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Cuticles of *Cordaites* from the Westphalian, Stephanian and Autunian of the Bohemian Massif (Czech Republic)

(a preliminary study)

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ABSTRACT. Despite of the fact that only three or four species of *Cordaites* (*C. principalis*, *C. palmaeformis*, *C. borassifolius* and ?*C. angulosostriatus*) and some *Poacordaites* sp. from the territory of the Bohemian Massif was described in the past, the diversity of cuticular types is much higher than diversity of leaves. The venation itself, which is mostly only a single feature on *Cordaites* specimens preserved in bore cores, is insufficient for determination of these plants. Several types of cuticles can belong to one type of *Cordaites* venation. Cuticular analysis of 65 specimens from most of the basins of the Bohemian Massif revealed high diversity of cuticular types.

Investigated *Cordaites* comes from the 6 stratigraphical levels of 7 coal basins from the Bohemian Massif. Three cuticular types of *Cordaites* have been determined in the Langsettian (Westphalian A) of the Upper Silesian Basin and also three cuticular types have been described from the Langsettian and Duckmantian (Westphalian A, B) of the Intrasudetic Basin. Most diversity of *Cordaites* cuticular structures is in the Central Bohemian region, where 9 cuticular types have been described from Bolsovian (Westphalian C) and 6 or 7 cuticular types from Westphalian D strata. Stephanian and Autunian *Cordaites* have been poorly investigated up to now. Therefore only three cuticular types of Stephanian *Cordaites* and 2 cuticular types of Autunian *Cordaites* have been determined from the Bohemian Massif up to now.

In total 26 or 27 *Cordaites* cuticular types have been determined in the Bohemian massif. *Cordaites principalis* is the most common morphological type (according to the venation pattern) from the Permo-Carboniferous basins of the Czech Republic. Cuticles of holotype *Cordaites borassifolius* have been studied.

Although cuticles of *Cordaites* from each strata are not completely known, it is evident that this genus was much diverse then it was thought before and its representatives were important plants of Carboniferous swamps of the Bohemian Massif.

KEY WORDS: *Cordaites*, Westphalian, Stephanian, Autunian, Bohemian Massif, cuticular analysis

INTRODUCTION

Remains of *Cordaites* leaves have been collected in large number in outcrops, spoil piles of mines and bore cores in the most of Permo-Carboniferous coal basins of the Bohemian Massif within last few decades.

The genus *Cordaites* Unger belongs to the order Cordaitales, class Cordaitopsida. This gymnospermous group had a great palaeoecological and evolutionary importance during the Carboniferous and Permian. *Cordaites* lived in different habitats – both in moisture conditions of peat-forming swamps and in the community of xerophilous upland flora (DiMichele in: Behrensmeyer et al 1992). They have common ancestors with conifers (Florin 1951).

Czech representatives of *Cordaites* have not been systematically studied since the time of Sternberg (1821). Although *Cordaites* have been mentioned in floral lists of many papers and unpublished reports of Šusta (1928), Němejc (1953), Havlena (1957), Šetlík (1967, 1968, 1970 and 1971) and Rieger (1971), only its 4 species and some *Poacordaites* are

Table 1. Morphological characteristics of selected *Cordaites* according different authors

