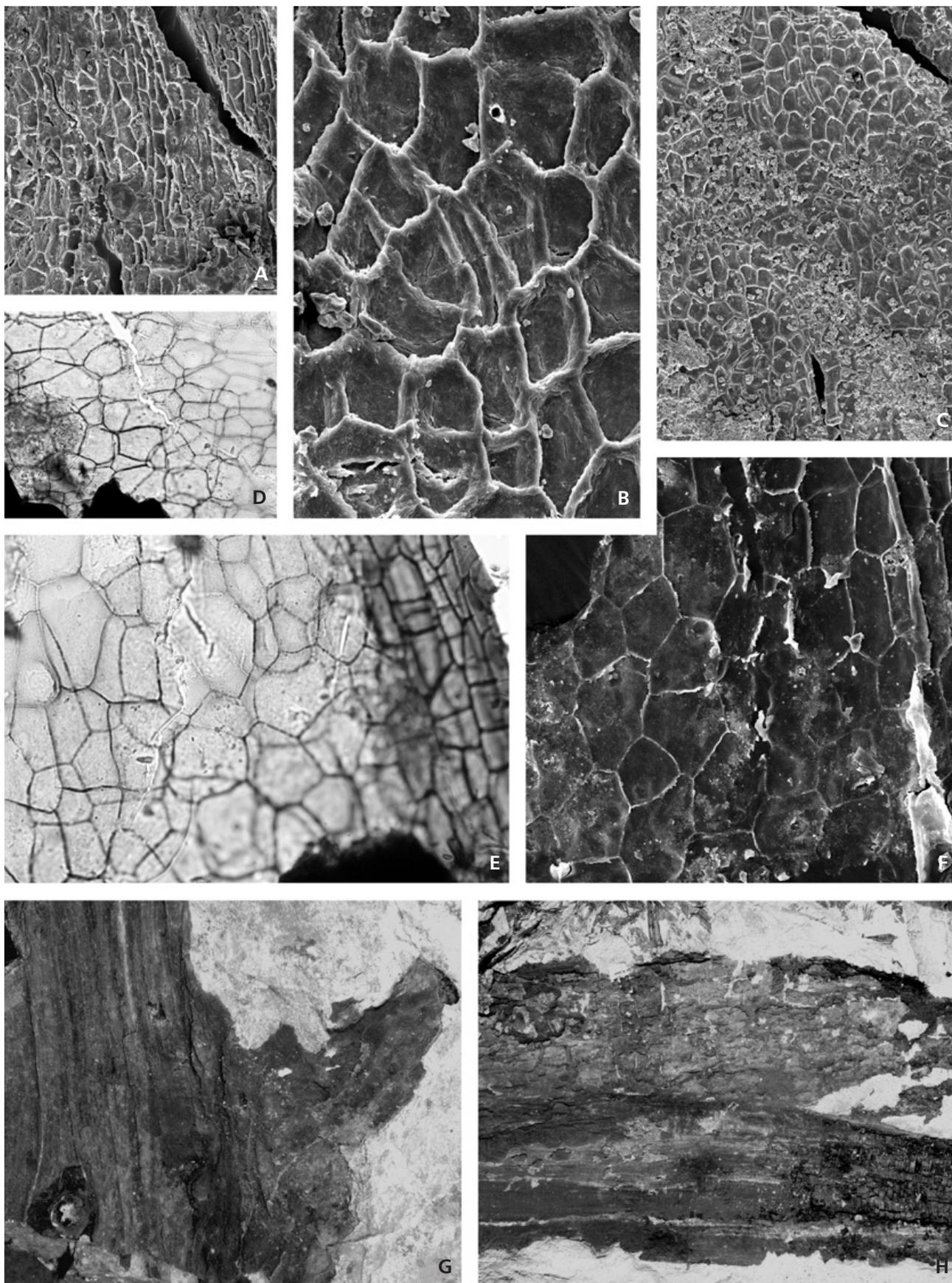
**Figure 21.** Part of the male cone *Florinanthus volkmannii* (Ettingshausen) nov. comb. (reconstruction by J. Svoboda), scale bar = 2 mm.



**Figure 23.** *Florinanthus volkmannii* (Ettingshausen) comb. nov., a male fertile organ of *Cordaites borassifolius.* Loc. Ovčín near Radnice, Pokrok Mine, Radnice Member, Bolsovian; National Museum in Prague, No. 5896. • A – a specimen with *Florinanthus* cones and *Cordaites borassifolius* leaves, × 1. • B – isolated part of *Florinanthus* cone from Fig. 23A with 5 fertile "buds" and bracts, Slide No. 416/22, × 5. • C – a detail of two cones from Fig. 23A, × 5.

shape, randomly orientated and 30–50 μm in diameter. The anticlinal cell walls are straight or slightly bent. The stomata are irregularly dispersed on the cuticle (Fig. 25A, B), but it is not known whether they occur on the adaxial or abaxial cuticle. The stomatal complex is simple, consisting of two guard cells surrounded by 4 to 6 subsidiary cells of the same shape as the ordinary epidermal cells. The visible part of the guard cells is somewhat oblong, 22–28 μm long, and 10–15 μm wide. The stomatal density varies from none to 40 stomata per 1 mm$^2$ (measured on 0.1 mm$^2$ area) and the stomatal index is less than 1. Three rows of trichomes are prominent along the scale margin (Fig. 26A, C, D). They are simple, uniseriate, 100–150 μm long and 12–20 μm wide (Fig. 25F), and are formed by 3 to 4 barrel-shaped cells and a terminal cell that is elongate triangular in shape arising almost perpendicular to the other cells. The anticlinal cell walls are moderately developed. The periclinal walls are slightly arched and bear papillae and small depressions. Papillae are small with a bluntly pointed tip, their base is elliptical, 25–35 μm long and 10–15 μm in height (Fig. 26H). Small elliptical depressions of unknown function are seen on some periclinal walls (Fig. 26H). These depressions are 12–18 μm long and 4–7 μm wide (Fig. 26B, E). They appear to be small stoma and represent true holes, 7 μm long and 2 μm wide, through the cuticle. They are transversely orientated to the cell direction.

*Cuticle of the bract* (Figs 27, 28A–E). – The adaxial and abaxial cuticles are difficult to distinguish from one anot-
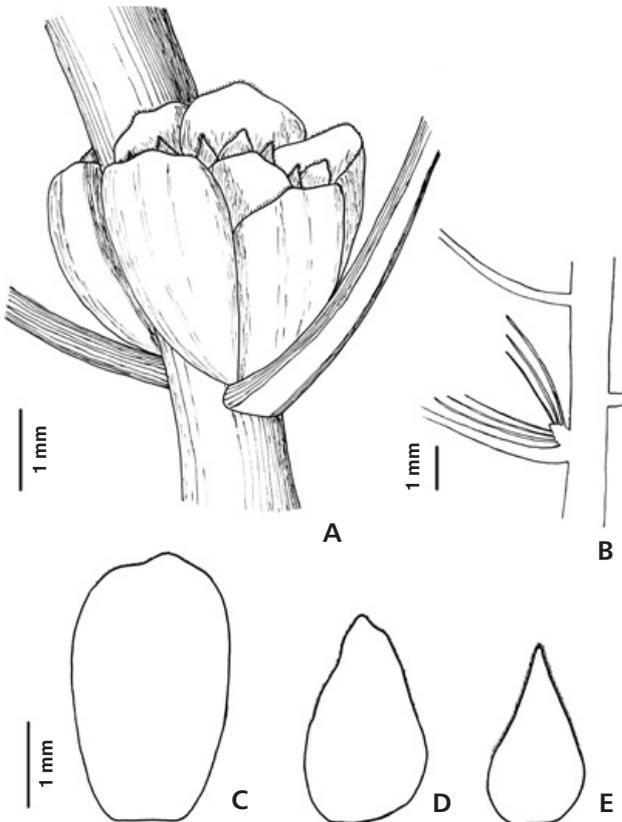


**Figure 22.** *Florinanthus volkmannii* (Ettingshausen) comb. nov. – reconstruction of a bud (A) and its section (B), scale bars = 1 mm. • C–E – sterile scales of the cone with different shape, scale bar = 1 mm.
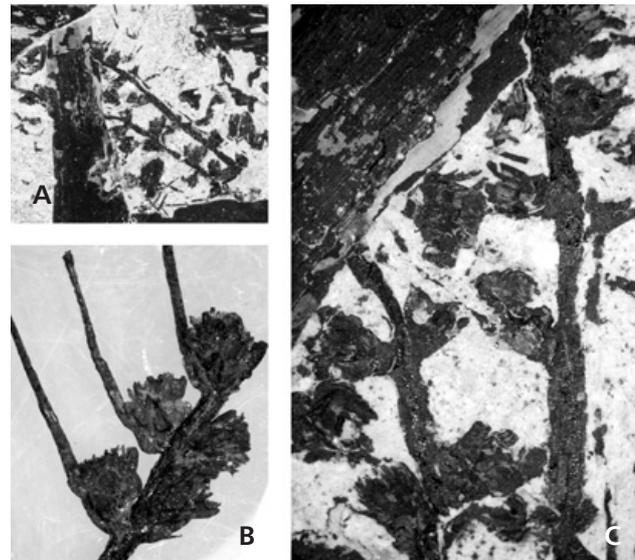
her, but the adaxial cuticle probably has less stomatal rows (Fig. 27D). The presumed abaxial cuticle with 4 stomatal rows is illustrated in Fig. 27B. The normal epidermal cells are oblong with straight, thin anticlinal walls, 50–110 μm long and 10–20 μm wide (Fig. 27C, D). The stomata are evenly spaced, between 50 to 150 μm apart, within a stomatal row. Stomatal rows are 120–200 μm apart. The stomatal complex is formed by a pair of guard cells that are 25–30 μm long and *ca* 22 μm wide, two bean-shaped lateral subsidiary cells and two square to oblong polar subsidiary cells, similar to normal epidermal cells. The guard cells are sunkenand elliptical (Fig. 28D). The outer stomatal crypt is round, 20–25 μm in diameter (Figs 27A, F, 28A, E), and resembles the Florin rings of younger conifers (Buchholz & Gray 1848) seen in the Podocarpaceae (Stocky *et al.* 1992, 1995, 1998) and Araucariaceae (Stockey & Atkinson 1993). Not including the polar cells, the stomatal complex is 48–55 μm wide and 40–50 μm long (the stomatal complex with polar cells would be up to 150 μm long). The lateral cells are 40–50 μm long and 15–20 μm wide, the polar cells are 25 to 60 μm long and 12–18 μm wide (Table 1).

