

Contribution to the knowledge of *Cordaites* species from the Kladno-Rakovník Basin, Middle Pennsylvanian (Bolsovian), Czech Republic



Zbyněk Šimůnek^{1*} and Jan Haldovský²

¹ Czech Geological Survey, Klárov 3/131, 118 21 Praha 1, Czech Republic; (zbynek.simunek@geology.cz)

² Modřínová 259, 273 08 Pchery – Theodor, Czech Republic

doi:10.4154/gc.2015.11

Geologia Croatica

ABSTRACT

New collections from the spoil piles of the Theodor mine in Pchery and the Schoeller mine in Libušín (Kladno-Rakovník Basin, Czech Republic) yielded a new *Cordaites* species and improved knowledge of the extent of the cuticular variability of the species *Cordaites wartmannii* ŠIMŮNEK. Based on the cuticles, it has been proven that the species *Cordaites polynervus* ŠIMŮNEK is conspecific with *Cordaites kladnoensis* ŠIMŮNEK. The new species, *Cordaites theodorii* ŠIMŮNEK & HALDOVSKÝ sp. nov., established on strongly papillate cuticles, is characterized by the presence of small teeth on the leaf margin. This feature is new for the genus *Cordaites*. The palaeoecological significance of papillae on *Cordaites* cuticles is discussed and is probably an adaptation to living on a peat substrate. Comparison of the species *Cordaites wartmannii* ŠIMŮNEK and *Cordaites barthelii* ŠIMŮNEK is made. Adaxial cuticles of *Cordaites kladnoensis* and *Cordaites wartmannii* are so similar that it is difficult to distinguish these species by means of the adaxial cuticle alone.

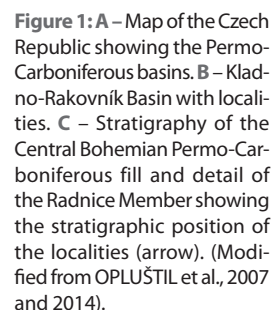
Keywords: *Cordaites*, cuticular analysis, Central Bohemian basins, Carboniferous, Bolsovian

1. INTRODUCTION

Cordaitaleans are an extinct group of gymnosperm trees and shrubs characterized by large strap-shaped leaves, and woody stems (RAYMOND et al., 2010). Their closest living relatives are the modern conifers (ROTHWELL, 1988). The group is divided into families Cordaitanthaceae, Ruffloriaceae and Vojnovskyaceae (CLEAL & THOMAS, 1995). Only the family Cordaitanthaceae is widespread in the Pennsylvanian and Permian of the Euramerican Realm (JONGMANS & DIJKSTRA, 1968 and DIJKSTRA & VAN AMEROM, 1998). Their representatives lived in different

habitats from coastal and lowland peat-swamps to intramountain peat swamps (DIMICHELE & PHILLIPS, 1994, ŠIMŮNEK et al., 2009, RAYMOND et al., 2010), to clastic and mineral soils of seasonally dry and dry habitats (FALCON-LANG, 2003a,b, FALCON-LANG & BASHFORTH, 2004, DIMICHELE et al., 2010, FALCON-LANG et al., 2006, 2011, BASHFORTH et al., 2014).

The first reference to cordaitaleans from the Kladno-Rakovník Basin is by FEISTMANTEL (1876). He mentioned *Cordaites borassifolius* (STERNBERG) UNGER from the Kladno “Opuka” locality. However, he understood this species in a very broad sense and identified it from all



1942-2002). Cordaitaleans were neglected in the Czech literature for a long time as stratigraphically uninteresting plants. For instance, NĚMEJC (1936a, 1940, 1947) published monographs of different plant groups (alethopterids, pecopterids, lepidodendrids), where the Libušín, Schoeller Mine locality is mentioned, but he was never interested in cordaitaleans. For all that, FLORIN (1931) published a drawing of the abaxial cuticle of *Cordaites* sp. 1 from the Rakovník locality in the Kladno-Rakovník Basin, and it seems

that this species is different to all 30 later described cordaitalean species (ŠIMŮNEK, 2007), classified by means of their cuticles. Five of those species occur in the Kladno region. Their leaves were collected by the first author (ZŠ) from the Tuchlovice and Libušín localities from the 1980s until the closure of the mines. The second author (JH) put together a large collection from the spoil pile of the Theodor mine, at the Pchery locality during recent years. Maceration of the new samples provided new data which required a subsequent revision of cordaitalean cuticles.

The biostratigraphy of the Radnice Member has been known since the beginning of the 20th century, when NĚMEJC (1932) placed the Radnice Member in the upper Westphalian C (Bolsovian). The Radnice Member is assigned to the *Paripteris linguaefolia* Zone of WAGNER (1984).

2. GEOLOGICAL SETTING

The Kladno-Rakovník Basin is a part of the Central and Western Bohemian Complex, which is characterised by a stratigraphic range from the middle Westphalian (Bolsovian) to the end of the Stephanian (PEŠEK 1994) and the lower part of the Permian (ZAJÍC, 2012). Sedimentary fill in this complex is subdivided into four formations (Fig. 1) based on alternating red (coal-barren) and grey (coal-bearing) strata (WEITHOFER, 1902). The Radnice Member (Bolsovian) comprises the most important coal-bearing strata of the basins in central and western Bohemia. Sediments of this unit are interpreted as the fill of river valleys that either were incised into the basement or with tectonically driven valley margins (OPLUŠTIL 2005a). In the Kladno-Rakovník 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 up to 1 m thick. The Upper Radnice Coal is the most important seam of the basin being locally up to 8 m thick. Both coal seams are separated by the volcanic Whetstone Horizon, which tends to be a few metres thick. This horizon consists of an approximately 60 cm thick pale yellow fossiliferous tuff bed (the “bělka”), followed by poorly- to well-laminated tuffitic claystone and mudstone (the “whetstone”).

3. MATERIAL AND METHODS

The majority of flora collected in the Libušín, Pchery and Tuchlovice localities comes from the tuffaceous partings called “Opuka”. The cordaitalean remains were collected predominantly in the 20 cm thick parting called “Velká Opuka” that occurs in the lower third from the footwall of the Upper Radnice (Main Kladno) coal seam (OPLUŠTIL, 2005a,b and OPLUŠTIL et al., 2007).

The material used in this study is stored in the Czech Geological Survey, Prague and comes from the following localities: Tuchlovice, Nosek mine (holotype of *Cordaite polynervus* ŠIMŮNEK, No. ZŠ 247), Libušín, Schoeller mine (holotype of *Cordaite wartmannii*, No. ZŠ 246 and additional specimens ZŠ 302–306), Pchery, Theodor Mine

(holotype of *Cordaite theodorii* ŠIMŮNEK & HALDOVSKÝ sp. nov., and specimens of *Cordaite wartmannii* ŠIMŮNEK, ZŠ 350; and *Cordaite kladnoensis*, ZŠ 358a,b). From these samples, cuticular slides No. 113/1-2, 182/1-3, 395/1-8, 518/1-13 and 543/1-4 were prepared by the method described by KERP (1990), KRINGS & KERP (1997) and KERP & KRINGS (1999). Coalified fragments of leaves were separated from the rock by means of a needle or hydrofluoric acid (HF). These fragments were bleached in Schulze's reagent (40% HNO₃ with crystals of KClO₃) for 3–18 hours (depending on preservation). After treatment in Schulze's reagent, cuticles were washed in water, subsequently immersed in 2% or 10% potassium hydroxide (KOH) and finally rinsed in distilled water. Some cuticles were stained with safranin, Bismarck brown, malachite green or neutral red (KRINGS, 2000) for 1 to 2 hours to accentuate the anticlinal walls and stomata. Before embedding in glycerine-gelatine slides, the cuticles were dehydrated in pure glycerine. The remaining cuticular fragments were affixed to metal stubs for observation under a Cam Scan CS 3200 scanning electron microscope at the Czech Geological Survey, Prague.

Stomatal index (SI) is calculated for specimens analysed here. It was first employed by SALISBURY (1927) and describes the number of stomata expressed as a percentage of the total number of cells per unit area: $SI = 100 \times \text{total number of stomata} / (\text{total number of stomata} + \text{total number of epidermal cells})$. Stomatal density represents the number of stomata per unit area, usually the number of stomata per 1 mm². The minimum area for calculation of stomatal density is 0.3 mm² (POOLE & KÜRSCHNER, 1999).

4. SYSTEMATIC PALAEOBOTANY

Order Cordaitanthales MEYEN, 1984

Family Cordaitanthaceae MEYEN, 1984

Genus *Cordaite* UNGER, 1850

4.1. *Cordaite wartmannii* ŠIMŮNEK emend. nov.

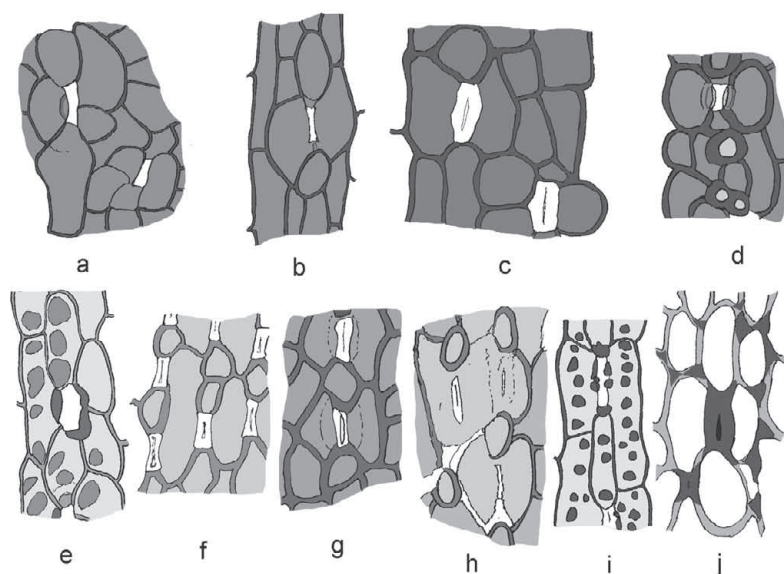
(Fig. 2a, b, g–h, Pl. 1A–D, Pl. 2, 3, 4, 5, Pl. 7G–H)

2007 *Cordaite wartmannii* ŠIMŮNEK, p. 147–148, text-fig. 38, pl. 3, fig. 15, pl. 41, figs 5, 6, pls 42, 43, figs 1–2.

Emended diagnosis (ŠIMŮNEK, 2007, p. 147): Leaves revolute, adaxial cuticle composed of oblong cells, cells of dark stomatal band tetragonal to pentagonal shape, subsidiary cells oval, lateral subsidiary cells semicircular. Abaxial cuticle papillate with oblong to trapezoidal cells, stomata in stomatiferous bands, polar subsidiary cells circular to oval, lateral subsidiary cells elongated, tetragonal to oval.

Description: The holotype is the narrowest leaf fragment of this species – 18 mm wide (Pl. 1A). The largest leaf fragments are up to 190 mm long and the widest 45 mm wide. The leaf margins are nearly parallel or somewhat divergent (narrow leaves) and revolute (inrolled toward the lower surface) in some cases. Such leaves may seem to be as little as only 20 mm wide. The veins have a small furrow

Figure 2: Comparison of the described cordaitalean stomatal types from the Kladno-Rakovník Basin. Scale bar = 50 μm . a–d. Adaxial cuticles that have similar pattern; stomata in dark stomatiferous bands; a–b. *Cordaitea wartmannii* ŠIMŮNEK, Libušín locality, a – Holotype, slide 113/1 (Pl. 2C), b – Type with circular to oval polar subsidiary cells, slide 395/5 (Pl. 3B); c–d. *Cordaitea kladnoensis* ŠIMŮNEK, c – Tuchlovice locality, holotype of "*Cordaitea polynervus*", slide 182/1, (Pl. 8D), d – Pchery locality, slide 543/4 (Pl. 9C), small rounded objects are damage to cuticles due to bacterial or fungal infection (maybe post mortum). e–j. Abaxial cuticles; e–h. *Cordaitea wartmannii* ŠIMŮNEK; e–f. Libušín locality, e – Holotype, slide 113/1, with elongated polar subsidiary cells and many flat papillae, f – A specimen with more or less circular polar subsidiary cells, resembling the Stephanian *Cordaitea barthelii* ŠIMŮNEK. Slide 395/5 (Pl. 3A); g–h. Pchery locality, cuticles with rounded polar subsidiary cells as in Fig. 2f, g – Slide 518/6 (Pl. 5G), h – This cuticle is a somewhat disorganized. Slide 518/2 (Fig. 9h); i – *Cordaitea theodorii* HALDOVSKÝ & ŠIMŮNEK sp. nov. Pchery locality. Cuticle with many dark, prominent papillae. Slide 518/2 (Pl. 7C); j – *Cordaitea kladnoensis* ŠIMŮNEK, holotype of "*Cordaitea polynervus*" Tuchlovice locality, slide 182/1 (Pl. 8E). Guard cells are sunken below strongly cutinised crypt. Triangular cutin thickenings and projections are in the cell corners.



in the middle, so they look like double veins. The vein density is low – 10 to 16 prominent veins per cm. Exceptionally one, but usually 2–3 narrow strips of sclerotic strands alternate with each vein. The leaves have stomata on both sides (amphistomatic).