Cordaites	Author	Length of leaf [cm]	Width of leaf [cm]	Number of veins per 1 cm	Number of fine veins between 2 thick veins
angulosostriatus	Crookal 1970	35–80	4–12	15–30	2–5
	Rabitz 1966		1–2.7	30–40	1–5
	Ledran 1966	20–80	4–12	20–30	2–5
	Doubinger et al. 1995	20–30	4–12		2–5
		20–80	**1–12**	15–40	1–5
borassifolius	Crookal 1970	25–60	3–12	20–30	1
	Rabitz 1966		0.8–3	20–54	1
	Ledran 1966	10–60	3.5–8	18–20	2–3
	Doubinger et al. 1995	10–60	3.5–8	18–20	2
	Josten 1991	20–50	up to 5	20–30	1
		10–60	0.8–12	18–54	1 – (3)
lingulatus	Zeiller 1906		1.5–6	20–35	
	Seward 1963	up tp 35	4–11		1–3 at the
	Ledran 1966	10–50	2–15	20–25	basal part
	Doubinger et al. 1995	10–50	up to 15		
		10–50	1.5–15	20–35	(0) 1–3
microstachys	Crookal 1970	3–30	0.4–0.8	30–40	1–2
	Ledran 1966	up to 20	0.4–1	60–70	2–3
		3–30	0.4–1	30–70	1–3
palmaeformis	Crookal 1970	up to 80	up to (10)	35–50	0
	Rabitz 1966		0.8–2.5	52–140	0
	Ledran 1966	30–60	1.5–5	30	0
	Doubinger et al. 1995	30–60	1.5–5		
		30–80	0.8–5(10)	30–140	0
principalis	Crookal 1970	20–50	3–6	16–32	1–6
	Rabitz 1966	33.3	5.1	14–38	1–7
	Ledran 1966	50–60	4–15	30–36	2–5
	Doubinger et al. 1995	50–60	4–15		2–5
	Josten 1991	20–50	about 5		2–7
	Remy – Remy 1977	30–90	up to 5	18–22	2–5
		20–90	3–15	14–38	1–7

Table 2. Artificial sorting of investigated *Cordaites* from the Bohemian Massif using venation density

Number of thick veins per 1 cm	Number of fine veins between 2 thick veins	Width of leaf [mm]	% of investigated specimens	Usually determined as
10–20	3 – 6(7)	18–56	32	*C. principalis*
20–30	(1)2–6(7)	8.5–95	41	*C. principalis*
30–40	1–2(3)	5.5–48	20	*C. principalis,,* *C. borassifolius* ? *C. palmaeformis* *Poacordaites*
40–50	0–1	40–50	7	*C. borassifolius* *C. palmaeformis*

referred from the territory of the Bohemian Massif.

Tab. 1 shows that numerical characteristics of many *Cordaites* species are overlapping and therefore it is very difficult to determine them from small leaf fragments.

Results of measuring of some investigated *Cordaites* from the Bohemian Massif is shown