*Cuticle of the strobilar axis* (Figs 27H, 28F–H). – The cuticle is very thick, up to 30 μm (Fig. 28F). The outer surface is nearly flat, whereas the inner surface has very distinct, strongly developed anticlinal cellular walls (Fig. 28F–H). The cells are elongate, tetragonal, usually oblong, 30–60 μm long, and 10–20 μm wide and orientated parallel to the axial length of the strobilus. Irregular, oval to ellipsoid structures, 10–15 μm long and 5–8 μm wide, occur on the outer axial surface. They occur most commonly on the tips of very flat papillae (Fig. 28G), their function is not known.

*Remarks*. – The syntypes of *Florinanthus volkmannii* were described from Stradonice (Hýskov relict) by Ettingshausen (1852), who considered the species to belong to *Calamites*. He figured 14 specimens on five figures, only seven of which are cordaitalean fertile organs, the other eight are in fact sphenopsids. The Ettingshausen's (1852) seven cordaitalean fertile organs (pl. 5, figs 1–3) are assignable to *Florinanthus volkmannii.* Ettingshausen's (1852) pl. 5, fig. 1 (see Fig. 29) represents 5 specimens. The four fertile organs belong to *Florinanthus volkmannii* [Fig. 29, Ettingshausen (1852), pl. 5, fig. 1]. The different specimen in the middle belongs to some calamite cone. The specimen in Ettingshausen's pl. 6, fig. 1 also represents a calamite cone and that in fig. 2 is a *Calamites* pith cast.

*Florinanthus volkmannii* is a small cordaitalean fertile organ. This name is frequently used in the literature, but presumably represents several different species. *F. volkmannii* sensu stricto is characterised by a very narrow axis that is usually 1 to 1.5 mm wide whereas axes figured by different authors are usually wider: 2 mm (Zeiller 1886),



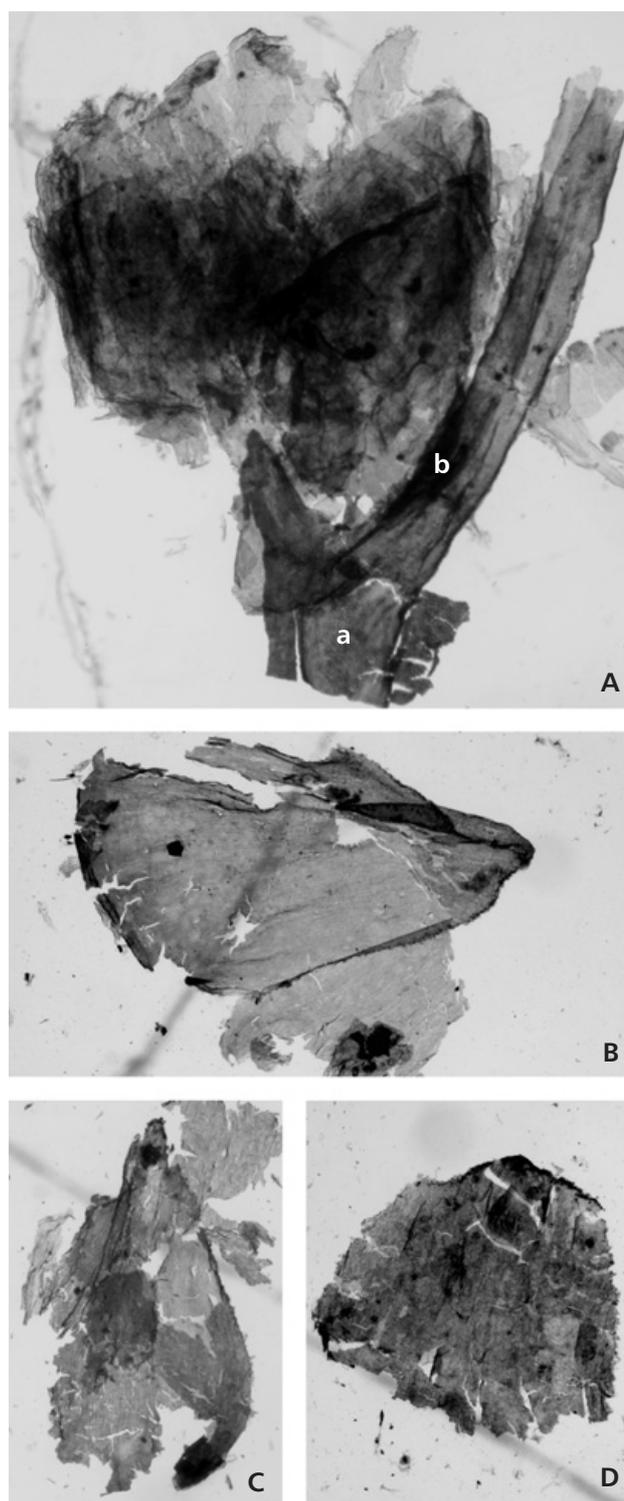**Figure 24.** *Florinanthus volkmannii* (Ettingshausen) nov. comb. • A – a macerated "bud", a – fertile organ axis, b – bract, slide 416/12, × 20. • B–D – macerated sterile scales; B – from the central part of a "bud", C – from the terminal part of a "bud", slide 416/20, D – terminal fragment of a scale from the basal part of a "bud", and B and C slide 416/19, all × 25.
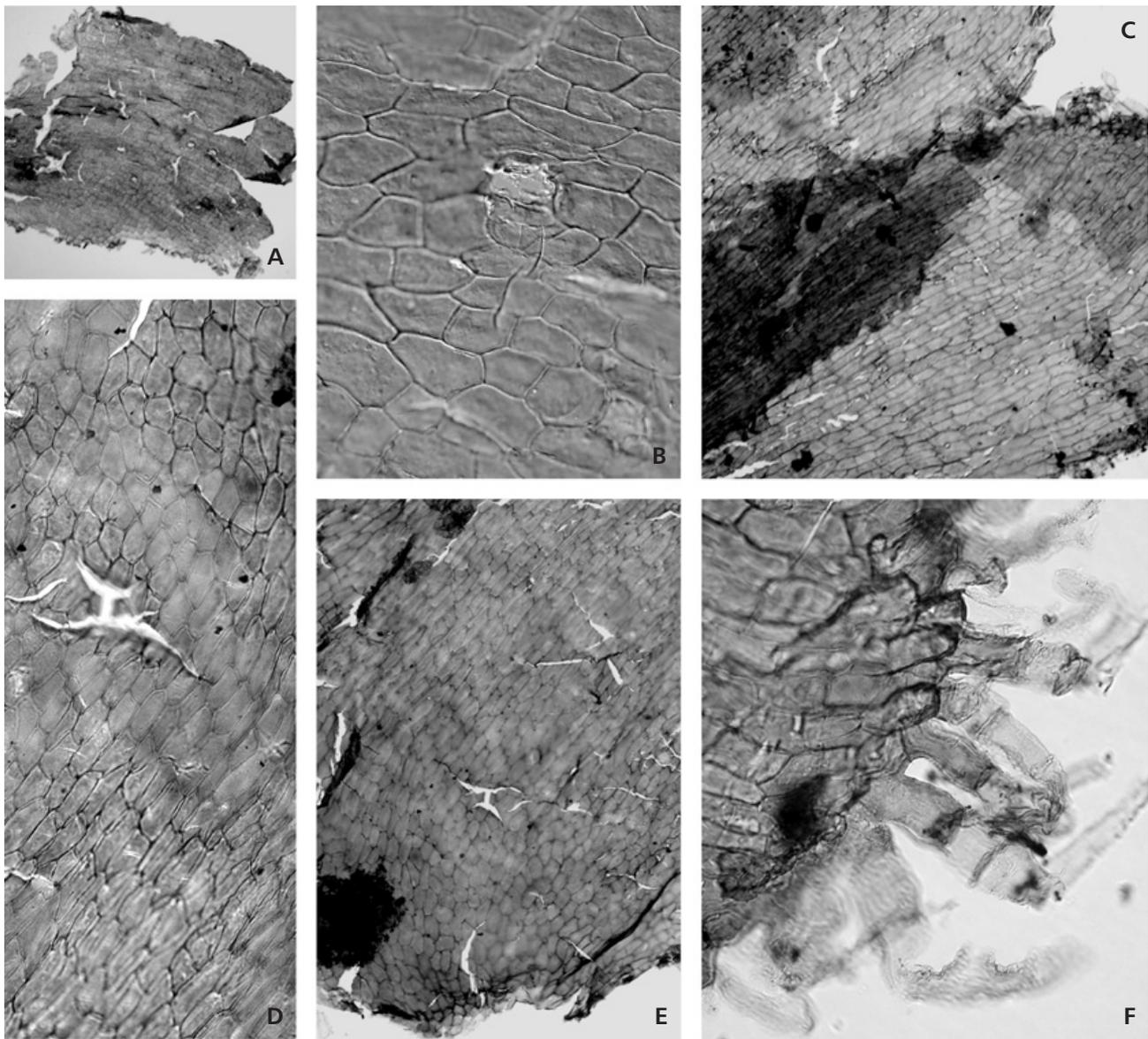
**Figure 25.** Cuticles of sterile scales of *Florinanthus volkmannii* (Ettingshausen) comb. nov. (from Fig. 25A). • A – a scale fragment (abaxial side) with few stomata, × 50. • B – abaxial cuticle of a scale with two stomata (a detail from Fig. A), 416/10, × 400. • C – adaxial and abaxial cuticles of a scale, slide 416/11, × 100. • D – detail of cells from Fig. 25E, × 200. • E – adaxial cuticle of a scale in the basal part, slide 416/11, × 100. F – margin of a scale with trichomes, slide 416/11, × 400.