Cuticular characteristics: It is not necessary to repeat the whole description from ŠIMŮNEK (2007, p. 147). Only new observations based on new material from the Libušín and Pchery localities will be mentioned. The comparison of cuticular characteristics is in Table 1.

Adaxial cuticle (Figs 2a–b, Pls 2A–C, 3A–D, 4G–L): Dark stomatal bands, 60–120 μm wide, are formed by one or two incomplete stomatal rows. Non-stomatiferous (costal) bands are formed by ordinary cells, they are usually of uneven width and can be 50–200 μm wide (depending on the specimen). The costal cells (in non-stomatiferous bands) are tetragonal, mostly oblong, 40–100 μm long and 16–30 μm wide. The cells of the dark (stomatiferous) bands are usually smaller.

The stomata in dark stomatiferous (intercostal) bands are unevenly spaced. They can be up to 150 μm apart but sometimes touch. The stomatal complex is formed by two guard cells and two lateral and two polar subsidiary cells. On better preserved cuticles, it is evident that only polar subsidiary cells are circular or oval, whereas lateral subsidiary cells tend to be more reniform. Specimens from the Pchery, Theodor mine show prominent proximal papillae growing from the lateral subsidiary cells towards the stoma (Pl. 4K, L). The stomatal density is 54–68 stomata per mm^2 and the stomatal index varies between 5 and 7.

Abaxial cuticle (Figs. 2e–h, Pls. 2D–F, 3E–G, 4A–F, 5, 7G–H): The stomata are arranged into stomatiferous and non-stomatiferous bands. Depending on specimens, their width is very variable, from 150 μm to 450 μm (Pl. 3E, F)

in the stomatiferous bands, and 100–350 μm in the non-stomatiferous bands. Because all the stomatiferous bands almost entirely comprise stomatal complexes, they markedly differ from the non-stomatiferous bands. In certain planes of focus, small flat papillae are visible on cells of the stomatiferous and non-stomatiferous bands (Pls. 2D–F, 3E, F). The stomatal rows are more or less regular within the stomatal band, but a lateral subsidiary cell is usually shared by two stomatal complexes, so the course of the stomatal rows is not as regular as in the species forming regular rows. The cells of the non-stomatiferous bands are tetragonal, oblong to trapezoidal, 45–95 μm long and 12–25 μm wide.

In the holotype, lateral and polar subsidiary cells are elongated and of the same dimensions (Pl. 2G, F). However, cuticles from another specimen (Pl. 3F, G) show that polar subsidiary cells can be very short, circular or oval, 15–30 μm long and 10–25 μm wide. Sometimes polar cells are elongate as lateral cells 30–60 μm long. The anticlinal walls of these cells are convex, so they differ from the cells of the non-stomatiferous band. A lateral subsidiary cell is usually shared by two stomatal complexes. The stomatal density is 400 to 600 stomata per mm^2 depending, on how wide the stomatiferous and non-stomatiferous bands are. This factor also influences the stomatal index (SI) with ranges from 12 to 23.

In the non-stomatiferous bands, circular, strongly cutinised structures occur on periclinal cell walls (Pls. 3E, F, 6I). Their function is not known.

Another cuticle assigned to this species (Fig. 2h, Pl. 7G, H) displays oval polar subsidiary cells, whereas the stomatal slit and the lateral subsidiary cells are not prominent. It is probably a more disorganized cuticle of *Cordaitea wartmannii* where even papillae are not preserved.

Remarks: *Cordaitea wartmannii* was compared with *Cordaitea* sp. of WARTMANN (1969) from the Bolssovian

Table 1: Comparison of *Cordaite* species from the Radnice Member of the Kladno-Rakovník Basin and *Cordaite bartheleii* from the Stephanian of the Krkonoše Piedmont Basin.

Reference	ŠIMŮNEK (2007) <i>Cordaite kladnoensis</i> Tuchlovice, Pchery	ŠIMŮNEK (2007) <i>Cordaite polynervus</i> Tuchlovice	ŠIMŮNEK (2007), this paper <i>Cordaite wartmannii</i> Libušín, Pchery	This paper <i>Cordaite theodorii</i> Pchery	ŠIMŮNEK (2014) <i>Cordaite bartheleii</i> Syřenov
Species					
Locality					
Leaf length (mm)	>230	>130	>150	?	>90
Leaf width (mm)	30–90	25	18–45	?	21–29
No. of true veins per 1 mm	10–22	10–12	10–6	?	25
No. of sclerotic strands between veins	(4–7)(2–3) dependence on position and side of the leaf	4–6	(1) 2–3	?	? (very fine)
Leaf margin	Smooth	Smooth	Smooth	Dentate	Smooth
Leaves	Amphistomatic	Amphistomatic	Amphistomatic	Hypostomatic	Amphistomatic
Adaxial cuticle	Cell shape of stomatal rows	Oblong (40–70) × (10–25)	Tetragonal to oval (25–50) × (10–30)	–	Oblong or elongated hexagonal (45–80) × (20–30)
	Size of stomatiferous cells (µm)	Square to oblong (30–60) × (10–20)	Rectangular – oblong (30–70) × (25–35)	Strongly papillate, longitudinally tetragonal (40–150) × (8–12)	Oblong or elongated hexagonal (45–80) × (20–30)
	Cell shape of non-stomatiferous bands	In dark bands 30–45	In dark bands 40–45	–	In stomatal rows 40
	Size of non-stomatiferous cells (µm)	3–3.5 (including non-stomatiferous band)	About 10 in dark band	–	–
	Stomatal density on 1 mm ²	–	–	–	–
	Stomatal index	–	–	–	–
	Size of 2 guard cells (µm)	–	–	–	–
	Size of stomatal complex (µm)	–	–	–	–
	Polar subsidiary cells – number	2–3	2	–	2
	Shape	Oval	Oblong to oval (35–52) × (25–30)	–	Polygonal (elongated) (15–45) × (10–18)
	Size in µm	10–15 in diameter	–	–	–
	Lateral subsidiary cells – number	2–3	2–4	–	2
Abaxial cuticle	Shape	Oblongate	Oblong to oval (25–60) × (25–30)	–	Polygonal (oblong to hexagonal) (38–55) × (10–25)
	Size v µm	11–15 in the diameter	–	–	–
	Differentiation of cells	Stomatiferous band (150–250 µm); non-stomatiferous band (150–250 µm)	Poorly preserved	Stomata in stomatal rows	Stomatiferous band (450–550 µm); non-stomatiferous band (100–150 µm)
	Cell shape of stomatiferous band	Oval to irregularly pentagonal	?	Tetragonal	Pentagonal to heptagonal (mostly hexagonal)
	Cell size of stomatiferous band (µm)	(25–50) × (12–25)	?	–	(30–70) × (10–18)
	Anticlinal walls	rounded	?	straight to bent	straight to bent
	Cell orientation of stomatiferous band	Random	?	Parallel to veins	Parallel to veins
	Cell shape of non-stomatiferous band	Longitudinally tetragonal	Rectangular – oblong (30–75) × (20–30)	Longitudinally tetragonal (35–130) × (8–20)	Oblong
	Cell size of non-stomatiferous band (µm)	(30–80) × (10–25)	–	–	(50–110) × (10–22)
	Stomata in the stomatiferous bands	In stomatiferous bands	In stomatiferous bands	In stomatal rows	In stomatiferous bands
	– Distribution	350–400 (in stomatiferous band) 13–15 (in stomatiferous band)	?	180–240	600 (775 in stomatiferous band) 20 (22 in stomatiferous band)
	Stomatal density on 1 mm ²	–	?	11–13	–
Outer stomatal cavity	Stomatal index	elliptical	?	elliptical	elliptical
	Guard cell pair shape	(20–30) × (10–15)	?	(25–30) × (8–14)	(16–25) × (8–14)
	Guard cell pair size (µm)	(50–65) × (40–50)	?	(60–75) × (32–42)	(55–70) × (32–40)
	Stomatal complex size (µm)	–	?	–	–
	Polar subsidiary cells – number	2	?	2	2
	Shape	Same as ordinary cells	?	Oblong	Trigonal, rhomboidal, oval.
	Size in µm	–	?	(30–45) × (8–12)	(20–30) × (10–20)
	Lateral subsidiary cells – number	2–3	?	2	2
	Shape	Same as ordinary cells	?	Oblong	Pentagonal to heptagonal (mostly hexagonal)
	Size in µm	–	?	(30–60) × (10–25)	(30–70) × (10–18)
	Outer stomatal cavity	Strongly cutinized above sunken guard cells	Stronger cutinization or presence of proximal papillae from lateral subsidiary cells	Strongly cutinised papillae towards the stoma	Stronger cutinization or presence of proximal papillae from lateral subsidiary cells

* Original description (ŠIMŮNEK, 2007), here assigned to *Cordaite kladnoensis*

of the Saar region (Germany) by ŠIMŮNEK (2007) based on the presence of papillae in both species. However, *Cordaite* sp. of WARTMANN (1969) has much larger and more prominent papillae than *Cordaite wartmannii* ŠIMŮNEK. In this feature, *Cordaite* sp. of WARTMANN (1969) bears more resemblance to *Cordaite theodorii* ŠIMŮNEK & HALDOVSKÝ sp. nov., which also has many strongly cutinised papillae. Because papillae occur in several species, to date it has been difficult to decide to which species WARTMANN's *Cordaite* sp. belongs.

The most similar species to *Cordaite wartmannii* ŠIMŮNEK is *Cordaite barthelii* ŠIMŮNEK, 2014 from the Stephanian B of the Krkonoše Piedmont Basin. The abaxial cuticles in particular of both species are very similar. Stomata of both species form wide stomatiferous bands, up to 550 µm wide, and are arranged in a stomatal row. *Cordaite barthelii* has polar subsidiary cells common to two stomatal complexes, whereas *Cordaite wartmannii* has polar and usually also lateral cells common to two stomatal complexes. *Cordaite wartmannii* differs from *Cordaite barthelii* by the presence of small papillae, visible in certain planes of focus on the light microscope. Small "holes" in the centre of certain cells of the non-stomatiferous bands occur in both *Cordaite barthelii* and *C. wartmannii*. The function of these holes is unknown. It is possible that these holes were the result of distortion of the cuticle but, as they also occur in *Cordaite wartmannii*, it is evident that they are not an artificial feature and the cracks may be related to differential cutinisation of certain cells and their subsequent torsion. The similarities provide further evidence that *Cordaite barthelii* and *Cordaite wartmannii* are related species.

The adaxial cuticle of *Cordaite barthelii* and *Cordaite wartmannii* have stomata in rare stomatiferous bands. The stomatiferous bands of *Cordaite barthelii* are not as dark coloured as in *Cordaite wartmannii*. Also, the shape of the subsidiary cells of both species differs. Polar subsidiary cells of *Cordaite wartmannii* are circular to oval, whereas those of *Cordaite barthelii* are elongated and usually oblong; lateral subsidiary cells of *Cordaite wartmannii* are broad reniform, whereas those of *Cordaite barthelii* are narrow and oblong. Furthermore, the venation density of both species differs. *Cordaite wartmannii* has 10–16 veins per 1 cm of the leaf, whereas *Cordaite barthelii* has about 25 veins per 1 cm of the leaf.