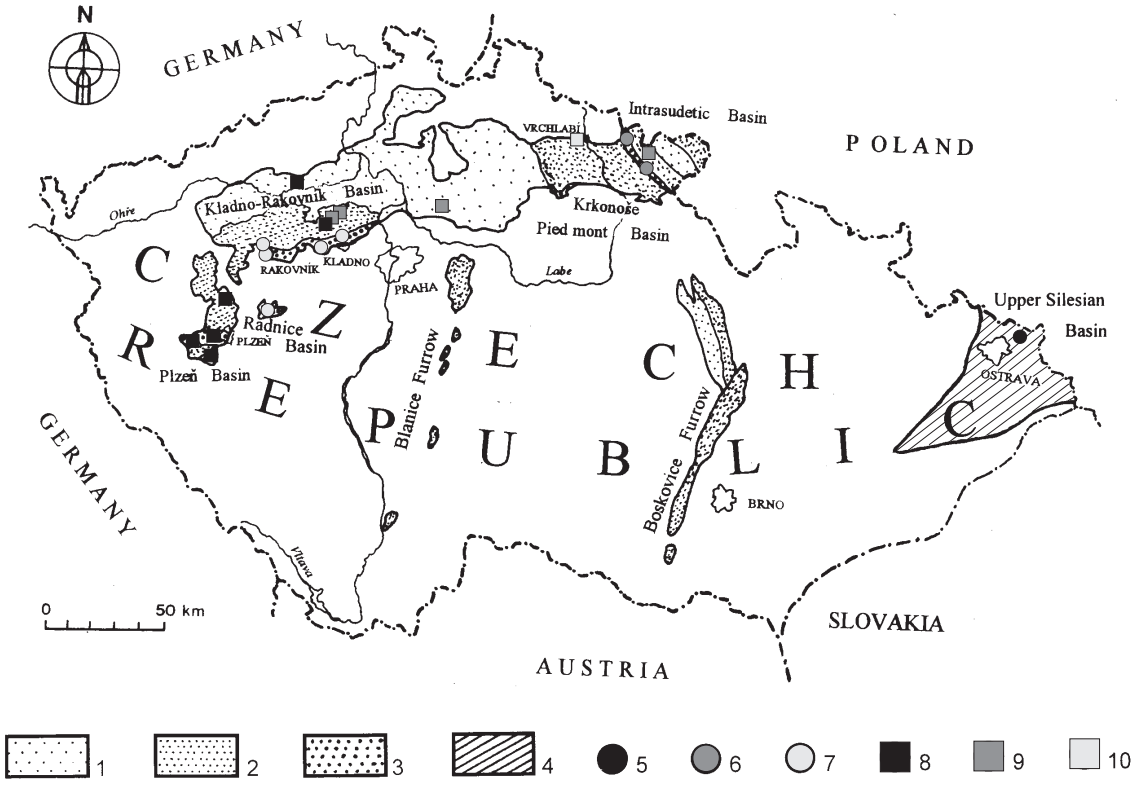

Fig. 1. Localities of investigated *Cordaites* from the Bohemian Massif. Explanation: **1** – Permo-Carboniferous (Westphalian, Stephanian and Permian) covered by younger sediments (mostly Cretaceous), **2** – Stephanian and Permian (mostly Autunian), **3** – Westphalian, **4** – Namurian to Langsettian (mostly covered by the Tertiary and Carpatian napes). 5–10 – localities of investigated cordaites: **5** – Langsettian, **6** – Duckmantian, **7** – Bolsovian, **8** – Westphalian D, **9** – Stephanian, **10** – Autunian

on Tab. 2. It is evident from this table that most specimens according to the venation patterns could be determined as *Cordaites principalis* (Germar) Geinitz. Only few specimens could be regarded as *Cordaites borassifolius* (Sternberg) Unger and *Cordaites palmaeformis* (Goeppert) Weiss.

Investigated localities are demonstrated on Fig. 1. The studied *Cordaites* come from the seven coal basins and from six formations of the Czech Republic.

CUTICLES OF INVESTIGATED *CORDAITES*

Cordaites from the Langsettian of the Karviná Formation (Upper Suchá Member, Upper Silesian Basin)

Fig. 2: 1, 2, 3

All specimens belong to Šusta's collection of the Ostrava Museum. Hypostomatic leaves of numbers 1 and 2 were determined as *Cordaites principalis* (Germar) Geinitz, amphistomatic leaf of number 3 as *Cordaites borassifolius* (Sternberg) Unger. Longitudinally tetragonal, mostly oblong cells, 35 to 100 μm in length and 15 to 25 μm in width belong to the adaxial cuticles. Stomatal density of "*Cordaites borassifolius*" is 60 stomata per mm^2. Stomatal index is 9–10.

Cells of abaxial cuticles are smaller 25 to 60 μm in length and 15 to 30 μm in width (in the intercostal field). Stomata occur in ill-defined stomatal rows. Guard cells are 20 to 30 μm long and 10 to 20 μm wide. Normal epidermal cells serve as subsidiary cells. Prominent papillae are present on specimen number 2. Stomatal density varies from 96 to 112 stomata per mm^2, stomatal index is from 7 to 10.