4 mm (Seward 1917), 4.5 mm (Crookall 1970), 2 mm (Havlena 1971), or narrower, < 1 mm (Lee 1963). Disregarding axis width, the fertile organs "*Cordaitanthus volkmannii*" Ettingshausen of the above mentioned authors, differs from Ettingshausen's (1852) species. The most similar to Ettingshausen's species is the specimen figured by Crookall (1970). The shape and dimension of axillary shoots are very similar, however, the bracts of Crookall's specimen are shorter and bent differently. Lee's (1963) specimen has obovate axillary shoots and very short bracts. Zeiller's (1886) specimen has oval axillary shoots without scales, very different from Ettingshausen's (1852)

specimens. Preservation is a problem however, as many fertile organs are not well enough preserved for detailed comparison. Fertile organs of this *Florinanthus volkmannii* have been described as being female cones (Seward 1917, Lee 1963, Crookall 1970). However, this study shows that *F. volkmannii* is a male fertile organ which is proved by accumulations of prepollen clusters on sterile scales and pollen sacs on some Stradonice samples. Moreover, Halle in 1942 wrote on some labels for Ettingshausen's collection in the "Geologische Bundesanstalt" in Vienna a remark that *Florinanthus volkmannii* is a male fertile organ.

**Figure 26.** Cuticles of sterile scales of *Florinanthus volkmannii* (Ettingshausen) comb. nov. under SEM. • A – outer surface of a scale with small trichomes situated on the margin, stump 30, photo E5896-10, × 110. • B – small slit (arrow) on the cuticle of unknown function (from Fig. 26A), × 110. • C, D – margin of a scale with trichomes (from Fig. 26A), × 550. • E – scale surface showing oriented cells and a "slit" (arrow) (from Fig. 26A, B), × 1100. • F – inner surface of scale with well visible anticlinal cell walls, × 110. • G – detail of cells from Fig. 26F, × 440. • H – detail of outer view of the scale surface with papillae and elongate oval structures of unknown function, × 440.

**Figure 27.** Cuticles of bracts (A–G) and axis (H) of *Florinanthus volkmannii* (Ettingshausen) comb. nov. (from Fig 23A). • A – details of stomatal row with three stomata from Fig. 27B, × 340. • B – "Abaxial" side of a bract with four stomatal rows, slide 416/1, × 42.5. • C – details of two stomatal rows from Fig. 27B, × 170. • D, E – probably part adaxial and part abaxial cuticle with stomatal row, slide 416/12, D × 85, E × 340. • F – detail of a stoma, slide 416/15, × 680. • G – detail of stomata of double stomatal row, slide 416/14, × 340. • H – cuticle of fertile organ axis with thick–walled cells, slide 416/12, × 170.

## Pollen grains

### *"Cordaianthus"* and *"in situ"* prepollen grains

Pollen grains isolated from pollen sacs of the male reproductive organ "*Cordaianthus*" Grand'Eury, 1877 were very credibly described by Renault (1879) in his comprehensive study of reproductive cordaitalean parts from silicified material of Stephanian age collected from the Grand-Croix locality near Saint-Étienne, France. The general diagnoses for "*in situ*" and dispersed pollen grains was fixed by Renault (1879) and used in subsequent publications dealing with "*Cordaianthus*" pollen grains (Renault 1881, 1896). Florin (1936) described "*in situ*" pollen of *C. saportanus* Renault from the typical locality. Schopf *et al.* (1944, pp. 58, 59) proposed the genus *Florinites* to circumscribe all sporae dispersae pollen grains of known

cordaitalean affinity. The genus *Florinites* was defined (Schopf *et al.* 1944) as: bilateral pollen grains, broadly elliptical in outline. Body somewhat more spherical and nearly entirely enclosed by bladder. Bladder and body walls are joined distally. Trilete imprint (where discernible) is vestigial.

However, the diagnosis of *Florinites* became broadly interpreted and a great number of species with a wide range of sizes, morphologies, and haptotypic features were ascribed to the genus *Florinites* Schopf, Wilson & Bentall, 1944 (see Kosanke 1950, Butterworth & Williams 1954, Balme & Henelly 1955, Potonié & Kremp 1956, Wilson & Hoffmaister 1956, Bhardwaj 1957, Dybová & Jachowicz 1957, Alpern 1959, Kalibová 1965, Felix & Burdbridge 1967, Peppers 1970).

Millay & Taylor (1974) studied in detail numerous well preserved *Florinites*-type pollen grains isolated from