Cordaite kladnoensis ŠIMŮNEK (2007) is another species similar to *Cordaite wartmannii*. Both have stomata of the adaxial cuticle arranged in dark stomatiferous bands. In the case of *Cordaite kladnoensis*, the distances between stomatiferous bands are more regular than in *Cordaite wartmannii*. Both species have similar vein densities: *Cordaite kladnoensis* has 10–22 veins per 1 cm, and *Cordaite wartmannii* has 10–16 veins per 1 cm of the leaf. However, the abaxial cuticles of these species are quite different. Guard cells of *Cordaite kladnoensis* are sunken and covered by a strongly cutinised crypt. Subsidiary cells are oval with strongly cutinised corners; in contrast, *Cordaite wartmannii* does not have such a crypt, but has at most two proximal papillae from the lateral subsidiary cells. The subsidiary cells

are narrower and longer than in *Cordaite kladnoensis*, and only the polar subsidiary cells can be rounded in *Cordaite wartmannii*.

4.2. *Cordaite theodorii* ŠIMŮNEK & HALDOVSKÝ sp. nov.

(Fig. 2i, Pls. 6. and 7A–F)

Derivation of name: After the Theodor mine, which is the type locality of this species.

Holotype: designated here on Pl. 1E, is stored in the Czech Geological Survey under the no. ZŠ 350, slides no. 518/1–13

Type locality: Pchery, Theodor mine, Kladno-Rakovník Basin, Czech Republic.

Type horizon: Tuffaceous parting (opuka) of the Upper Radnice coal seam, Radnice group of coals, Radnice Member, Kladno Formation, Bolsovian, Middle Pennsylvanian.

Material: Only one sample (holotype).

Diagnosis: Very small and rare teeth on the leaf border, hypostomatic leaves, strongly papillate cells on abaxial and adaxial epidermis. Adaxial epidermis: parallel oriented, elongate tetragonal cells. Abaxial epidermis: elongated cells, stomata in rows.

Description: Much of the macromorphology and venation of the leaves is uncertain, because cuticles of *Cordaite wartmannii* were also obtained from the same sample, and because the adpressions on Pl. 1E, F, G resemble other *Cordaite wartmannii* leaves. We know for certain that the leaf margin was dentate. The distances between the teeth were 0.3–0.5 mm (Pl. 6A), and teeth were acroscopically oriented and 30–40 µm long (Pl. 6B).

We can speculate, however, that the leaf surface had little relief, because the cuticular structure is uniformly flat.

Adaxial cuticle (Pl. 6C–F): It is not possible to differentiate costal and intercostal bands. The cells are tetragonal, elongated, very narrow and oriented parallel to veins. They are 40–150 µm long and 8–12 µm wide. Each cell bears many small, strongly cutinised papillae, 3–5 µm in diameter and visible as black spots.

Abaxial cuticle (Figs. 2i, Pl. 7A–F): The cells of the abaxial cuticle resemble the cells of the adaxial cuticle. They are strongly papillate, with an elongated tetragonal shape, 35–130 µm long and 8–20 µm wide (Pl. 7E). Stomata are arranged into stomatal rows. Polar and lateral subsidiary cells are oblong, similar to normal epidermal cells. A row of papillae runs from one end to another in the middle of the cell. In addition, proximal papillae point into the stoma centre, above the sunken guard cells. The stomatal complex (including 4 subsidiary cells) is 60–75 µm long and 32–42 µm wide.

Stomatal density and stomatal index were calculated from 3 measurements. Stomatal density varies from 180 to 240 stomata per mm²; stomatal index varies from 11.1 to 12.9. Some inaccuracy could have been caused by the small area used for these calculations.

Remarks: This species is strongly papillate and differs from all other known species of *Cordaite* in being hypostomatic and in having a dentate margin. It is also a distinct species based on the cuticular micromorphology.

4.3. *Cordaites kladnoensis* ŠIMŮNEK emend nov.

(Figs. 2c, d, j; Pl. 8A–I; Pl. 8J–L; Pl. 9)

2007 *Cordaites kladnoensis* ŠIMŮNEK, p. 143–144, text-figs. 36a–i, pl. 3, fig. 14, pl. 38, figs. 2–6, pls. 39, 40, figs. 1–3.

2007 *Cordaites polynervus* ŠIMŮNEK, p. 148–149, text-figs. 39a–f, pl. 43, figs. 3–7, pl. 44, figs. 1–3

Emended diagnosis (ŠIMŮNEK, 2007, p. 143): Amphistomatic, large leaves with sparse venation, 2–7 thin sclerenchymatous bands alternate with each thick vein. Cells of adaxial cuticle oblong, stomata in infrequent stomatal rows, subsidiary cells circular to oval. Proximal papillae on lateral subsidiary cells. Cells of abaxial cuticle oval or irregularly pentagonal, stomata in stomatiferous bands without discernible stomatal rows.

Material: Tuchlovice, Nosek mine, Pchery, Theodor mine, Kladno-Rakovník Basin. Czech Geological Survey, Prague, inv. No. ZŠ 247, coll. Z. ŠIMŮNEK. Radnice Member, Bolsovian.

Description: Here we redescribe the specimen selected as a holotype of *Cordaites polynervus* and the specimen from Pchery, Theodor mine.

The holotype from Tuchlovice is a leaf fragment 25 mm wide and about 130 mm long with nearly parallel margins. The leaf surface relief is flat. There are 10–12 veins per 1 cm of the leaf surface. On the impression (Pl. 8I, right), positive and negative relief of vascular and sclerotic bundles are visible. Usually one to two sclerotic bundles alternate with one true vein. On the phytolite (thin carbon layer on a plant compression) (Pl. 8I, left), 4–6 very fine strips occur between two veins, probably representing stomatiferous bands (or non-stomatiferous bands?). A similar pattern is found on the specimen from Pchery (Pl. 1H, Inv. No. ZŠ 358a). The leaf fragment is 160 mm long and 23 mm wide with non-parallel margins, but, as the leaf margins are revolute, the true leaf width was probably 33 mm. 4–6 very fine sclerotic bundles alternate with each true vein (Pl. 1I), and the same pattern is seen on the imprint (Pl. 1J, right). The imprint itself (Pl. 1J, left) shows more prominent true veins separated by one or two sclerotic strips. The leaves are amphistomatic.

Adaxial cuticle of the Tuchlovice specimen (Figs. 2c, Pl. 8A–D): The dark stomatiferous (intercostal) bands are 80–140 μm wide, whereas non-stomatiferous (costal) bands are 120–200 μm wide. The ordinary cells are tetragonal to oval, 25–50 μm long and 10–30 μm wide. The costal cells are larger than the intercostal cells; they are rectangular, usually oblong, 30–70 μm long and 25–35 μm wide. The stomatal complexes are in irregular distances from each other within dark stomatiferous bands that are formed by single or double stomatal rows oriented parallel to the veins. Sunken guard cells are usually surrounded by 4 subsidiary cells that slightly differ from the ordinary epidermal cells of the dark bands – polar cells are square to oblong; lateral cells are oblong to reniform. The stomatal complexes (including subsidiary cells) are 90–125 μm long and 60–75 μm wide. The stomatal density is about 40–45

stomata per 1 mm^2 on the leaf blade. The stomatal index is 4.2 and for the dark bands about 10.

Adaxial cuticle of the Theodor Mine specimen (Figs. 2d, Pls. 8J–L, 9): The cells are differentiated into dark stomatiferous bands and non-stomatiferous bands (Pls. 8J–L, 9). The stomata are relatively sparse in the dark bands. The cells are usually of oblong shape. The cells of the non-stomatiferous bands are longer, 30–70 μm long and 12–18 μm wide, whereas those of the dark stomatiferous bands are only 25–35 μm long and 15–20 μm wide. The stomata are relatively rare and are dispersed within the dark bands. The stomatal complexes are formed by 6 cells: two guard cells, two lateral and two polar subsidiary cells. Lateral subsidiary cells are usually oblong or reniform and polar subsidiary cells are oblong to oval. Guard cells are sunken and partly covered by proximal papillae growing from lateral subsidiary cells (Figs. 2d, Pl. 9C). The stomatal density is 45 stomata per mm^2 (95 in the stomatal band) and the stomatal index is 3.2 (6 in the stomatal band).

Abaxial cuticle of the Tuchlovice specimen (Fig. 2j, Pl. 8E–H): ŠIMŮNEK (2007, p. 149) considered a poorly preserved cuticle as an abaxial one and described it as *Cordaites polynervus* (ŠIMŮNEK, 2007, pl. 43, figs. 3–6 and pl. 44 figs. 1–2). In slide 182/1, the holotype of *Cordaites polynervus*, a cuticular fragment of known abaxial cuticle has been discovered that proves the identity of *Cordaites polynervus* as *Cordaites kladnoensis*, thus allowing these synonymy of these two species to be recognised.

The cells are differentiated into stomatiferous (intercostal) and non-stomatiferous (costal) bands, both of which vary in width between 150–200 μm (Pl. 8F). The cells of the stomatiferous bands are oval to irregularly pentagonal, 25–50 μm long and 12–25 μm wide. The anticlinal walls are rounded. The costal (non-stomatiferous) cells are elongated and tetragonal, 30–80 μm long and 10–25 μm wide. The stomata are not prominent and they occur in stomatiferous bands with poorly defined stomatal rows. The sunken guard cells are dark, convex and oblong (Figs. 2j, Pl. 8E, H). The corners and anticlinal walls of cells are strongly cutinised, so it is sometimes difficult to distinguish cutinisation from stomata. The stomatal complexes (including subsidiary cells) are 50–65 μm long and 40–50 μm wide. The subsidiary cells, 4–5 per stoma, are of the same shape as the ordinary epidermal cells, usually oblong to oval with convex anticlinal walls. The stomatal density is about 280 stomata per mm^2 , and about 570 stomata per mm^2 in the stomatiferous band, which, is more than for *Cordaites kladnoensis* as described by ŠIMŮNEK (2007). Stomatal index is 15 for the whole leaf surface and 17 for the stomatiferous band.

The abaxial cuticle of this species from the Theodor Mine was not preserved.

Remarks: Comparison of *Cordaites kladnoensis* with *Cordaites wartmannii* was mentioned in the description of the latter species. The abaxial cuticle of two other species is similar to *Cordaites kladnoensis*. Adaxial and abaxial cuticles of *Cordaites principalis* (GERMAR) GEINITZ morphotype 5 of ZODROW et al. (2000) are very similar to the abaxial cuticle of *Cordaites kladnoensis*. The cell corners

are strongly cutinised in the stomatiferous band and a strongly cutinised crypt is present above the guard cells in *Cordaites kladnoensis* abaxial cuticle.

Essentially, the same pattern as in *Cordaites kladnoensis* occurs in *Cordaites radcicensis* ŠIMŮNEK (2008), which also has sunken stomata on the abaxial cuticle that are covered by a strongly cutinised crypt. The cell corners are strongly cutinised with projections that fill the intercellular space. The adaxial cuticles of *Cordaites radcicensis* and *Cordaites kladnoensis* both have stomata in dark stomatiferous bands. *Cordaites radcicensis* has a lower stomatal density (only 8–11 stomata per 1 mm²) than *Cordaites kladnoensis*, which has 30–45 stomata per 1 mm² in the adaxial cuticle. *Cordaites principalis* (GERMAR) GEINITZ morphotype 5 of ZODROW et al. (2000) occurs in the Bolsovian of the Maritimes Basin, Canada, whereas *Cordaites radcicensis* occurs in the Asturian of the Plzeň Basin, Czech Republic.

5. DISCUSSION

The flora of the Radnice Member in the studied localities includes about 90 species that represent 50 to 60 “natural” species of lycopsids, sphenopsids, ferns, progymnosperms, pteridosperms and cordaitaleans that are represented mostly by trees, bushes, lianas and creeping forms. The diversity of flora indicates a wet tropical forest. Practically all cordaitalean remains come from tuffaceous partings (“Opuky”) of the Upper Radnice coal seam, and in particular from the Velká Opuka (Fig. 1).