Cordaites from the Duckmantian of the Žacléř Formation (Intrasudetic Basin)

Fig. 2: 4, 5, 6

Specimens are not determined except of a narrow-leafed specimen number 5 which is

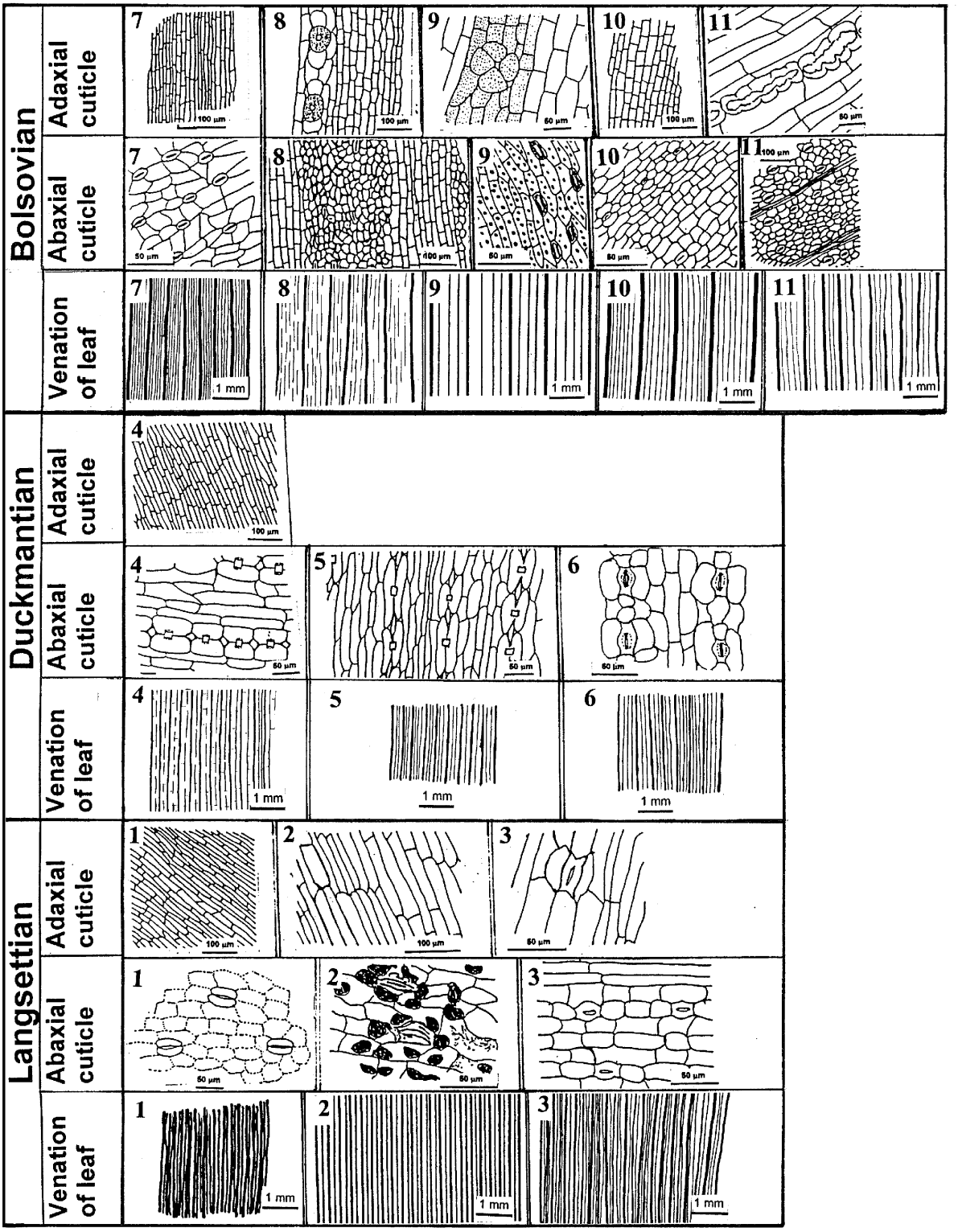

Fig. 2. Adaxial and abaxial cuticles and venation diagrams of *Cordaites* leaves from the Langsettian, Duckmantian and Bolsovian of the Bohemian Massif. **1** – "*Cordaites principalis*", loc. Karviná, Hlubina mine, 19th coal seam, No. A 5999, slide No. 173, Upper Silesian Basin, Upper Suchá Member, **2** – "*Cordaites principalis*", loc. Karviná, Hlubina mine, 19th coal seam No. A 6581, slide No. 299, Upper Silesian Basin, Upper Suchá Member, **3** – "*Cordaites borassifolius*", Karviná, Františka mine, 22nd coal seam No. A 5989, Upper Silesian Basin, Upper Suchá Member, slide No. 301, **4** – *Cordaites* sp., loc. Rtyně v Podkrkonoší, Nejedlý mine (Ida gallery), Intrasudetic Basin, Prkenný Důl-Žďárky Member, **5** – *Cordaites* cf. *microstachys*, loc. Rtyně v Podkrkonoší, Nejedlý mine (Ida gallery), slide No. 186, Intrasudetic Basin, Prkenný Důl-Žďárky Member, **6** – *Cordaites* sp., loc. Žacléř, Šverma mine, slide No. 312, Intrasudetic Basin, Lampertice Member, **7** – *Cordaites* sp., loc. Tuchlovice, Nosek mine, slide No. 184, Kladno Basin, Radnice Member, **8** – *Cordaites* sp., loc. Tuchlovice, Nosek mine, slide No. 183, Kladno Basin, Radnice Member, **9** – *Cordaites* sp., loc. Libušín, Schoeller mine, slide No. 113, Kladno Basin, Radnice Member, **10** – *Cordaites* sp., loc. Tuchlovice, Nosek mine, slide No. 182, Kladno Basin, Radnice Member, **11** – *Cordaites* sp., loc. Tuchlovice, Nosek mine, slide No. 185, Kladno Basin

comparable to *Cordaites microstachys* Goldenberg. This cuticular type is probably amphistomatic, the others are hypostomatic. Adaxial cuticle has also longitudinally tetragonal (oblong) cells, 35 to 160 μm long and 12 to 25 μm wide. Both adaxial and abaxial cuticles of *Cordaites microstachys* are probably very similar.