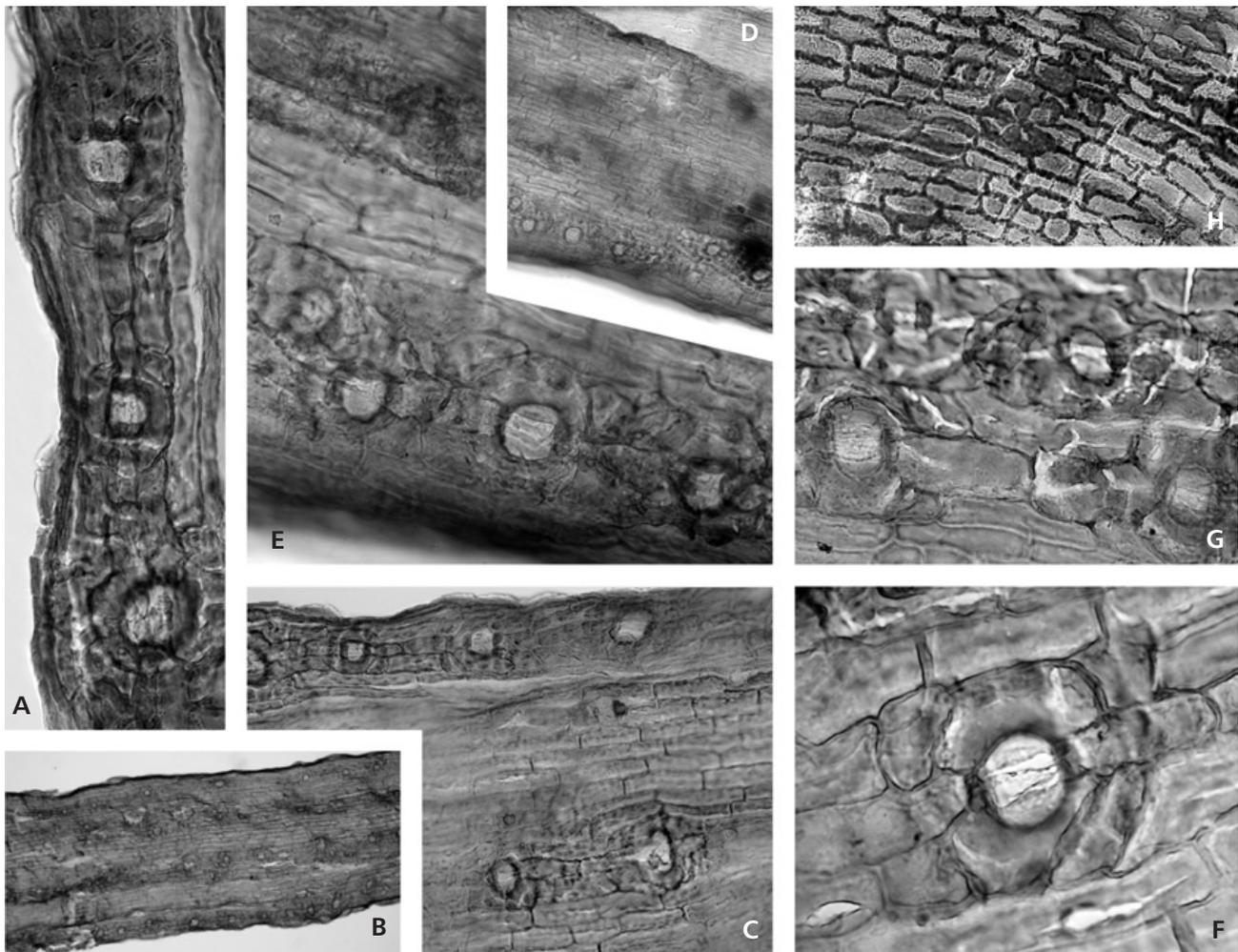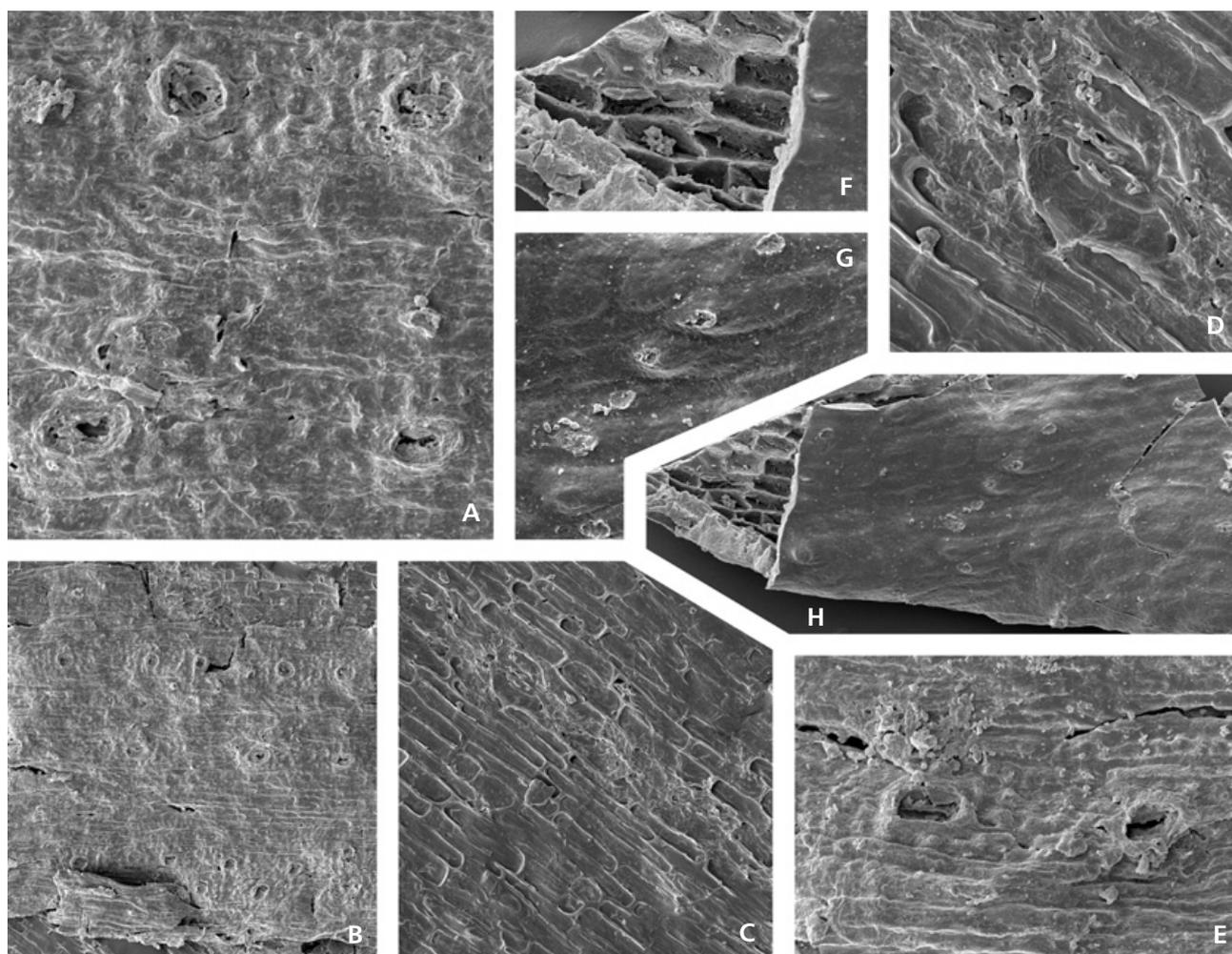**Figure 28.** Cuticles of bracts of *Florinanthus volkmannii* (Ettingshausen) comb. nov. under SEM. • A – detail of 4 stomata from Fig. 28B with slightly developed crypt, × 340. • B – outer view of abaxial cuticle of a bract with three stomatal rows, stump 30, photo E5896-22, × 85. • C – inner view on abaxial cuticle with a stomatal row, photo E5896-23, × 170. • D – a detail of a stoma from Fig. 28C, × 510. • E – a detail of two stomata with crypts, photo E5896-22det3, × 340. • F – inner view on well-developed anticlinal cell walls – a detail from Fig. 28H, × 340. • G – a detail from Fig. 28H with oval structures of unknown function, × 340. • H – cuticle of the fertile organ axis. In front, outer view of the cuticle with slightly marked cellular outlines; behind, inner view with prominent anticlinal walls; SEM stump 30, photo E5896-28, × 170.

"*Cordaianthus*" concinnus Delevoryas, 1953 and "*Cordaitanthus*" schueleri (Darrah) Fry, 1956, together with other dispersed pollen from Kansas and Iowa. They defined *Florinites* as bilaterally symmetrical alete pollen grains consisting of a circular to oval central body surrounded by a large equatorial saccus. The saccus is attached to the corpus on both the proximal and distal surfaces (see Millay & Taylor 1974, p. 81).

*Florinites pellucidus* (Wilson & Coe) Wilson, 1958 was chosen as the type species. This implies that only alete pollen grains are accommodated in the genus *Florinites*, whereas other pollen grains with a monolete, triletoid or trilete scar have been expelled from the genus *Florinites*.

Millay & Taylor (1974) also described pollen grains from a pollen sac dispersed among cone scales of "*Cordaianthus*-like" reproductive structures, and established two new monosaccate genera. The characteristic features of *Sullisaccites* and *Felixipollenites* are given in Table 3. These authors also discussed the ultrastructural organization of saccate pollen and evolution of cordaitalean pollen. Saccate pollen grains have a two-layered exine, with an outer wall layer (sexine) and an inner wall layer (nexine). Millay & Taylor (1976) also proposed an evolutionary sequence for cordaitalean pollen grains.

**Description of pollen grains from *Florinanthus volkmannii* (Ettingshausen) comb. nov.**

Pollen grains of *F. volkmannii* are monosaccate, bilateral, 60 (75) 85 µm × 32(55) 62 µm, with an amb that is broadly elliptical from a polar view and elongate oval from an equatorial view. The central body is hexagonal, oval to

**Table 2.** Overview of some *in situ Florinites* isolated from cordaitalean fertile organs. Abbreviation: * type species of *Florinanthus* Ignatiev & Meyen, 1989, ** D3 – petrified specimens, D2 – compression/impression specimens.

| Parent plants | ** | Diameter | Shape and features | Name | Age and country | References |
|---|---|---|---|---|---|---|
| *Florinanthus* (al. *Cordaitanthus*) *saportanus* (Renault, 1879) Ignatiev & Meyen, 1989 | D3 | 78–93 μm | Oval, monosaccate, leptomate, corpus subcircular | *Florinites* sp. (isolated from anther sacs) | Carboniferous, France | Florin (1936), Renault (1879), Scott (1923), Potonié (1962), Balme (1995) |
| *Cordaianthus gemmifer* Grand'Eury, 1877 | D3 | About 60 μm broad | A small trilete mark on the proximal face of the corpus | *Florinites* sp. | Carboniferous, France | Brush & Barghoorn (1962); Potonié (1962, 1967) |
| *Florinanthus* (al. *Cordaianthus*) *concinnus* (Delevoryas, 1953) Ignatiev & Meyen, 1989 * | D3 | 44–71 μm | Oval, monosaccate, corpus circular smooth proximally and granulate distally | *Florinites pellucidus* (Wilson & Coe) Wilson | Carboniferous, USA | Millay & Taylor (1974, 1976); Brush & Barghoorn (1962); Meyen (1984, 1987); Taylor (1981, 1988); Taylor & Taylor (1993); Balme (1995) |
| *Renaulticonus* (al. *Cordaianthus*) *grandeuryi* (Brongniart) Ignatiev & Meyen, 1989 | D3 | About 100 μm | Oval, monosaccate, corpus subcircular | *Florinites* sp. (recovered from the canal of the pollen chamber) | Carboniferous, France | Renault (1879) |
| *Florinanthus* (al. *Cordaitanthus*) *schueleri* (Darrah) Ignatiev & Meyen, 1989 | D3 | 62–89 μm | Oval, monosaccate, corpus circular smooth proximally and granulate distally | *Florinites* sp. (isolated from anther sacs) | Carboniferous, USA | Millay & Taylor (1974); Darrah (1952); Fry (1956); Brush & Barghoorn (1962); Potonié (1962, 1967); Balme (1995) |
| *Lesqueranthus* (*Gothania*) cones attached to stems of *Mesoxylon priapi* (Trivett & Rothwell, 1985) | D3 | 80 μm | Oval, monosacate, trilete, ?flexed monolete, corpus circular | Sullisaccites | Carboniferous, USA | Millay & Taylor (1974), Trivett & Rothwell (1985), Taylor & Taylor (1993) |
| *Lesqueranthus* (al. *Gothania*) *lesliana* (Daghlian & Taylor, 1979) Ignatiev & Meyen, 1989 | D3 | 180 μm | Oval to subcircular, monosacate, trilete, distally leptomate | Felixipollenites | Carboniferous, USA | Millay & Taylor (1974), Taylor & Taylor (1993) |
| *Florinanthus volkmannii* (Ettingshausen) comb. nov. | D2 | 58–85 μm | Oval, monosaccate, corpus oval smooth proximally and granulate distally | *Florinites* cf. *ovalis* *Florinites* cf. *guttatus* | Carboniferous, Czech Republic | Herein |