The topography of the coal-bearing strata was formed by wide valleys up to 2 km wide and up to 10 km long (OPLUŠTIL, 2005a,b). The altitude is estimated to be 900–1200 m (OPLUŠTIL, 2005b). Plant assemblages of the tuffaceous partings (“Opuky”) comprise both peat-forming plants that were buried in place (OPLUŠTIL et al., 2007), and partly also non-peat-forming plants that were transported to the place of deposition from non-peat accumulating areas and also from valley slopes. The marginal parts of these coal deposits are enriched by non-peat-forming flora (progymnosperms, some cordaitaleans and pteridosperms). These elements disappear towards the valley centre. Cordaitaleans were very common in the Tuchlovice, Nosek mine locality. As they were commonly found together with a primitive lycopsid *Omphalophloios feistmantelii* (FEISTMANTEL) BEK et al. (2015), it is supposed that these cordaitaleans belonged to peat-forming plants. *Omphalophloios feistmantelii* (FEITMANTEL) BEK et al. is a major producer of *Densosporites* and it grew in the “densospore phase”, which probably represents wet conditions in the peat swamp, when domed peat suffered nutrient deficiency and only well adapted plants could grow there (DiMichele, pers. com.). Cordaitalean remains were locally common, up to 10 to 20 % of the assemblage in the Velká Opuka parting in both the Tuchlovice and Theodor mines. This is in concordance with the observation of RAYMOND et al. (2010), where they found a coal plant assemblage comprising 29–81 % cordaitaleans in lowland and coastal peat-swamp settings in Iowa, USA. A similar situation occurs in Kentucky and Tennessee, where cordaitaleans form 33–40 % of a plant assem-

blage of the same or slightly younger age – middle to upper Bolsovian. American cordaitalean-dominated assemblages are accompanied by a primitive lycopsid *Chaloneria* PIGG & ROTHWELL (RAYMOND et al., 2010), whereas it seems that *Omphalophloios* WHITE prevails with cordaitaleans in the Czech assemblages.

The Libušín, Schoeller mine locality is an exception. Cordaitaleans, represented by only one species, *Cordaites wartmannii*, were very rare here; extrabasinal and other “exotic” elements are also rare or absent. The cuticles of *Cordaites wartmannii* were newly discovered (not published) in the dispersed cuticular spectrum from coal from the Wanieck coal mine, Srby locality (near Tuchlovice). The study of dispersed cordaitalean cuticles from the coal (ŠIMŮNEK & FLORJAN, 2013) revealed that cuticles bear considerably more papillae than do cuticles prepared from compression/impression specimens. Papillae have been described on cordaitalean cuticles by many authors: *Cordaites* sp Types 2 and 3 (BARTHEL, 1962), *Cordaites* sp. Types 6 and 7 from the Permian Schweinsdorf coal seam in the Döhlen Basin, Germany (BARTHEL, 1964); *Cordaites* sp. from the Bolsovian of the Saar Region of Germany (WARTMANN, 1969); and *Cordaites neimengensis* from the Lower Permian of Inner Mongolia, China (LIU et al., 1998). This could be further evidence that papillate *Cordaites wartmannii* is a peat-forming plant. The reasonable interpretation of the presence of the papillae on plants growing in tropical rain forest was given by CLEAL AND SHUTE (2012). They argue that papillae in medullosan pteridosperms could protect the stomata from water ingress into the stomatal pore. The papillae in the cordaitaleans could have a similar function. *Cordaites theodorii* from the Pchery locality is also supposed to be a peat-forming plant because its cuticles are strongly papillate and it was found on the same specimen together with the previously mentioned *Cordaites wartmannii*. Seven of the nine abaxial cuticular species of the genus *Cordaia* *abaxicutis* ŠIMŮNEK & FLORJAN, 2013 were papillate. These species came from different strata and localities of the Upper Silesia Basin (Poland). In contrast, only a few of the c. 30 species from the Bohemian Massif that were prepared from compressions bear papillae on the abaxial cuticle (ŠIMŮNEK, 2007). The evidence thus suggests that cordaitaleans living in saturated peat substrates tended to have more papillate epidermal surfaces. However, the function of these papillae remains unknown (ŠIMŮNEK & FLORJAN, 2013).

A different situation occurs in *Cordaites kladnoensis*. It is not papillate and resembles *Cordaites radcicensis*, which comes from mudstones of the Cantabrian Plzeň Basin, Czech Republic, where coal was not developed. If we suppose a similar habitat, it maybe grew in the marginal parts of the swamp.

We can deduce the original habitat of cordaitaleans from the facies in which they are preserved. BASHFORTH et al. (2014) described a flora from different rocks of a mega fan structure of Langsettian age in New Brunswick, Canada. The predominance of cordaitalean, mostly in coarse deposits, suggested to these authors that these plants lived in better-drained substrates and also on river banks. The rooting system of these huge trees enabled them to live in “dry” soils, where the wa-

ter table was low. Alternatively, smaller cordaitalean forms were able to grow directly in the peat swamps (COSTANZA, 1985). Wetland and dryland floras with cordaitaleans were discussed by DIMICHELE (2014) using as an example the Pennsylvanian floras from North America.

The study of dispersed cuticles from the central Bohemian region is in its infancy, so it is not possible to produce a list of peat-forming cordaitaleans from this region. The clear evidence for the Radnice Member is that *Cordaite borassifolius* (STERNBERG) UNGER (ŠIMŮNEK et al., 2009) and possibly also *C. wartmannii* ŠIMŮNEK and *C. theodorii* ŠIMŮNEK & HALDOVSKÝ sp. nov. lived in coal swamps. DIMICHELE & PHILLIPS (1994) demonstrated the greatest abundance of cordaitaleans in the Duckmantian, Bolsovian and early Asturian peat swamps in America. In comparison with the Bohemian Massif, the greatest diversity of cordaitaleans occurs in the lower Bolsovian Radnice Member (ŠIMŮNEK, 2007), however, these cuticles were isolated from specimens from roof shales or clastic and tuffitic partings, and therefore mostly from species that predominantly lived in clastic-swamp wetlands, but not directly in the peat swamps (GASTALDO et al., 1995). The relatively high diversity of cordaitaleans in the Bohemian Massif is also seen in the middle Asturian Nýřany Member in Central Bohemia, (the zircon dating revealed an older age for these strata that was previously supposed; Opluštil, pers. com.). The Asturian records fit with the observations by DIMICHELE & PHILLIPS (1994) based on peat substrate floras. A relatively rich and diversified cordaitalean assemblage is known from roof-shales (clastic deposits) from the upper Asturian of Bohemia (ŠIMŮNEK, 2007). This provides further evidence that the peat substrate wetland flora might differ from the clastic substrate flora.

6. CONCLUSION

A new species *Cordaite theodorii* ŠIMŮNEK & HALDOVSKÝ sp. nov. from the Bolsovian of the Kladno-Rakovník Basin is erected. This species is remarkable in having dentate leaf margins, not known from other cordaitaleans; both of its cuticles are strongly papillate.

Great variability has been observed on additional cuticles of *Cordaite wartmannii* ŠIMŮNEK from the Libušín and Pchery localities. In contrast to the holotype, new samples of *Cordaite wartmannii* have much wider stomatiferous bands on the abaxial cuticle (up to 450 µm) and thus they resemble the Stephanian *Cordaite barthelii* ŠIMŮNEK. They also have smaller polar subsidiary cells than the holotype.

Cordaite polynervus ŠIMŮNEK has been shown to be conspecific with *Cordaite kladnoensis* ŠIMŮNEK, based on the similarity of their abaxial cuticles. The species *Cordaite kladnoensis* (abaxial cuticle) resembles *Cordaite principalis* morphotype 5 of ZODROW et al. (2000) from Canada and *Cordaite radcicensis* ŠIMŮNEK from the Asturian of the Plzeň Basin. The latter was found in mudstone, thus the habitat of *Cordaite kladnoensis* is considered to be non-peat-forming.

Cuticles of peat-forming cordaitaleans are often strongly papillate, and *Cordaite wartmannii* and *Cordaite theodorii* have such characteristics.

ACKNOWLEDGEMENT

This research was conducted by the support of the Grant Agency of the Czech Republic, grant no. P210/10/0232. The authors thank to Dr. C. J. CLEAL (Cardiff, UK) for checking the English in the text, two anonymous reviewers of *Geobios* and an anonymous reviewer of *Geologia Croatica* and Dr. W. A. DIMICHELE (Washington D.C., USA) for their comments that improved the manuscript.

REFERENCES

- BARTHEL, M. (1962): Mikropaläobotanische Untersuchungen im Rotliegenden des Döhlener Beckens. Teil I.– Jahrbuch des Staatlichen Museums für Mineralogie und Geologie zu Dresden. 1962, 157–175.
- BARTHEL, M. (1964): Coniferen und Cordaiten-Reste aus dem Rotliegenden des Döhlener Beckens.– *Geologie*, 13, 1, 60–89.
- BASHFORTH A.R., CLEAL, C.J., GIBLING, M.R., FALCON-LANG, H.J. & MILLER, R.F. (2014): Paleoeecology of Early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada).– *Review of Palaeobotany and Palynology*, 200, 229–263.
- BEK, J., OPLUŠTIL, S., DRÁBKOVÁ, J. & PŠENIČKA, J. (2015): The sub-arborescent lycopod *Omphalophloios feistmantelii* (O. FEISTMANTEL) comb. nov. emend. from the Middle Pennsylvanian of the Czech Republic.– *Bulletin of Geosciences*, 90/2.
- CLEAL, C.J. & SHUTE, C.H. (2012): The systematic and palaeoecological value of foliage anatomy in Late Palaeozoic medullosalean seed-plants.– *Journal of Systematic Palaeontology*, 10/4, 1–36. DOI: 10.1080/14772019.2011.634442.
- Cleal, C.J. & Thomas, B.A. (1995): *Palaeozoic Palaeobotany of Great Britain*.– Chapman & Hall. London, 295 p.
- COSTANZA, S.H. (1985): *Pennsylvanioxylon* of Middle and Upper Pennsylvanian coals from the Illinois Basin and its comparison with *Mesoxylon*.– *Palaeontographica*, Abt. B, 197, 81–121.
- DIJKSTRA, S.J. & van AMEROM, H.W.J. (1998): *Fossilium Catalogus II: Plantae*. Pars 99 – Backhuys Publishers, Leiden, 1–195.
- DIMICHELE, W.A. (2014): Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics.– *International Journal of Plant Sciences*, 175/2, Special Issue, 123–164.
- DIMICHELE, W.A. & PHILLIPS, T.L. (1994): Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica.– *Palaeogeography, Palaeoclimatology, Palaeoecology*, 106, 39–90.
- DIMICHELE, W.A., CECIL, C.B., MONTAÑEZ, I.P. & FALCON-LANG, H.J. (2010): Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea.– *International Journal of Coal Geology*, 83/2–3, 329–344.
- FALCON-LANG, H.J. (2003a): Late Carboniferous tropical dryland vegetation in an alluvial plain setting, Joggins, Nova Scotia, Canada.– *Palaios*, 18/3, 197–211.
- FALCON-LANG, H.J. (2003b): Anatomically preserved cordaitalean trees from a dryland alluvial plain setting, Joggins, Nova Scotia.– *Atl. Geol.*, 39/3, 259–265.
- FALCON-LANG, H.J. & BASHFORTH, A.R. (2004): Pennsylvanian uplands were forested by giant cordaitalean trees.– *Geology*, 32/5, 417–420.