Stomata of abaxial cuticles are organised into well-defined single or double stomatal rows separated by longitudinally tetragonal (oblong) epidermal cells, 30–100 μm long and 5–22 μm wide. Stomatal complex is formed by 2 guard cells, 12 to 25 μm long and 6 to 15 μm width, 2 big oblong to kidney-shaped lateral subsidiary cells and 2 small rounded, rhombic or spindle-forming polar subsidiary cells. Transverse oblong outer stomatal cavities are developed in specimens of numbers 4 and 5. Stomatal density varies from 180 to 250 stomata per mm^2, stomatal index is from 11 to 15.

Cordaites from the Bolsovian of the Central Bohemian region (Kladno Formation, Radnice Member)

Fig. 2: 7 to 11, Fig. 3: 12 to 15

Bolsovian is the period of the highest diversity of the *Cordaites* cuticular structures in the Bohemian Massif. Most of the specimens are not determined up to now. Cuticles number 12 are very similar to that ones prepared from holotype of *Cordaites borassifolius* (Sternberg) Unger. There is many different types in organisation of stomatal complexes in adaxial and abaxial cuticles, that it is very difficult to give common description of all cuticular types. Leaf number 7 is hypostomatic, all other specimens are amphistomatic.

Stomata of adaxial cuticles of numbers 8 and 9 have the same shape and dimension of polar and lateral subsidiary cells. Lateral subsidiary cells are larger than polar subsidiary cells in numbers 10, 12 to 15. Number 12 and 14 have well developed outer stomatal cavities. Number 11 has stomata with very large lobed outer stomatal cavities. Normal cells serve as subsidiary cells. Stomata are arranged in different ways. Stomata are mostly organised in better or worse defined rare single (or double) stomatal rows (numbers 8–11, 14 and 15). Stomata of numbers 9 and 10 are distributed in markedly darker bands. Stomata of numbers 12 and 13 are dispersed more or less irregularly in the adaxial surface. Stomatal density is variable – from 4 (number 13) to 90 (number 15) stomata per mm^2. Stomatal index varies from 0.5 (number 4) to 13 (number 15).