nearly circular from the polar view 30–51 μm long and 25–38 μm broad, and is a distinct darker brown colour. The longer axes of the spore and those one of the central body are mutually perpendicular. The proximal body surface is without folds, it has 8–15 μm long monolete scars (Fig. 30D, H) which curve in the centre, sometimes with an indication of an additional long third ray that suggests a transition to a trilete scar. This feature is often indistinct in light microscopy. The body outline is trapezoidal in equatorial view and tapers towards the distal side of the pollen grain (Fig. 31D). The wall of the body on the distal side has folds or pleats running along its long axis. The central body is surrounded by a large equatorial saccus, which is attached to the central body on both the proximal and distal surfaces (Fig. 30C, E, I).

The equatorial saccus covers the proximal side of the central body. The saccus is attached at a narrow zone near the proximal surface of the central body (Fig. 30I). Only part of the central body, with an oval or sickle shape, remains uncovered on the distal side. The slit is usually indiscernible.

Most studied pollen grains have the saccus torn from the proximal side and the surface of the central body is well exposed. The central body is wrinkled. The saccus is laevigate from the outer side and reticulate from the inner side (Fig. 30J).

***Comparison of prepollen grains***. – Three species of the genus *Florinites* were originally described, which are in certain aspects similar to the pollen grains isolated from *Florinanthus volkmannii*. They are *Florinites ovalis* Bhardwaj, 1957, *Florinites guttatus* Felix & Burdbridge, 1967 and *Florinites diversiformis* Kosanke, 1950. These bilateral monosaccate species possess a central body with a darker colour, in which the longer axis is mostly perpendicular to the longer axis of the saccus. However, after the Taylor & Millay's (1974) revision of the heterogenous genus *Florinites*, only monosaccate alete species (inclusive of *Florinites ovalis*) were kept in the genus *Florinites*, and the remainder of species (inclusive of *Florinites guttatus* and *Florinites diversiformis*) were excluded from this genus.

The pollen grains of *Florinanthus volkmannii* from Pokrok Mine, Ovčín – Přívětice Radnice Basin are very similar in morphology to two other species of pollen, *Florinites ovalis* and *Florinites guttatus*. However *Florinanthus volkmannii* pollen, which has a diameter

**Table 3.** Comparison of some pollen taxa with "*in situ*" pollen isolated from *Florinanthus volkmannii.*

| Taxon | Symmetry an diameter | Haptotypic features | Attachement of equatorial saccus | Notice |
|---|---|---|---|---|
| *Florinites* | Monosaccate, radially–bilaterally symmetrical | Alete, with a distal aperture | On both proximal and distal surface | Proximal saccus corpus overlap slight to absent. Saccus levigate, intrareticulate. |
| *Sulisaccites* | Monosaccate, bilaterally symmetrical 55–80 µm | Trilete | On both proximal and distal surface | Proximal saccus corpus overlap slight. Distal overlap approximately 1/2. |
| *Felixipollenites* | Monosaccate, radially–bilaterally symmetrical 115 (150) 180 µm | Trilete, triletoid more seldom monolete | On both proximal and distal surface | Proximal saccus corpus overlap slight to absent. |
| *Florinites guttatus* | Monosaccate, bilaterally symmetrical 95–140 µm × 120–70 µm | Monolete-triletoid | On both proximal and distal surface | The spore body covered by thin granulose membrane proximally and coarser reticuloid membrane distally. |
| *Pseudoillinites* Basionym = *Florinites diversiformis* | Monosaccate, bilaterally symmetrical | Monolete | Proximal surface of central body free from saccus | Appearance of a bisaccate grain. Saccus coarsely intrareticulate proximal surface of central body free from saccus. |
| Pollen isolated from *Florinanthus volkmannii* | Monosaccate, bilaterally symetrical 60 (75) 85 µm × 32 (55) 62 µm | Monolete-triletoid | On both proximal and distal surface | The spore body covered by thin smooth to granulose membrane proximally and coarser granulate membrane distally. |

58–85 µm, is intermediate in size between *Florinites ovalis* (42–65 µm) and *Florinites guttatus* (95–135 µm) with a monolete-triletoid scar.

The central body of some Bohemian specimens from the Radnice Basin extends nearly the full width of the saccus, resulting in the appearance of a bisaccate grain. Such pollen grains could be morphologically similar to *Pseudoillinites* Ravn (1979), a genus erected to accommodate bilateral, monosaccate, monolete prepollen or pollen grains. *Pseudoillinites* (al. *Florinites*) *diversiformis* (Kosanke, 1950) Ravn, 1979 was chosen as its type species.

Pollen grains isolated from *Florinanthus volkmannii* differ from pollen grains of the morphogenera *Florinites* and *Sulisaccites* (Schopf, Wilson & Bental) Millay & Taylor, 1974 by the presence of a monolete – triletoid scar on the proximal side of the central body and by having a thicker exine.

These pollen grains are partly comparable with the genus *Felixipollenites* in the shape of the haptotypic feature (monolete-triletoid) and in the stronger nature of the central body exine. However, *Felixipollenites* pollen grains are radially – bilaterally symmetrical and the proximal surface of the grains (Millay & Taylor 1974, pl. 42, figs 5, 6) show a reticulate ornamentation that is clearly limited to the proximal saccus corpus attachment region. Millay & Taylor (1976, p. 68) consider this feature to be primitive.

*Potonieisporites* is a monosaccate, monolete spore, but pollen grains isolated from *Florinanthus volkmannii* show a gradation from monolete to trilete. It seems that the *Florinanthus volkmannii* pollen grains studied are not comparable with any of above-mentioned taxa (Table 3), and they belong, perhaps, to a new genus. However, the studied pollen grains are preserved as compression/impressions and they are not as well-preserved as pollen grains from coal balls described by Millay & Taylor (1974).

## Pith casts

### *Artisia* Sternberg, 1838

*Type species.* – *Artisia transversa* (Artis) Corda *in* Sternberg, 1838

### *Artisia approximata* Brongniart *ex* Lindley & Hutton, 1837
Figures 32A–D

> 1821 *Calamites fasciatus* Sternberg, p. 27, pl. 17, fig. 3.
> 1825 *Calamites fasciatus* Sternberg, tent. 24.
> 1828 *Sternbergia approximata* Brongniart, p. 137 (nomen nudum).
> 1837 *Sternbergia approximata* Brongniart *ex* Lindley & Hutton, p. 187, pls 224, 225.
> 1838 *Artisia approximata* (Brongniart *ex* Lindley & Hutton). – Corda *in* Sternberg, p. XXII (Skizzen).
> 1838 *Tithymalites biformis* Presl *in* Sternberg, p. 205, pl. 53, figs 1–6.

*Description.* – Casts more or less cylindrical, 15–30 mm in diameter and 50–200 mm-long fragments, bearing alternate approximately horizontal septa and spaces between the septa (Specimen numbers are given in the "Material" section). The spaces are usually rounded, 0.6 to 2.0 mm in height, rarely anastomosing. Connection between *Artisia* and a trunk or twig surface is illustrated in Fig. 20H.