- FALCON-LANG, H.J., BENTON, M.J., BRADDY, S.J. & DAVIES, S.J. (2006): The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada.— *Journal of the Geological Society of London*, 163, 561–576.
- FALCON-LANG, H.J., JUD, N.A., NELSON, W.J., DIMICHELE, W.A., CHANEY, D.S. & LUCAS, S.G. (2011): Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biomes.— *Geology*, 39/4, 371–374.
- FEISTMANTEL, O. (1876): Die Versteinerungen der Böhmschen Kohlenablagerungen. III. Abteilung.— *Palaeontographica*, 23, 223–316.
- FLORIN, R. (1931): Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales.— *Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien*, 10/1, 1–588.
- GASTALDO, R.A., PFEFFERKORN, H.W. & DIMICHELE, W.A. (1995): Taphonomic and sedimentologic characterization of roof-shale floras.— In: LYONS, P.C. & MOREY, E.D., WAGNER R.H. (eds.): *Historical perspective of early twentieth century Carboniferous papeobotany in North America* (W.C. Darrah volume), Boulder, Colorado.— *Geological Society of America Memoir*, 185, 341–352.
- JONGMANS, W.J. & DIJKSTRA, S.J. (1968): *Fossilium Catalogus*, II: Plantae – Pars 70. Cordaitales 1, 1–112.
- KERP, H. (1990): The Study of fossil gymnosperms by means of cuticular analysis.— *Palaiois*, 5, 548–549.
- KERP, H. & KRINGS, M. (1999): Light microscopy of fossil cuticles.— In: JONES, T.P. & ROWE, N.P. (eds.): *Fossil plants and spores. Modern techniques*. Geological Society, London, 52–56.
- KRINGS, M. (2000): The use of biological stains in the analysis of the late Palaeozoic pteridosperm cuticles.— *Review of Palaeobotany and Palynology*, 108, 143–150.
- KRINGS, M. & KERP, H. (1997): An improved method for obtaining large pteridosperm cuticles.— *Review of Palaeobotany and Palynology*, 96, 453–456.
- LIU, Z.-H., GENG, B.-Y., WANG, S.-J. & LI, C.-S. (1998): On *Cordaitea neimengensis* sp. nov from Lower Permian of Zhungeerqi, Inner Mongolia, China.— *Acta Botanica Sinica*, 40, 4, 383–388.
- MEYEN, S.V. (1984): Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record.— *The Botanical Review*, 50, 1, 1–112.
- NĚMEJC, F. (1932): Stratigraphické výzkumy, konané s hlediska paleobotanického v uhelných revírech jižní části plzeňské kamenouhelné pánve v letech 1928–1932.— *Hornický věstník*, 14/33, 241–245, 268–273, 295–300, 320–333, 345–350.
- NĚMEJC, F. (1936): Studies on the Alethopterids of the Permocarboiferous of Central Bohemia (with remarks on forms collected in other Bohemian coal districts).— *Vestník Královské České Společnosti Nauk, Tř. II*, 1–18.
- NĚMEJC, F. (1940): The Pecopterides of the coal districts of Bohemia.— *Sborník Národního Muzea (Praha), ř. B*, 1, 1–28.
- NĚMEJC, F. (1947): The Lepidodendraceae of the coal districts of Central Bohemia (A preliminary study).— *Sborník Národního Muzea (Praha), ř. B*, 3 (2), 1–28.
- OPLUŠTIL, S. (2005a): Evolution of the Middle Westphalian river valley drainage system in central Bohemia (Czech Republic) and its palaeogeographic implication.— *Palaeogeography, Palaeoclimatology, Palaeoecology*, 222, 223–258.
- OPLUŠTIL, S. (2005b): The effect of paleontology, tectonics and sediment supply on quality of coal seams in continental basins of central and western Bohemia (Westphalian), Czech Republic.— *International Journal of Coal Geology*, 64, 173–203. doi:10.1016/j.coal.2005.03.022
- OPLUŠTIL, S., PŠENÍČKA, J., LIBERTÍN, M. & ŠIMŮNEK, Z. (2007): Vegetation patterns of Westphalian and Lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic.— *Review of Palaeobotany and Palynology*, 143, 107–154. DOI 10.1016/j.revpalbo.2006.06.004
- OPLUŠTIL, S., PŠENÍČKA, J., BEK, J., WANG, J., FENG, Z., LIBERTÍN, M., ŠIMŮNEK, Z., BUREŠ, J. & DRÁBKOVÁ J. (2014): T⁰ peat-forming plant assemblage preserved in growth position by volcanic ash-fall: A case study from the Middle Pennsylvanian of the Czech Republic.— *Bulletin of Geosciences*, 89/4, 773–818. DOI 10.3140/bull.geosci.1499
- PEŠEK, J. (1994): Carboniferous of Central and Western Bohemia (Czech Republic).— *Czech Geological Survey, Prague*. 61 p.
- POOLE, I. & KÜRSCHNER, W.M. (1999): Stomatal density and index: the practice.— In: JONES, T.P. & ROWE, N.P. (eds.) *Fossil plants and spores. Modern techniques*. Geological Society, London, 257–260.
- RAYMOND, A., LAMBERT, L., COSTANZA, S., SLONE, E.J. & CUTLIP, P.C. (2010): Cordaites in paleotropical wetlands: an ecological re-evaluation.— *International Journal of Coal Geology*, 83/2–3, 248–265.
- ROTHWELL, G.W. (1988): Cordaites.— In: BECK, C.B. (ed.): *Origin and Evolution of Gymnosperms*. Columbia University Press, New York, 273–297.
- SALISBURY, E.J. (1927): On the causes and ecological significance of stomatal frequency with special reference to the woodland flora.— *Philosophical Transactions of the Royal Society (London) B*, 216, 1–65.
- ŠIMŮNEK, Z. (2007): New classification of the genus *Cordaitea* from the Carboniferous and Permian of the Bohemian Massif, based on cuticle micromorphology.— *Acta Musei nationalis. Pragae, Series B., Historia Naturalis*, 62/3–4, 97–210.
- ŠIMŮNEK, Z. (2008): The Asturian and Cantabrian floral assemblages with *Cordaitea* from the Plzeň Basin (Czech Republic).— *Studia Geologica Polonica*, 129, 51–80.
- ŠIMŮNEK, Z. (2014): First cuticles of *Cordaitea* Unger from the Stephanian B of the Krkonoše Piedmont Basin (Czech Republic).— *Palaeontographica Abt. B*, 290/4–6, 127–139.
- ŠIMŮNEK, Z. & FLORJAN, S. (2013): The Pennsylvanian cordaitalean dispersed cuticles from the Upper Silesian Basin (Poland).— *Review of Palaeobotany and Palynology*, 197, 26–49.
- ŠIMŮNEK, Z., OPLUŠTIL, S. & DRÁBKOVÁ, J. (2009): *Cordaitea borassifolius* (Sternberg) Unger (Cordaitales) from the Radnice Basin (Bolshevik, Czech Republic).— *Bulletin of Geosciences*, 84/2, 301–336.
- UNGER, F. (1850): *Genera et Species Plantarum Fossilium*.— *Wilhelmum Braumüller, Vienna*, 627 p.
- WAGNER, R.H. (1984): Megafloral zones of the Carboniferous.— *Compte rendu 9e Congrès International de Stratigraphie et de Géologie du Carbonifère* (Washington, 1979), 2, 109–134.
- WARTMANN, R. (1969): Studie über die papillen-förmigen Verdickungen auf der Kutikule bei *Cordaitea* an Material aus dem Westphal C des Saar-Karbons.— *Argumenta Palaeobotanica*, 3, 199–207.
- WEITHOFER, K.A. (1902): Geologische skizze des Kladno-Rakonitzer Kohlenbeckens.— *Verhandlungen K. K. Geologischen Reichsanstalt*, 399–420.
- ZAJÍC, J. (2012): Otázka stáří nejvyšší části línského souvrství (mšensko-roudnická pánev, Český masív) – nové indicie z vrhu Be-1 Bechlín [Contribution to the question of age of the uppermost part of the Líně Formation (Mšeno-Roudnice Basin, Bohemian Massif)].— *Zprávy o geologických výzkumech v roce 2011*, 59–62.
- ZODROW, E.L., ŠIMŮNEK, Z. & BASHFORTH, A.R. (2000): New cuticular morphotypes of „*Cordaitea principalis* (GERMAR) GEINITZ“ from the Canadian Carboniferous Maritimes Basin.— *Canadian Journal of Botany*, 78/2, 135–148.

Manuscript received January 19, 2015

Revised manuscript accepted May 29, 2015

Available online June 19, 2015

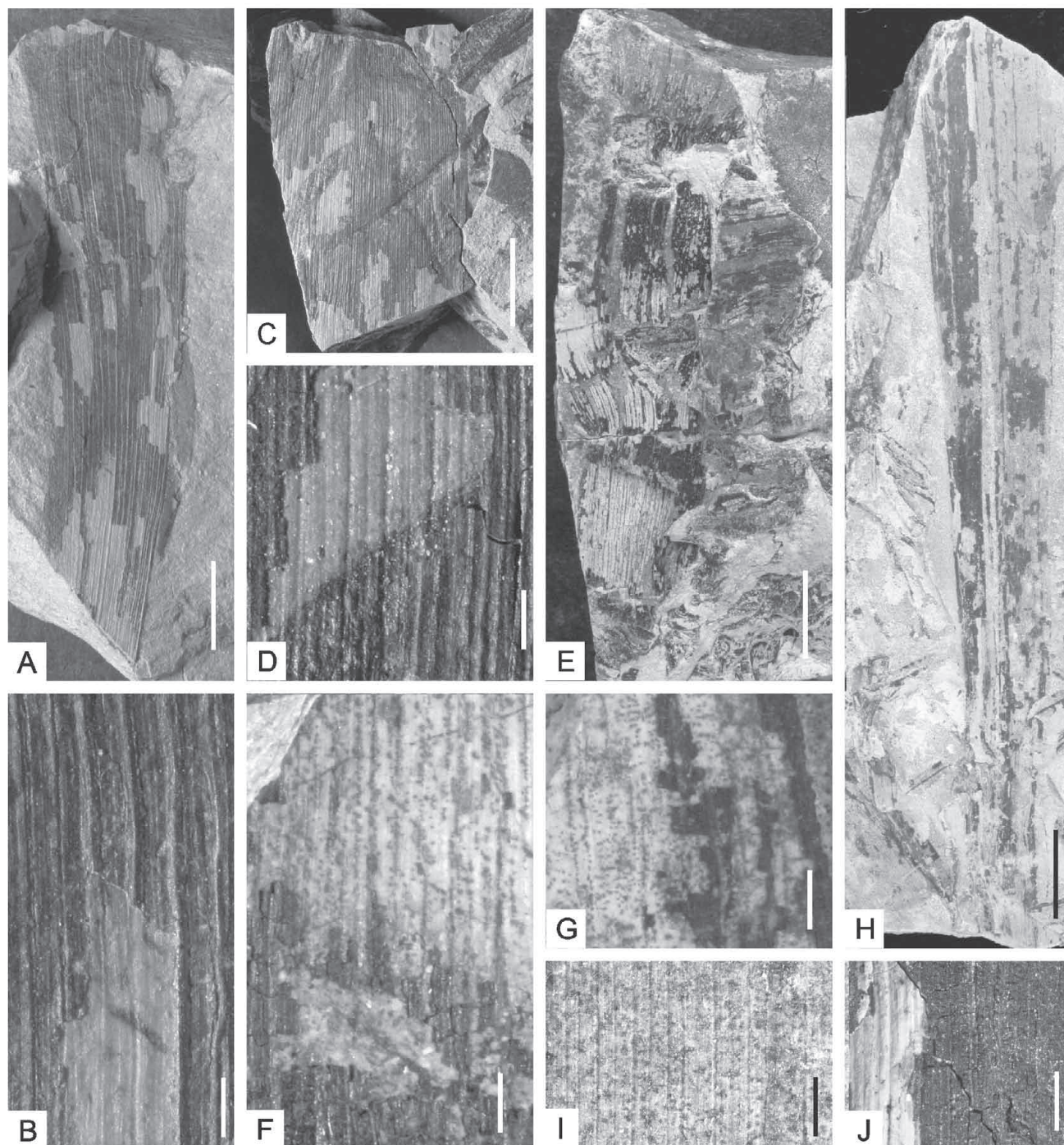


PLATE 1

- A–D** *Cordaite wartmannii* ŠIMŮNEK, Libušín, Schoeller mine, Kladno-Rakovník Basin, Radnice Member, Bolsovian (Coll. CGS, ZŠ 246). **A** – A leaf with venation (holotype), material of slides 113/1–2. Scale bar = 1 cm; **B** – Detail of the venation from Fig. A, Veins visible as doubled and alternating with sclerenchymatous strands. Scale bar = 1 mm; **C** – A wide leaf fragment from which slides 395/1–8 have been prepared (Coll. CGS, ZŠ 303). Scale bar = 1 cm; **D** – Detail of the venation from Fig C. It has the same pattern as Fig. B;
- E–G** Fragments of leaves of *Cordaite wartmannii* ŠIMŮNEK, and *Cordaite theodorii* ŠIMŮNEK et HALDOVSKÝ sp. nov. (holotype), Pchery, Theodor mine, Kladno-Rakovník Basin, Radnice Member, Bolsovian (Coll. CGS, ZŠ 350). Scale bar = 1 cm; **F** and **H** – Details of venation; **F** – from the large left leaf; **G** – from the small right leaf from the Fig. E. Both venations exhibit “doubled” veins and probably belong to *Cordaite wartmannii*. Scale bar = 1 mm;
- H–J** *Cordaite kladnoensis* ŠIMŮNEK, Pchery, Theodor mine, Kladno-Rakovník Basin, Radnice Member, Bolsovian; **H** – Leaf fragment, Scale bar = 1 cm; **I** – Detail of venation from the leaf impression with fine veins. Scale bar = 1 mm; **J** – Detail of venation from the opposite side of phytolite (Coll. CGS, ZŠ 358a). Scale bar = 1 mm.