Stomata of abaxial cuticles are organised in stomatiferous bands and stomatal rows. Stomata of numbers 7, 8, 9 are organised in stomatiferous bands of 150–280 μm in width. Stomata of number 8 are submerged, cells of number 9 are covered by many very tiny papillae. Subsidiary cells (of numbers 7, 8, 9, 11 and 13) do not differ from normal cells of the stomatiferous bands. Stomatal complex of number 12 consists of 2 guard cells, 2 large oblong lateral subsidiary cells and 2 very small rounded to elliptical polar subsidiary cells oriented into stomatal rows. Three to six rows form a stomatiferous band. Transverse outer stomatal cavity is well developed. Specimen number 14 is remarkable by very small stomatal complexes orientated in stomatal rows and stomatiferous bands. Lateral subsidiary cells do not differ from the normal cells. Polar subsidiary cells are big and oblong. A cuticular thickening like “Florin rings” is developed above the submerged guard cells. Stomatal rows of number 15 contain stomata with 2 big kidney-shaped lateral subsidiary cells and 2 to 4 small polar subsidiary cells. Stomatal density is very variable 70 stomata per mm^2 (number 15), 280 (number 13) to 400 (numbers 7, 8 and 9). Stomatal index varies from 10 (number 15) to 20 (number 12).

Cordaites of Westphalian D of the Central Bohemian region (Kladno Formation, Nýřany Member)

Fig. 3: 21 to 27, Fig. 4: 15 to 20

Westphalian D is also a period with large diversity of *Cordaites* cuticular structures. Hypostomatic specimen number 16 represents 3 ontogenetic stages of development of stomatal complexes (Šimůnek 1994). There are many others amphistomatic leaves, that have the same shape and distribution of stomatal complexes in the abaxial cuticle like number 16 (e. g. numbers 17 to 20 and 23). Slight differences can be explained in different way of preservation. Stomata in adaxial cuticle of this type are usually surrounded by 2 bigger lat-