*Remarks.* – Only two species of *Artisia*, *Artisia tranversa* and *Artisia approximata*, are generally accepted (Van Amerom 1998, Fossilium catalogues, pp. 6–9). The other "species" are considered synonyms of these two. The *Artisia approximata*-type does not have the longitudinal ridges

**Figure 29.** Copy of the Ettingshausen's (1852) pl. 5, fig. 1. Only four specimens belong to *Florinanthus volkmannii* (Ettingshausen) comb. nov. Loc. Stradonice (Hýskov relict), Bolsovian. The arrow represents a *Rhacopteris* pinnule. × 1.

of *Artisia transversa*. Only *Artisia approximata* has been found at the Ovčín locality and therefore it could belong to *Cordaites borassifolius*. The *A. approximata* stem type was possibly produced by more than one species of cordaitalean plants as only two species of *Artisia* have been described, whereas many more species of the *Cordaites* leaf morphology are known. For example, the pith cast of the newly described species *Cordaites schatzlarensis* Šimůnek & Libertín, 2006 is of the *A. approximata* type.
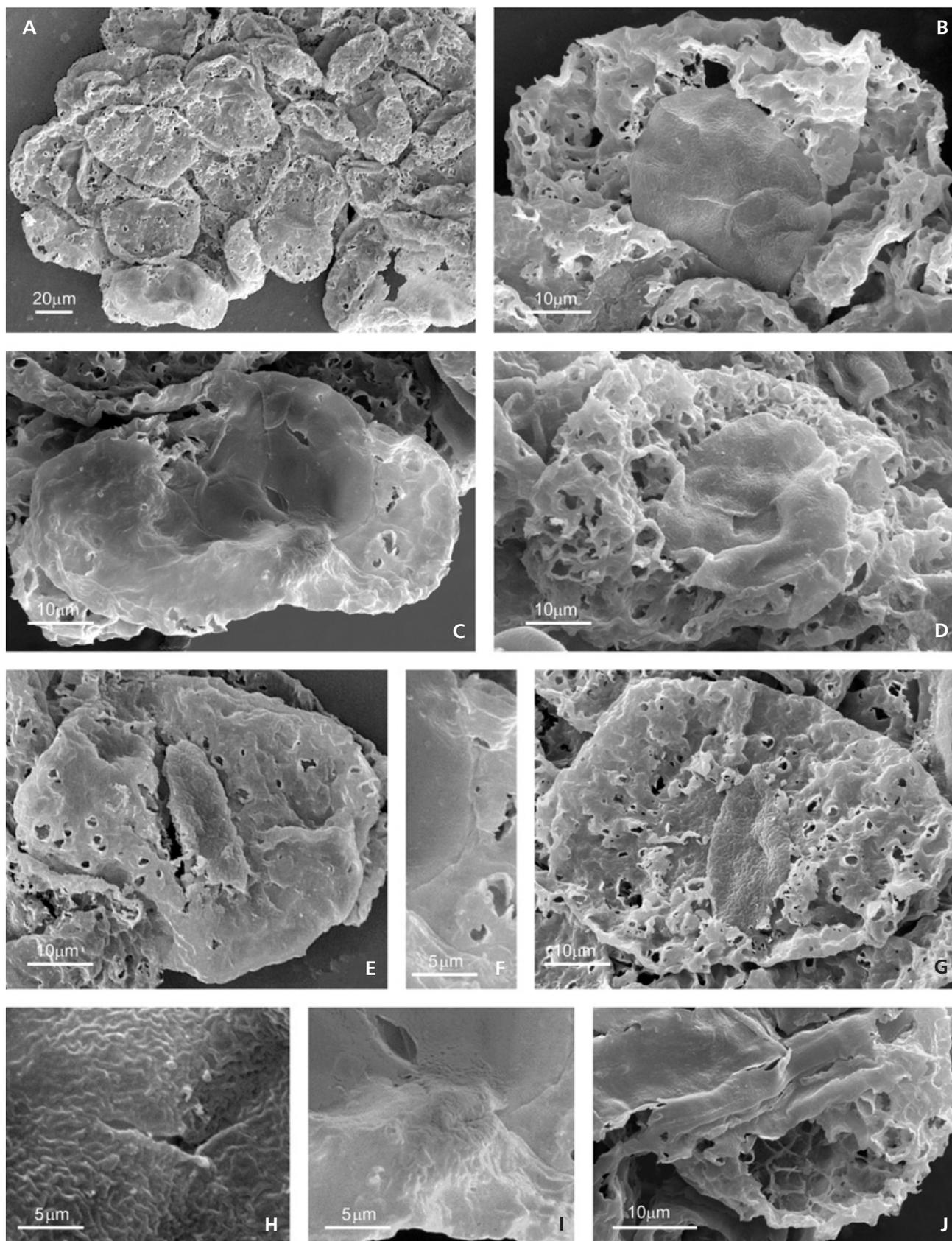
## Palaeoecology

The interpretation of the palaeoecological characteristics of *Cordaites borassifolius* is based on the occurrence of its remains in the bělka bed in the roof of the Lower Radnice Coal. Plant remains preserved there represent a peat-forming plant assemblage buried *in situ* by volcanic ash fall

(Opluštil *et al.* 2005). Therefore, *Cordaites borassifolius* is interpreted as a peat-forming representative of this genus, preferring a peat substrate. The Lower Radnice Coal is generally rich in volcanic ash and thin sedimentary partings (Andrusov *et al.* 1940). In excavations, the top of the seam is characterised by alternations of carbonaceous shale ranging to impure coal with occasional vitrain bands. This indicates the existence of an inundated planar eutrophic mire.

Excavations in the Radnice Basin provided information on the synecology of this species. Here, *Cordaites borassifolius* formed part of a diversified forest ecosystem with a well-developed shrubby storey and ground cover (Opluštil *et al.* 2007, 2009). More than 25 species have been identified in the vicinity of representatives of this species. These include sphenophytes (*Calamites* and *Sphenophyllum*), ferns (*e.g.*, *Corynepteris angustissima*, *Desmopteris longifolia*, *Senftenbergia plumosa*, *Hymenotheca* sp.), pteridosperms (*e.g.*, *Sphenopteris mixta*, *Palmatopteris furcata* and *Eusphenopteris nummularia*) and lycophytes among which the most common are *Lepidodendron lycopodioides*, *Lepidodendron simile sensu* Němejc (1947), which is a *Flemingites*-bearing species, *Lepidophloios* cf. *acerosus* and *Spencerites havlenae*. *Cordaites borassifolius* was probably among the tallest species of the ecosystem and together with lepidodendrids also the greatest contributor to bio mass.

Cordaitaleans were a diverse group and cumulatively encompassed a broad ecological amplitude ranging from dry substrates (Falcon-Lang & Scott 2000, Falcon-Lang 2003, Falcon-Lang & Bashforth 2004) to brackish environments (Falcon-Lang 2005) and waterlogged peats (DiMichele & Phillips 1994). Perhaps tolerance to physiological drought enabled cordaitaleans to live in mires. The cordaitaleans, for the most part, were a major, as well as probably the tallest component of the Bolsovian upland vegetation in southwest Newfoundland, Canada (Falcon-Lang & Bashforth 2004) where they reached nearly 50 m in height. On the other hand, the smallest forms, *Pennsylvanioxylon nauertianum* (= *Cordaixylon dumusum* Rothwell & Warner, 1984), were shrubs that grew in peat mires. The mangrove-like trees, *Pennsylvanioxylon birame* (Cridland 1964, Costanza 1985) that lived in brackish coastal habitats were probably no more than 5 m tall. Present in Upper Bolsovian coal balls from Iowa (USA), Falcon-Lang (2005) described the occurrence of similar

**Figure 30.** Pollen grains isolated from *Florinanthus volkmannii* (Ettingshausen) comb. nov., Ovčín locality, under SEM. • A – clump of pollen grains (part of the sporangium), × 340. • B – proximal view. Strongly corroded pollen grain. Central body with triletoid suture, × 1180. • C – proximal-lateral view. Relatively well-preserved pollen grain. It seems that the saccus overlaps all the proximal part of the central body. Saccus unevenly levigate, saccus corpus attachment levigate to finely granulate, × 1180. • D – proximal view. Strongly corroded pollen grain. Central body with monolete suture. Notice the distinct medial deflection of the suture, × 1180. • E – distal view. Relatively well-preserved pollen grain. Saccus unevenly levigate, saccus-corpus attachment granulate, × 1180. • F – distal view. Detail of the attachment of saccus from Fig. 30C, × 2320. • G – distal view, × 1180. • H – detail of the central body with open triletoid suture. Notice rugulate ornamentation of the body, × 2320. • I – detail of the saccus from Fig. 30C with central body attachment, × 2320. • J – pollen grain covered by some cuticle. Only part of broken equatorial saccus is exposed. Notice internal reticulation of the saccus, × 2320.
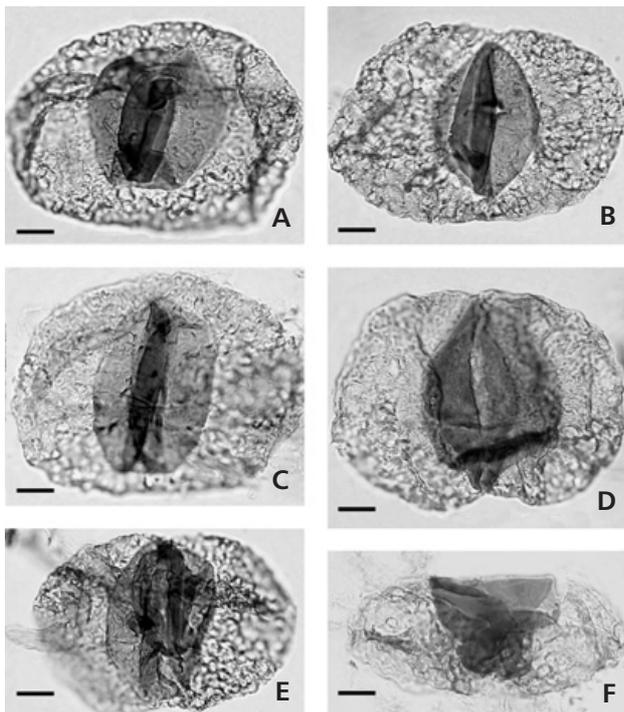
**Figure 31.** Pollen grains isolated from *Florinanthus volkmannii*, Ovčín locality. • A, C – *Florinites* cf. *ovalis* Bharadwaj, 1957, monolete suture is not seen, polar view, slide 416/17, × 500. • B – *Florinites* cf. *guttatus* Felix & Burdbridge 1967, pollen grains with monolete suture, polar view, B – slide 416/5, × 500. • D, E – cf. *Pseudoillinites* Ravn, 1979, pollen grains of a bisaccate appearance, polar view, D – slide 416/19, E – slide 416/11, × 500. • F – pollen grain of *Florinanthus volkmannii* in lateral view, slide 416/17, × 500.

cordaitalean trees from the Joggins Formation (Langsettian) of Nova Scotia, Canada. The trees from Joggings were of the same height as trees from Iowa and had a mangrove-like rooting system. Evidence of marine influence is unquestionably present in the Joggins Formation. The afore mentioned cordaitaleans are the extreme cases regarding overall height and are from unusual habitats. Cordaitalians that grew on clastic substrates probably grew to between 30 and 40 m (Grand'Eury 1877).