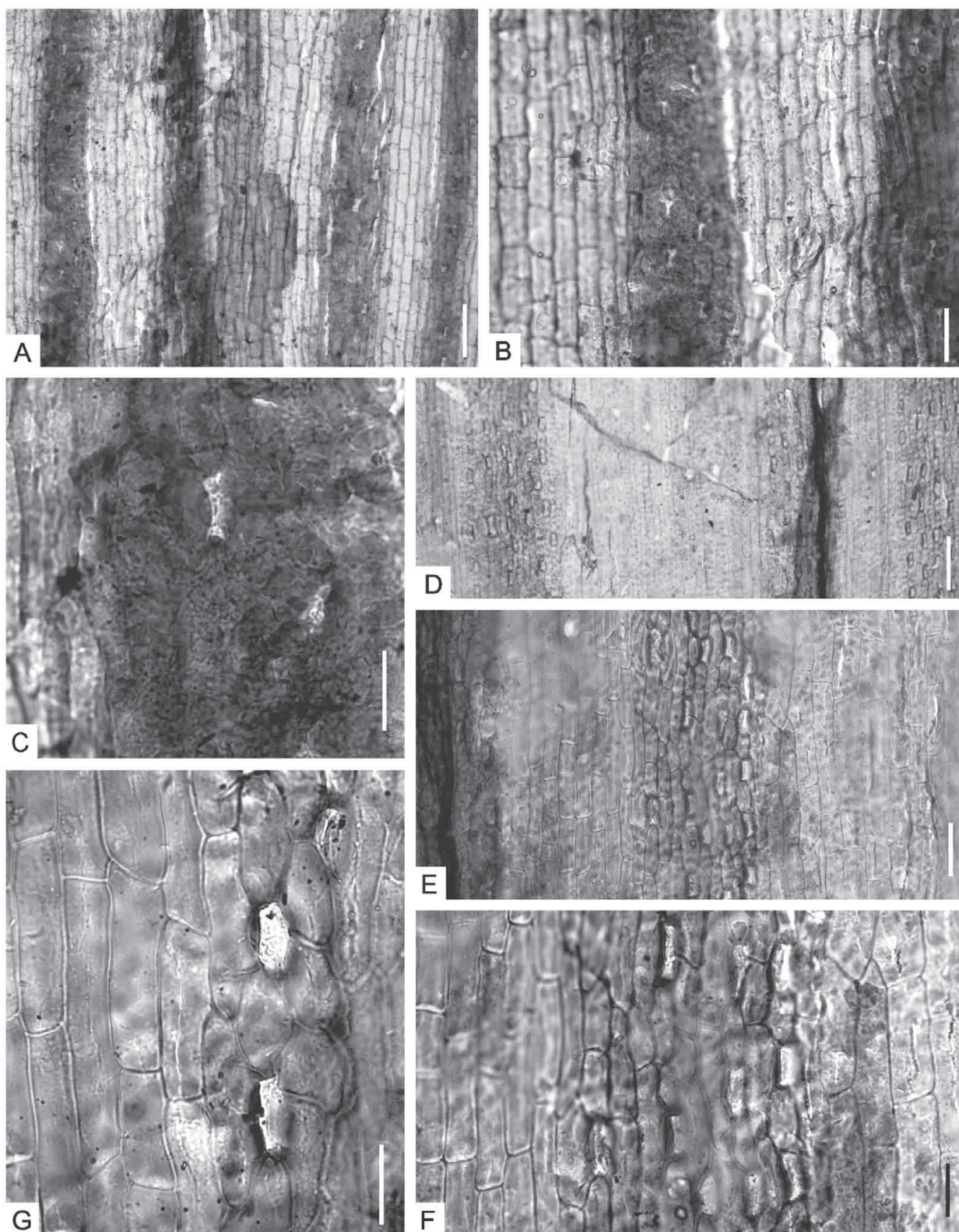
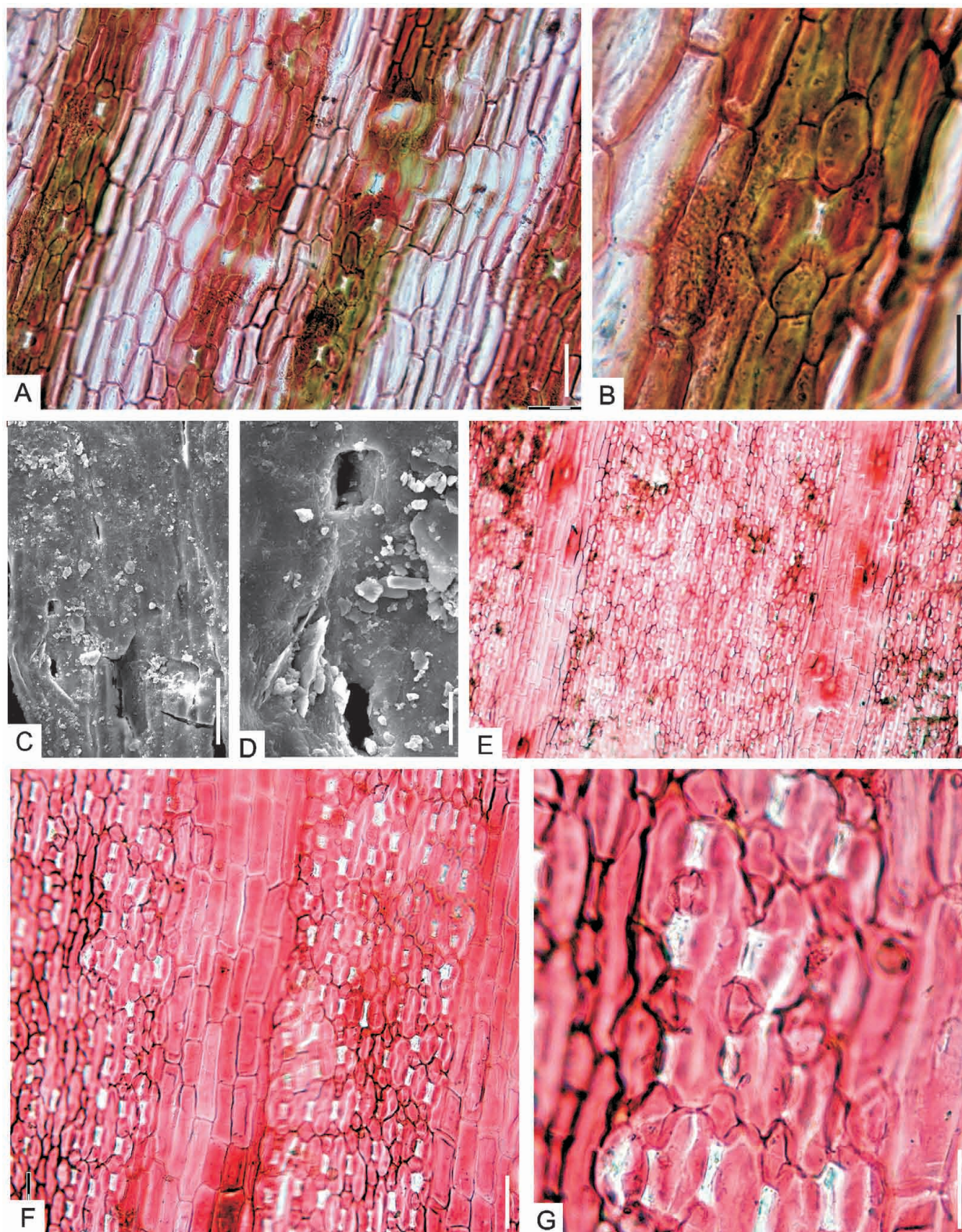


PLATE 2

Cuticles from *Cordaites wartmannii* ŠIMŮNEK (holotype, slide 113/1), Libušín, Schoeller mine.

- A–C** Adaxial cuticle. **A** – Adaxial cuticle with dark stomatal rows. Scale bar = 100 μ m; **B** – Details of dark stomatiferous bands. Scale bar = 50 μ m; **C** – Detail of two stomatal complexes. Scale bar = 25 μ m;
D–F Abaxial cuticle; **D** – Cuticle with three stomatiferous bands. Scale bar = 100 μ m; **E–F** Detail with a stomatiferous band and stomata and small papillae on epidermal cells; **E** – Scale bar = 50 μ m; **F** – Scale bar = 25 μ m; **G** – Detail of two stomatal complexes and epidermal cells. Scale bar = 25 μ m.

**PLATE 3**

Cuticles from *Cordaite wartmannii* ŠIMŮNEK, Libušín, Schoeller mine, slide no. 395/5;

- A** Adaxial cuticle with dark stomatal rows. Scale bar = 50 µm;
B Detail of dark stomatal row with a stomatal complex. Scale bar = 25 µm;
C–D Outer view of adaxial cuticle with openings above guard cells, SEM stub no. 25; **C** – Scale bar = 50 µm; **D** – Scale bar = 10 µm;
E–G Abaxial cuticle with stomatiferous and non-stomatiferous bands; **E** – Note relatively wide stomatiferous bands and some strongly cutinised cells in non-stomatiferous bands. Scale bar = 100 µm; **F** – Abaxial cuticle with relatively narrow stomatal bands and small papillae on epidermal cells. Scale bar = 50 µm; **G** – Detail of some stomatal complexes within stomatiferous band. Note small polar subsidiary cells. Scale bar = 25 µm.