Two stem-genera, based on anatomical features, have been recognized in mire habitats: *Mesoxylon* and *Pennsylvanioxylon* (DiMichele & Phillips, 1994). The stem anatomy of *Cordaites borassifolius* from the Radnice Basin is not known therefore direct comparison with *Mesoxylon* and *Pennsylvanioxylon* is not possible. DiMichele & Phillips (1994) mentioned that cordaitaleans were most common in marginal areas of coal bodies that were subject to clastic influx from adjacent channels or in association with mineral partings and adjacent high-ash coals. The typical floral assemblage that includes cordaitaleans also includes calamites, some tree ferns and arborescent lycopsids. Cordaitaleans grew in planar swamps that had seasonally high water tables. The cordaitaleans in Ovčín were known

to occur in the southeastern portion of the Pokrok (Ovčín – Přívětice) quarry, adjacent to our excavations, where they were also recovered.

Life in mire environments probably subjected the cordaitaleans to conditions that resulted in tolerance to physiological draught. This tolerance is suggested by the xerophyllous features observed in the cuticles such as stronger cutinisation and sunken stomata with special mechanism for transpiration reduction. Such features usually occur in two different environments: In primarily dry habitat with shortage of water on well-drained clastic substrates, and in wet peat-forming environments with a shortage of nitrogen. In such settings, plants attempt to diminish transpiration by various xerophyllous adaptations. *Cordaites borassifolius* had such adaptations. Its adaxial cuticle was significantly thicker and had a very low density of sunken stomata. Stomata on abaxial surface are also deeply sunken with a special crypt transverse to the guard cells, further reducing transpiration.

## Stratigraphic range and geographic distribution

*Cordaites borassifolius* leaf cuticles have been found at only several localities in the Radnice Basin and in Stradonice (= Hýskov relict) near Beroun locality and this species has been found only at the level of the Whetstone Horizon, early Bolsovian (middle Moscovian). Outside central and western Bohemia, the remains of *Cordaites borassifolius* have frequently been reported based on leaf morphology only. However, no reliable identification using cuticles has confirmed these identifications. Therefore, mapping the geographic distribution and stratigraphic range of the species requires further investigation.

## Discussion: The whole plant concept

The first cordaitalean reconstructions were made by Grand'Eury (1877). He figured several arborescent forms, 20 to 40 m high, that represent canopy trees from floodplain environments. These reconstructions were adopted by many palaeobotanical textbooks in the 20th century. It seems that Grand'Eury (1877) did not reconstruct a particular species, but rather combined features from species representing subgenera of *Cordaites*. Modern reconstruction, based on coal ball material, were published by Rothwell & Warner (1984) and Costanza (1985). Rothwell & Warner (1984) reconstructed *Pennsylvanioxylon nauertianum* (Andrews) Costanza (= *Cordaixylon dumusum* Rothwell & Warner). They found an endarch cordaitalean stem organically conected with *Cordaites* leaves and pollen cones of *Cordaitanthus* morphology. They classified

all these organs under a single name *Cordaixylon dumusum* Rothwell & Warner, 1984. Moreover, they found disarticulated ovules and ovulate cones. These they classified as seperate morphogenera, *Cardiocarpus* and *Cordaitanthus*, although their organic connection was not demonstrated, their affinity to *Cordaixylon dumusum*, however, is highly probable. This plant had a bush-like habit.

The reconstruction of another cordaitalean tree, based on material from coal balls was proposed by Costansa (1985). She found, in organic connection, the following plant organs: *Pennsylvanioxylon birame* (stems), *Amyelon iowense* (roots), *Cordaites principalis* (leaves), *Florinanthus (Cordaitanthus) concinuus* (pollen-bearing shoots), *Cordaitanthus* sp. (ovule shoots) and *Cardiocarpus spinatus* (ovules). The growth habit of this 5 m tall plant was mangrove-like. However, it must be noted that the name *Cordaites principalis* in fact comprises many natural species.

The individual species of cordaitaleans cannot be determined solely by venation. Only by obtaining cuticular material from a specimen is it possible to assign it to a species taxon (Šimůnek 2007). That means that cordaitalean leaves with the venation pattern of *Cordaites principalis* may in fact be a leaf from any number of cuticle based taxa that have different stem and fertile organ morphologies.

The reconstruction of adpression cordaitalean plants is different from those based on coal ball derived material. Rothwell & Warner (1984) and Costanza (1985) used the name applied to the stem to represent their completely reconstructed plant. It is not possible with the adpression preservation because anatomical features of two-dimensional stems are not preserved. Typically only the coalified surface of the trunk or the pith cast of *Artisia* is preserved in compression-adpression settings. It is thus impossible to determine whether the plant is *Mesoxylon* or *Pensylvanioxylon.* Therefore, we chose the leaf characteristics (including the cuticles) as the basic feature for naming the whole plant: *Cordaites borassifolius.* Leaves of *Cordaites borassifolius* were the first cordaitalean remains described by Sternberg (1821). Our excavations in the Radnice Basin yielded another cordaitalen organ genera that may or may not be assignable to *Cordaites borassifolius*.

The plants preserved in the bělka bed from the Radnice Basin were buried *in situ* by volcanic ash as indicated by common upright stems ranging from a few centimetres to nearly 1 m in diameter (Opluštil *et al.* 2009). These stems are associated with pre-eruption plant litter as well as branches broken due to volcanic ash load, found scattered in the tuff at the base of the upright parent trunk. Such associations of various plant organs with their parent stems provide a very good basis for whole plant reconstruction of several species, including *Cordaites borassifolius*. Specimens collected at the Ovčín localities come from a small area of about 200 m by 200 m and most probably represent the same plant
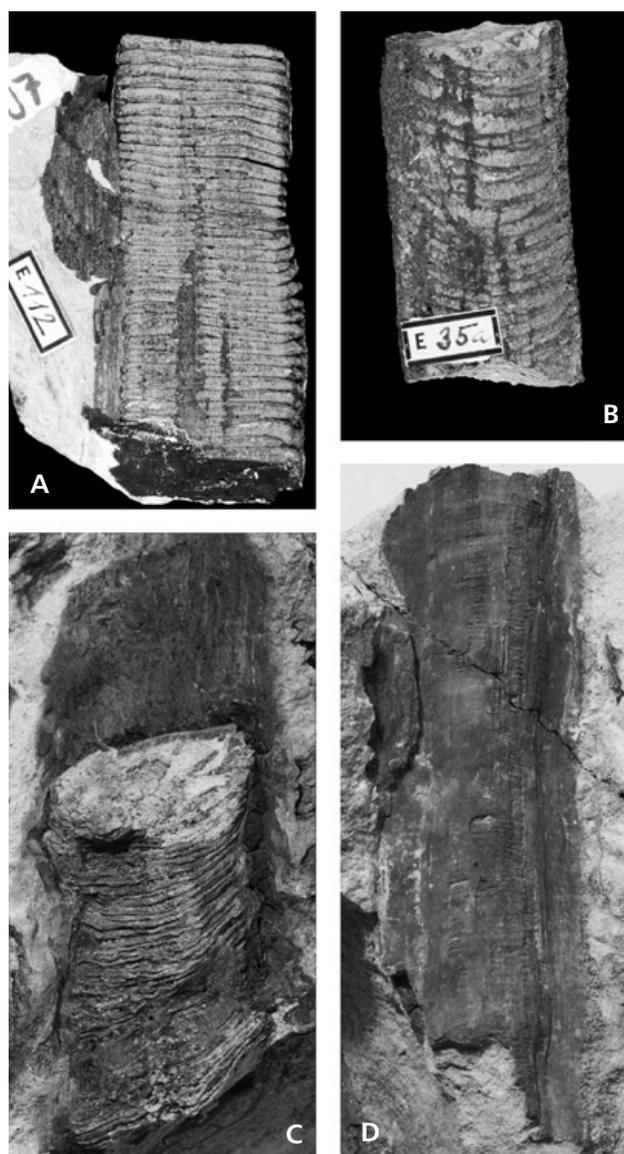


**Figure 32.** *Artisia approximata* Brongniart *ex* Lindley & Hutton. • A – pith cast of "*Tithynalites biformis* Presl *in* Sternberg", locality Radnice, Inv. No. E 112 (National Museum Prague), × 1. • B – pith cast of "*Calamites fascaitus* Sternberg", loc. Radnice, Inv. No. E 35a (National Museum Prague), × 1. • C – the pith cast and partly wood imprint, loc. Ovčín near Radnice, West Bohemian Museum in Plzeň, × 2. • D – an imprint of *Cordaites* wood, loc. Ovčín near Radnice, West Bohemian Museum in Plzeň, × 1.

assemblage in which only one cordaitalean species occurred. This is further supported by cuticle analysis of 11 cordaitalean leaves preserved in both the bělka and the tuffite above it. This analysis demonstrated that all these leaves belong to one species, although maybe in different ontogenetic stages as indicated by different crypt development. Furthermore, cuticles of these leaves are identical with those prepared from the holotype of *Cordaites borassifolius* from Svinná, about 6 km north of our excavations

**Figure 33.** Whole-plant reconstruction of *Cordaites borassifolius* (Sternberg) Unger (reconstruction by J. Svoboda).

(Fig. 3B, C). Abaxial cuticle from the holotype shows the same crypt as samples from Ovčín. Such a crypt does not occur in any other samples from the Czech Republic (similar crypt development is known from the Döhlen Basin, Germany) (Barthel 1964, Šimůnek 2007). Therefore we assign our specimens to the same species as Sternberg's original material. Unfortunately, the assignment of other plant organs such as seeds (*Cardiocarpus*) and strobili (*Florinanthus volkmannii*) to *Cordaites borassifolius* is not so straightforward because all organs were found isolated, not in organic connection to leafy twigs. However, as already stated above, these organs are associated with leaves which, based on cuticles, are identical to *Cordaites borassifolius*. Therefore we believe that *Florinanthus volkmannii* and *Cordaitanthus ovatus* strobili as well as *Cardiocarpus* seeds were produced by the same plant species, *Cordaites borassifolius*.

Although the seeds are platyspermic, they are not winged. They probably fell near the parent plant. We assign these seeds to *Cordaites borassifolius*.

The several specimens of the second fertile organ identified as *Cordaitanthus ovatus* were found in isolation. We consider these to also belong to *Cordaites borassifolius*, although we do not have organic attachment to prove this hypothesis. None of these fertile organs are well preserved. Thus, cuticular study is not possible. This type of fertile organ is more robust than *Florinanthus volkmannii* and therefore is considered to be female. No seeds were found *in situ* with this fertile organ so the gender of the cone remains in doubt.

*Florinanthus volkmannii* and "*in situ*" prepollen grains: Pollen sacs were probably overripe and not preserved in this fertile organ. However, accumulations of *Florinites* prepollen were found among the sterile scales (Fig. 30A), though this in itself does not prove beyond doubt that they are the prepollen of *Cordaites borassifolius*. However, it is more likely that this is the case than to suggest that they were transported by wind from an upland cordaitalean plant kilometres away. They have been classified as 3 species of cordaitalean prepollen, probably based on their maturity. Rare *Artisia* pith casts were also found in association with *Cordaites borassifolius* leaves. Even though their organic connection is not preserved, their affinity to *Cordaites borassifolius* is probable. It should be noted, however, that *Artisia approximata,* a species with few diagnostic features, occurs with many other cordaitalean species.

Summary of the whole plant concept: Based on cuticular studies, it has been proven that, of the possible cordaitaleans, only *Cordaites borassifolius* leaves are present in the bělka tuff bed in the roof of the Lower Radnice Coal, Radnice Basin. Given that the leaves are all of one type, then the other cordaitalean organs present, the seeds *Cardiocarpus annularis* and the male fertile organs *Florinanthus ovatus,* were found with accumulations of *Cordaites borassifolius* leaves. Therefore their affinity to *Cordaites borassifolius* is highly probable. The *Artisia approximata* pith cast and *Cordaitanthus ovatus* fertile organ were not found in organic connection with *Cordaites borassifolius* and their affinity to this species is less probable. However, there is only one cordaitalean species in the deposits thus the possibility that these organs belong to another cordaitalean species is not likely. The proposed reconstruction of *Cordaites borassifolius* can be seen in Fig. 33.

The Stradonice locality (Hýskov relict) is important to the current discussion because it is the type locality of *Florinanthus volkmannii*. At least four types of cordaitalean fertile organs have been discovered from this locality, including *Cordaitanthus triticus* (Andrae) and *Cardiocarpus orbiculare* type seeds (Ettingshausen 1852). The others are not yet described. Adequate cuticular recovery from the cordaitaleans from Stradonice has been unsuc-

cessful. It seems that at least two natural cordaitalean species occur at the Stradonice locality (Hýskov relict).

The cuticles of the different cordaitalean organs (leaves, cone scales, and seeds) found at the Ovčín localities exhibit different cellular details. These differences, however, are quite common and there are many examples in different plant groups. In the pteridosperm *Laveineopteris* for example, the cuticle of the pinnules differes from the cuticle of the cyclopterid of the same species (Cleal & Shute 2003). In the cordaitaleans it has been demonstrated that the leaf cuticle of *Cordaites schatzlarensis* Šimůnek & Libertín differs from the seed cuticle of *Samaropsis newberryi* (Andrews) Seward. Nevertheless, both morphogenera belong to one biological species (Šimůnek & Libertín 2006). The fact that cuticles of different organs are not identical in all details does not preclude them from belonging to the same biological species. We believe this to be case for the cordaitalean remains found in the bělka bed at Ovčín; several cuticular types representing one biological species.

Concerning the botanical affinity of the large trunk fragment found in SE1, its identification as a cordaitelan remain is mostly indirect since no leaves were found attached to the branches. Nevertheless the character of branching and surface of the trunk clearly differentiate this specimen from associated calamites, medullosans, tree ferns and lepidodendrid (even decorticated) stems. Moreover, this stem is associated with leaves of *Cordaites borassifolius*, which again points to the conclusion that this is most likely the trunk of the same species. If so, this species was a fairly large tree.

## Conclusions

*Cordaites borassifolius* represents a distinct cordaitalean leaf known from several localities in the Radnice Basin. Some cordaitalean leaves from Stradonice (Hýskov relict) probably also belong to this species. The venation of *Cordaites borassifolius* exhibits two patterns: the abaxial surface shows the typical venation of *Cordaites borassifolius* with alternating wide and narrow veins, whereas the adaxial side shows veins of approximately equal width.

Morphological features of the cuticle are significant for recognition of this species. The adaxial cuticle has orientated oblong cells and rare stomata more or less regularly dispersed on the leaf surface. Stomatal complexes of the abaxial cuticle, however, are arranged in multiple stomatal rows, forming stomatiferous bands. Each stoma (guard cells) is covered by a transverse outer stomatal cavity (crypt) that is a reliable diagnostic feature for this species. This feature has only been observed in *Cordaites* sp. type 6 by Barthel (1964) from the Permian strata of the Döhlen Basin in Germany.

Fertile organs found associated with the *Cordaites borassifolius* leaves are classified as two species. In accordance with the system of Ignatiev & Meyen (1989), the male inflorescence found at both Stradonice (Hýskov relict) and the Radnice Basin is named *Florinanthus volkmannii* (Ettingshausen) nov. comb. [Representatives of "*Cordaianthus*" *volkmannii* described from other areas (United States, Great Britain and China) do not belong to this species. They are usually described as female fertile organs, and according to Ignatiev & Meyen (1989), should be classified within the genus *Grandeuryconus* Ignatiev & Meyen.] *F. volkmannii* has long bracts and very small fertile buds. The cuticle of the bracts shows orientated tetragonal cells and stomatal complexes arranged into single stomatal rows. The fertile axillary complexes are composed of 20 to 30 spatulate to lanceolate shaped scales. Small uniseriate trichomes grew from the scale margins. Pollen grains associated with these scales resemble dispersed *Florinites ovalis* Bharadwaj, *Florinites guttatus* Felix & Burdbridge, and *Pseudoillinites* sp. Comparison of Bohemian "*in situ*" pollen grains with other cordaitalean "*in situ*" species could not be accomplished, because it was necessary to use SEM and TEM analysis for exact determination.

The second fertile organ is comparable to the North American Westphalian D species *Cordaitanthus ovatus* (Lesquereux) Ignatiev & Meyen. Even though it is presumed to be female, its gender could not be unquestionably demonstrated. The sex of this inflorescence is indeterminate, and therefore it is classified as *Cordaitanthus* Feistmantel, which was established to accommodate cordaitalean fertile organs of indeterminate sex.

The seeds from SE, discovered in 2006 are similar to *Cardiocarpus annularis* (Sternberg) Lesquereux. The cuticle of seed integuments consists of polygonal cells. The strongly cutinised cells with thick walls probably covered the sclerotesta whereas the two-layerd thin cuticle covered the sarcotesta.

Twigs and pith casts were previously described by Sternberg (1821, 1825) as *Calamites fasciatus* Sternberg and as *Tithymalites biformis* Presl by Presl *in* Sternberg (1838). The valid name is *Artisia approximata* Brongniart *ex* Lindley & Hutton.

*Cordaites borassifolius* was an important element of the peat-forming floras of the Radnice Basin and shared the ecosystem with peat-forming lepidodendrids. In life, it was a tree of medium height, reaching 20 m high.

## Acknowledgement

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