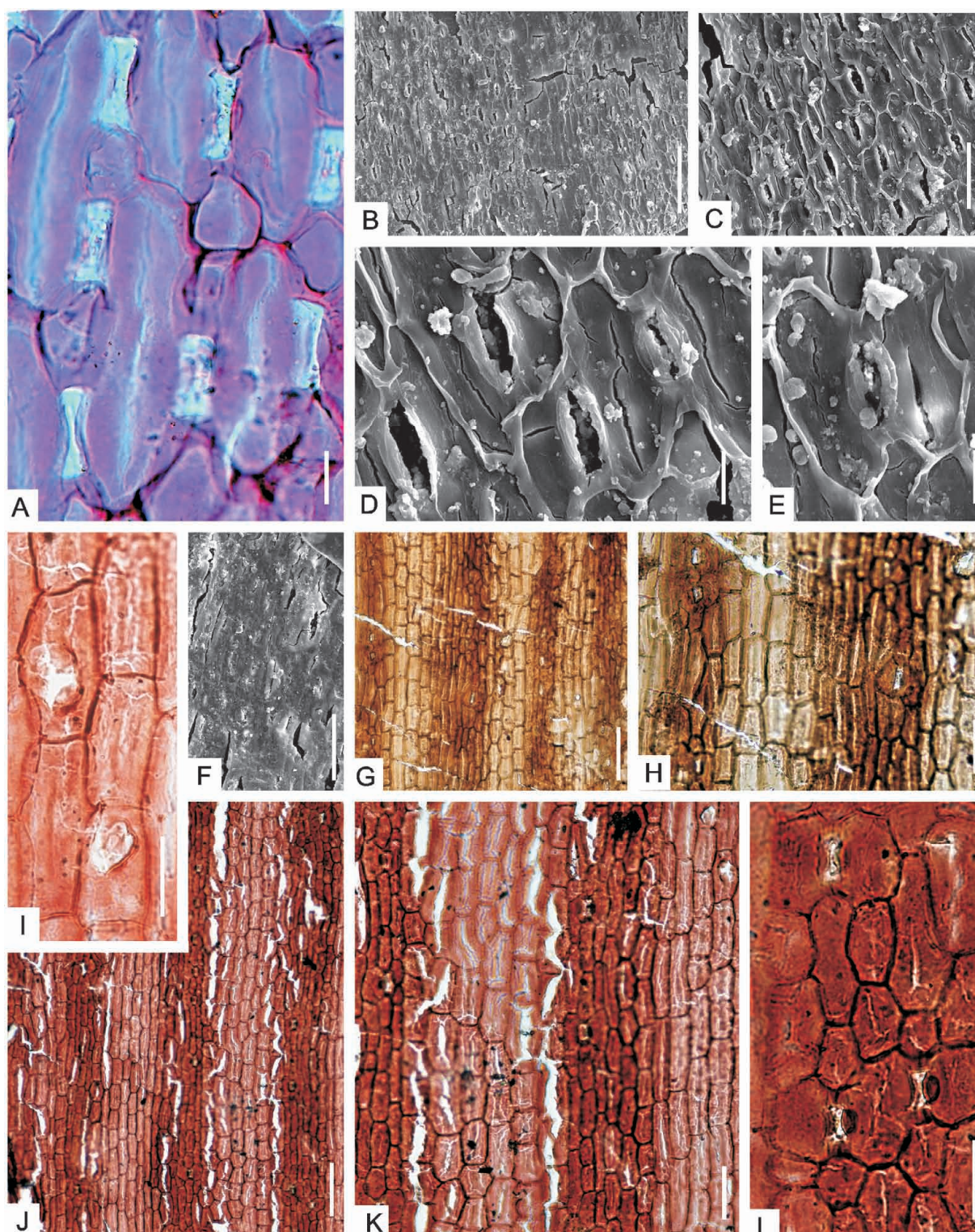
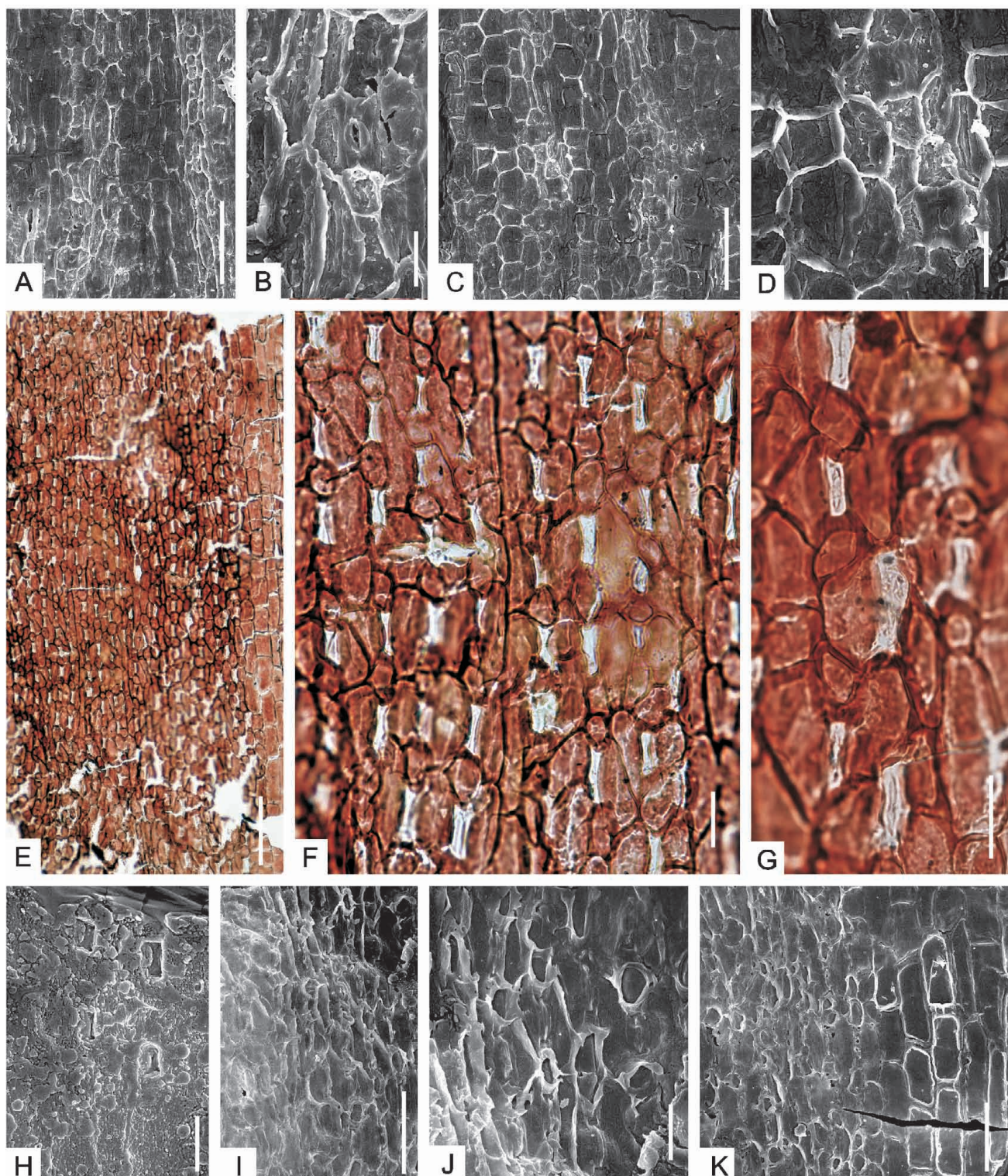


PLATE 4

Cuticles from *Cordaites wartmannii* ŠIMŮNEK

- A–F** Libušín, Schoeller mine locality; **A** – Detail of stomatal complexes from Pl. 3F. Scale bar = 10 μ m; **B–F** Abaxial cuticle in SEM, stub 25, outer view; **B** – Low magnification with stomatal bands and stomatal openings. Scale bar = 100 μ m; **C** – Stomatiferous band with guard cells visible. Scale bar = 50 μ m; **D** and **E** – Inner view of stomatal complexes with very visible guard cells. Scale bar = 10 μ m; **F** – Outer view on the abaxial cuticle. Scale bar = 100 μ m;
- G–L** Adaxial cuticle, Pchery, Theodor mine locality **G–H** Alternating non-stomatiferous and dark stomatiferous bands. slide 518/8. Scale bars = 100 (**G**) and 50 (**H**) μ m; **I** – Detail of cells of non-stomatiferous band with burst papillae-like objects, slide 518/13. Scale bar = 25 μ m; **J–K** Adaxial cuticle with dark stomatiferous bands, slide 518/13; **J** – Scale bar = 100 μ m; **K** – Scale bar = 50 μ m; **L** – Detail of the dark stomatiferous band from Pl. 4K with stomata. Note proximal papillae on lateral subsidiary cells. Scale bar = 25 μ m.

**PLATE 5**Cuticles from *Cordaite wartmannii* ŠIMŮNEK Pchery, Theodor mine locality

- A–D** SEM images from inner side of the adaxial cuticle, SEM stub 56; **A** – General view of abaxial cuticle. Scale bar = 100 μ m; **B** – view to stomatal complex. Scale bar = 20 μ m; **C** – Another view of adaxial cuticle. Scale bar = 100 μ m; **D** – Adaxial cuticle with stomata – detail from Pl. 5C. Scale bar = 25 μ m;
- E–G** Abaxial cuticles, Slide 518/6; **E** – Abaxial cuticle with stomatiferous and non-stomatiferous bands. Scale bar = 100 μ m; **F** – Detail of the stomatiferous band with stomatal complexes from Pl. 5E. Scale bar = 50 μ m; **G** – Detail of stomatal complexes from Fig. F. Scale bar = 25 μ m;
- H–K** SEM images of abaxial cuticle. SEM stub 56; **H** – Outer view of abaxial cuticle with stomatal openings above guard cells and papillae on the surface. Scale bar = 25 μ m; **I** – Inner view of the abaxial cuticle with prominent anticlinal walls, guard cells are not very discernible. Scale bar = 50 μ m; **J** – Abaxial cuticle with indiscernible guard cells, but with very prominent anticlinal walls of polar subsidiary cells. Scale bar = 20 μ m; **K** – Inner view of the abaxial cuticle. Cells of stomatiferous and non-stomatiferous bands are clearly distinguishable. Scale bar = 50 μ m.

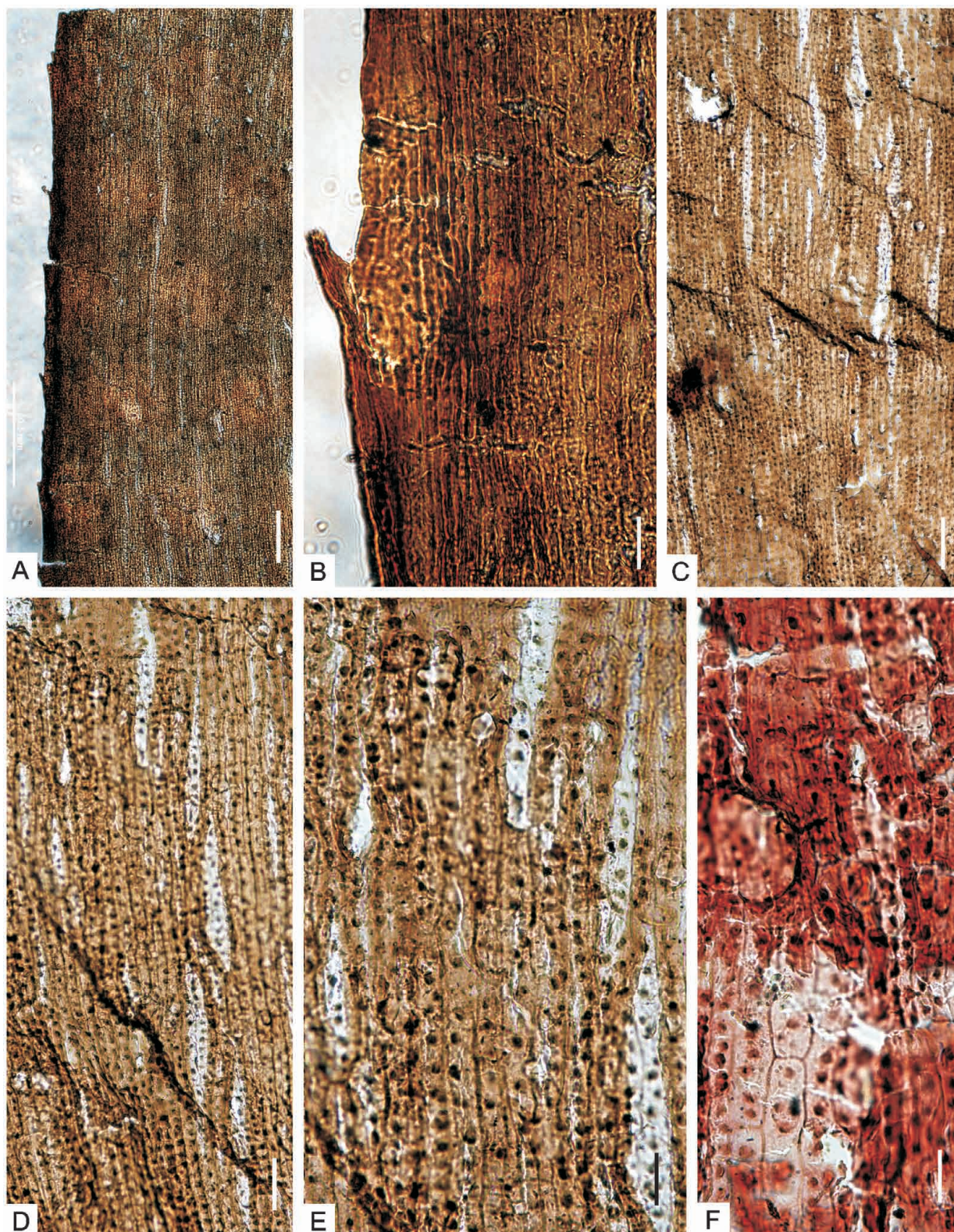


PLATE 6

Cordaites theodorii ŠIMŮNEK & Haldovský sp. nov., Pchery, Theodor mine locality.

- A Leaf margin with teeth. Slide 518/1. Scale bar = 250 μ m;
- B detail of a tooth from Pl. 6A. Scale bar = 25 μ m;
- C Surface of the adaxial cuticle with elongated cells and many papillae. Slide 518/8, Scale bar = 100 μ m;
- D Detail of adaxial cuticle from Pl. 6C. Scale bar = 50 μ m;
- E Detail of strongly papillate cells of the adaxial cuticle from Pl. 6D. Scale bar = 25 μ m;
- F Papillate cells of adaxial cuticle, Slide 518/13. Scale bar = 25 μ m.

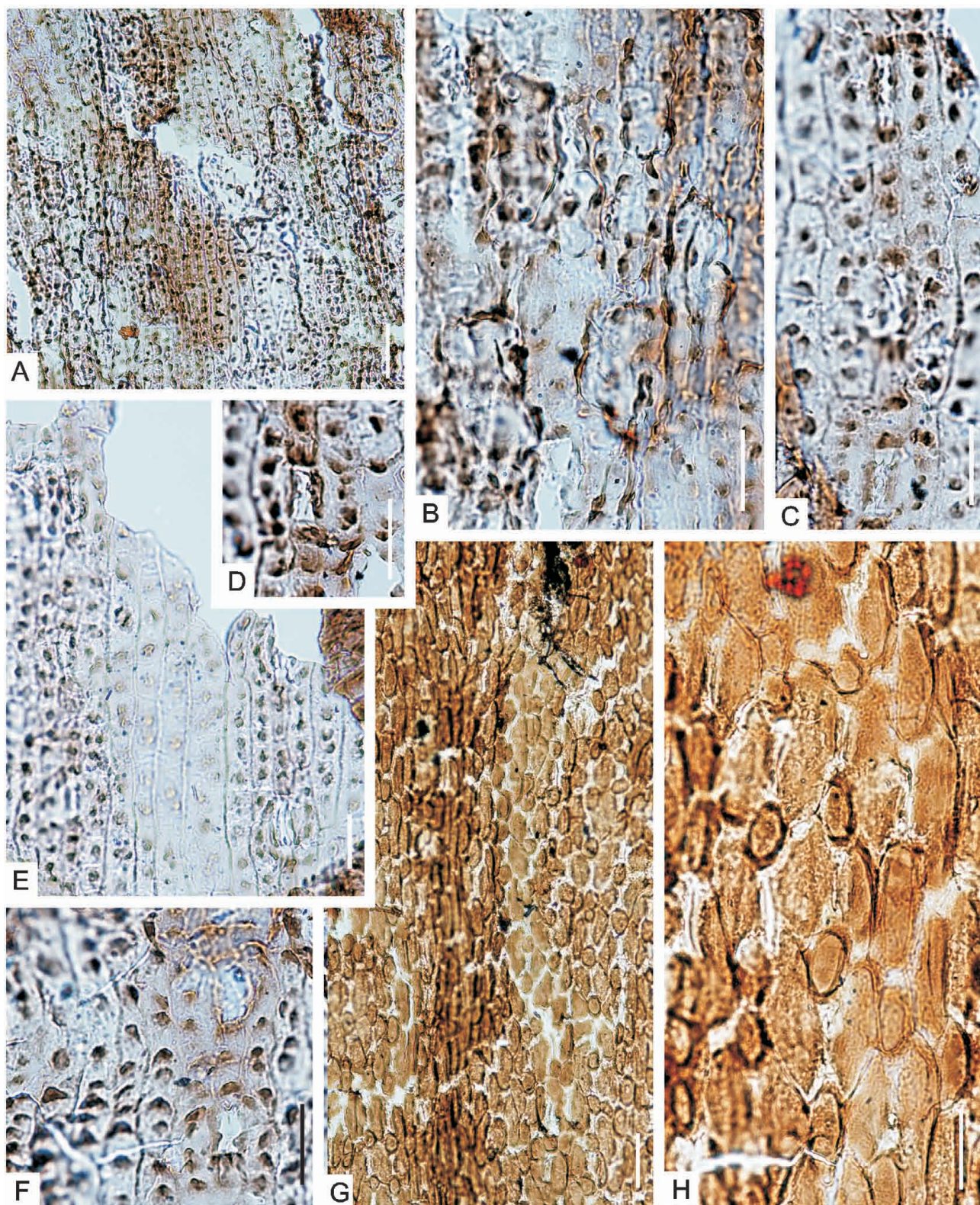


Plate 7

- A–F** *Cordaites theodorii* ŠIMŮNEK & HALDOVSKÝ sp. nov., Pchery, Theodor mine locality; **A** – Strongly papillate abaxial cuticle. Slide 518/1. Scale bar = 50 µm; **B** – Detail of abaxial cuticle from Pl. 7A with stomata. Scale bar = 25 µm; **C–D** Strongly papillate cells of abaxial cuticles. Note proximal papillae on subsidiary cells pointing to the center of the stoma. Slide 518/2. Scale bar = 25 µm; **E** – Stomata arranged in rows, Slide 518/2. Scale bar = 25 µm; **F** – Detail of two stomata. Note many papillae. Slide 518/2. Scale bar = 25 µm;
- G–H** *Cordaites wartmanni* ŠIMŮNEK. Pchery, Theodor mine locality. Poorly preserved cuticles with prominent polar subsidiary cells. The other cells, including the guard cells are poorly discernible. **G** – Scale bar = 50 µm; **H** – Scale bar = 25 µm.

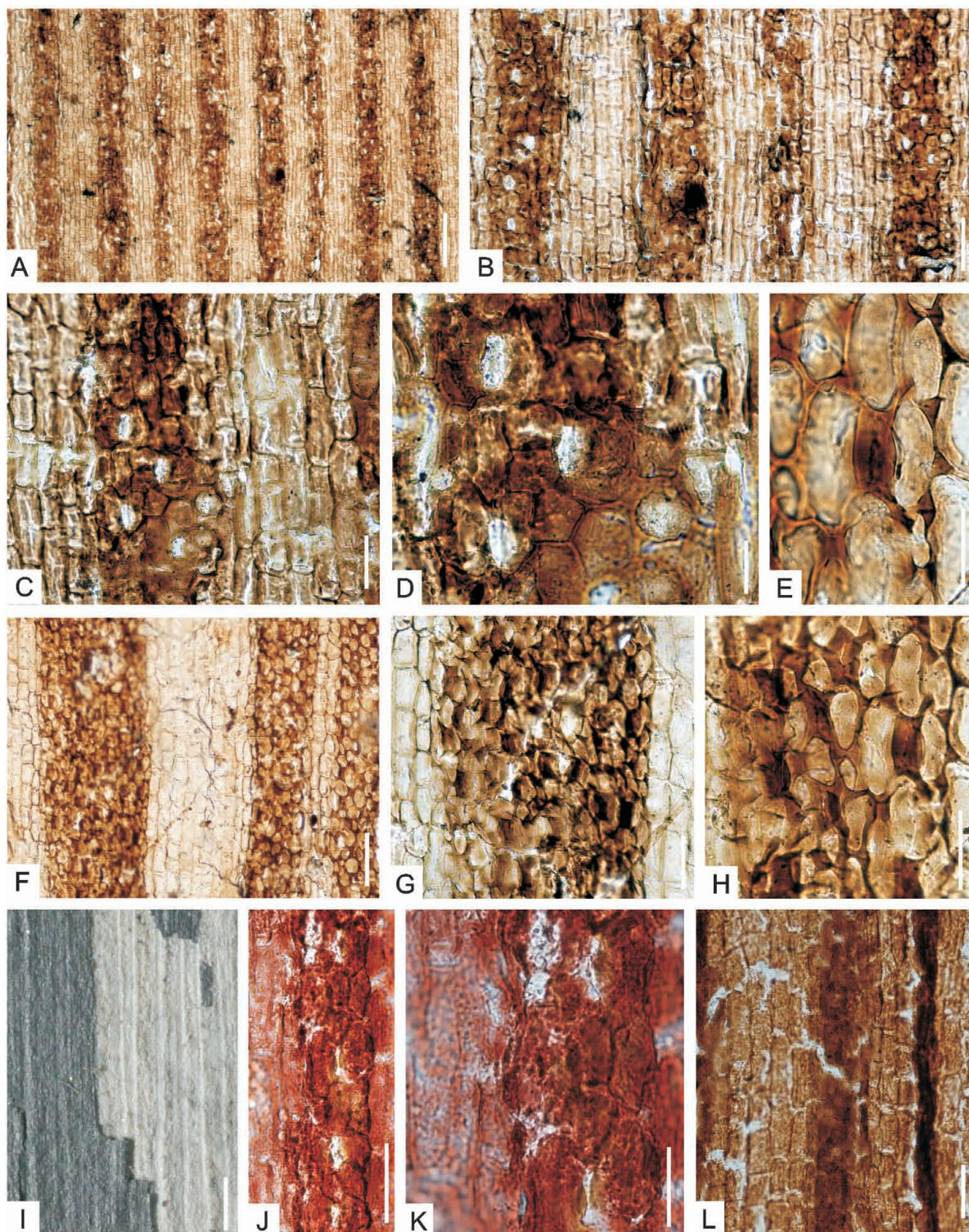


Plate 8

- A–D** *Cordaites kladnoensis* ŠIMŮNEK (holotype of *Cordaites polyneurus* ŠIMŮNEK, slide 182/1) Tuchlovice, Nosek mine locality; **A–D** Adaxial cuticles; **A** – daxial cuticle with more or less regular dark stomatal rows. Scale bar = 250 µm; **B** – Detail from Fig. A. Scale bar = 100 µm; **C** – Detail of a dark stomatiferous band with stomatal complexes from Pl. 8B. Scale Bar = 50 µm; **D** – Detail of three stomatal complexes from Pl. 8C. Scale Bar = 25 µm;
- E–H** Abaxial cuticle; **E** – A stomatal complex with strongly cutinised crypt above guard cells, detail from Fig. H. Scale bar = 25 µm; **F** – View of an abaxial cuticle with three stomatiferous bands. Scale bar = 100 µm; **G** – Detail of a stomatiferous band from Fig. F. with strongly cutinised crypts above guard cells and anticlinal walls in the corners of cells. Scale bar = 50 µm; **H** – Close up of a stomatiferous band from Pl. 8G to see in more detail strongly cutinised crypts and anticlinal walls. Scale Bar = 25 µm;
- I** Venation pattern of *Cordaites kladnoensis* ŠIMŮNEK (holotype of *Cordaites polyneurus* ŠIMŮNEK) Inv. No. ZŠ 247, Scale bar = 1 mm;
- J–L** Adaxial cuticle of *Cordaites kladnoensis* ŠIMŮNEK, Pchery, Theodor mine locality, **J** – Dark stomatiferous band with stomata. Slide 543/1. Scale bar = 50 µm; **K** – Close up of stomatal complexes from Fig. J. Scale bar = 25 µm; **L** – Adaxial cuticle with a dark stomatiferous band. Slide 543/3 Scale bar = 50 µm.

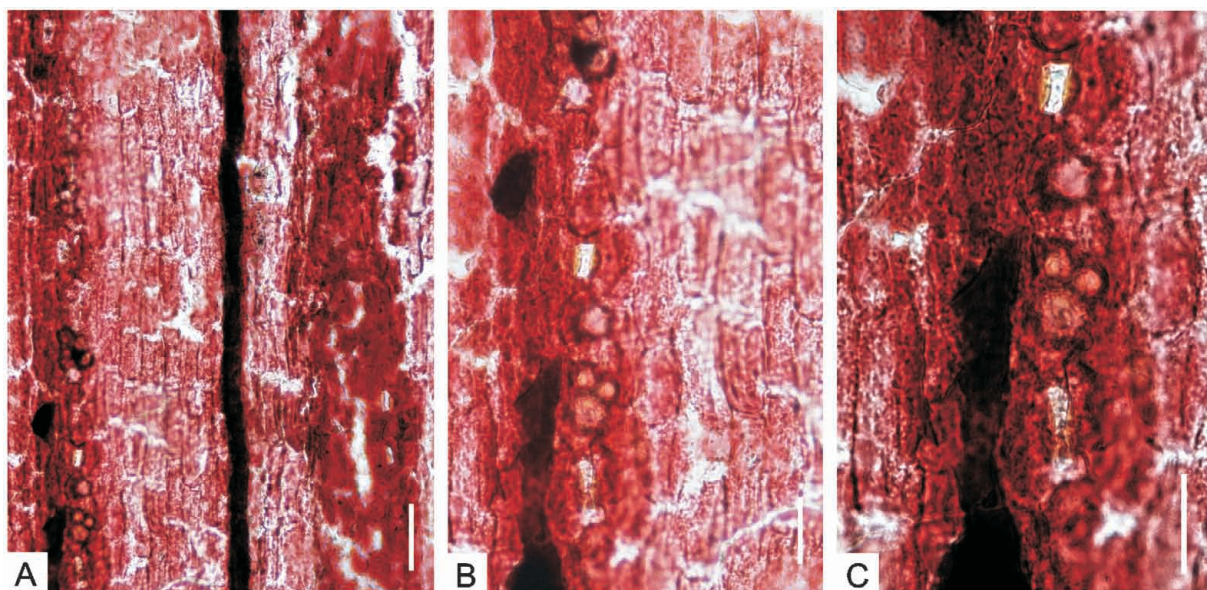


PLATE 9

Adaxial cuticle of *Cordaites kladnoensis* ŠIMŮNEK, Pchery, Theodor mine locality. Slide 543/4;

- A Adaxial cuticle with two dark stomatiferous bands. Scale bar = 50 μm ;
- B Close up of dark stomatiferous band from Pl. 9A. Scale bar = 25 μm ;
- C Close up of two stomata from the stomatiferous band on Pl. 9B. Scale bar = 25 μm .