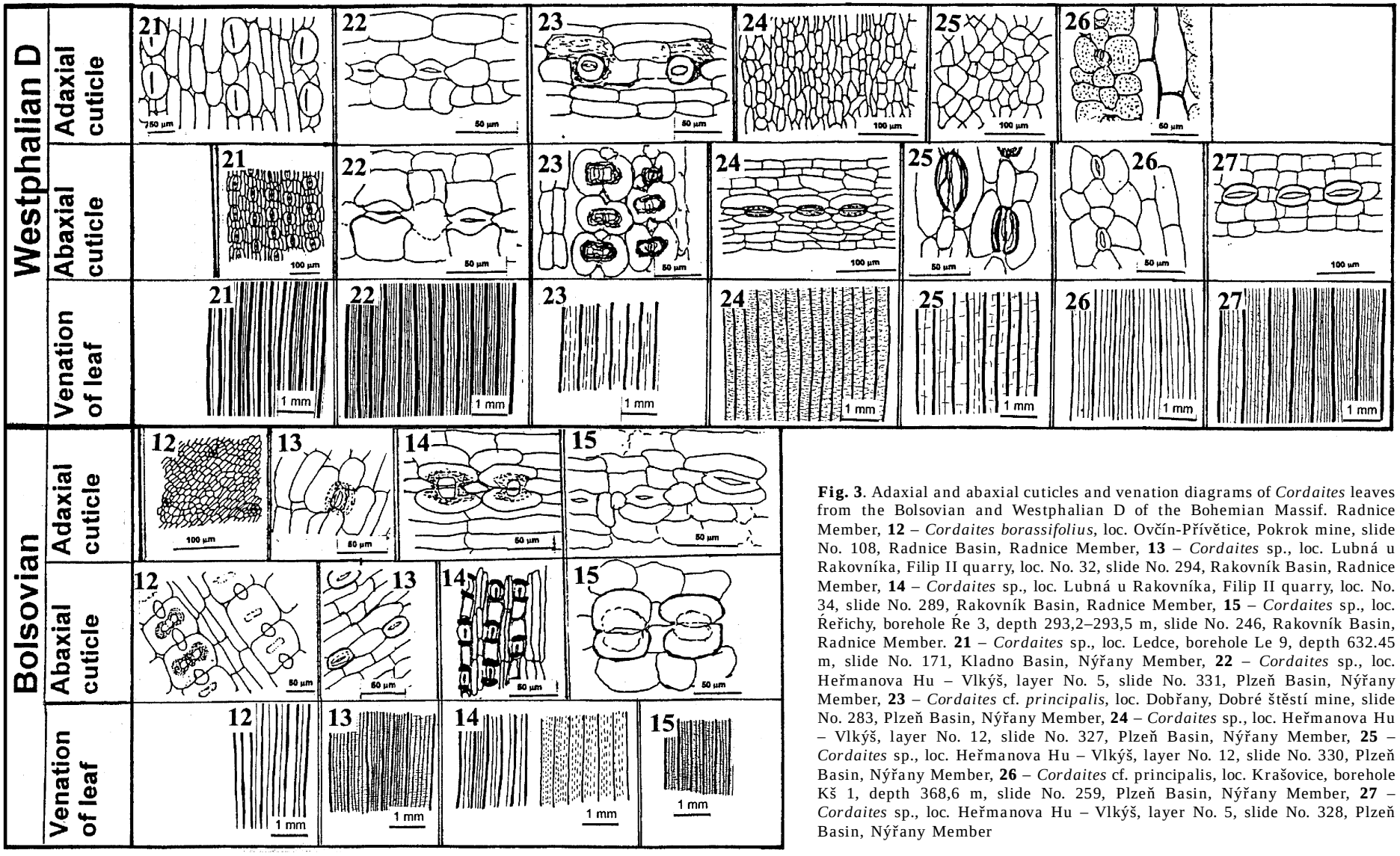

Fig. 3. Adaxial and abaxial cuticles and venation diagrams of *Cordaites* leaves from the Bolsovian and Westphalian D of the Bohemian Massif. Radnice Member, **12** – *Cordaites borassifolius*, loc. Ovčín-Přívětice, Pokrok mine, slide No. 108, Radnice Basin, Radnice Member, **13** – *Cordaites* sp., loc. Lubná u Rakovníka, Filip II quarry, loc. No. 32, slide No. 294, Rakovník Basin, Radnice Member, **14** – *Cordaites* sp., loc. Lubná u Rakovníka, Filip II quarry, loc. No. 34, slide No. 289, Rakovník Basin, Radnice Member, **15** – *Cordaites* sp., loc. Řeřichy, borehole Ře 3, depth 293,2–293,5 m, slide No. 246, Rakovník Basin, Radnice Member. **21** – *Cordaites* sp., loc. Ledce, borehole Le 9, depth 632.45 m, slide No. 171, Kladno Basin, Nýřany Member, **22** – *Cordaites* sp., loc. Heřmanova Hu – Vlkýš, layer No. 5, slide No. 331, Plzeň Basin, Nýřany Member, **23** – *Cordaites* cf. *principalis*, loc. Dobřany, Dobré štěstí mine, slide No. 283, Plzeň Basin, Nýřany Member, **24** – *Cordaites* sp., loc. Heřmanova Hu – Vlkýš, layer No. 12, slide No. 327, Plzeň Basin, Nýřany Member, **25** – *Cordaites* sp., loc. Heřmanova Hu – Vlkýš, layer No. 12, slide No. 330, Plzeň Basin, Nýřany Member, **26** – *Cordaites* cf. principalis, loc. Krašovice, borehole Kš 1, depth 368,6 m, slide No. 259, Plzeň Basin, Nýřany Member, **27** – *Cordaites* sp., loc. Heřmanova Hu – Vlkýš, layer No. 5, slide No. 328, Plzeň Basin, Nýřany Member

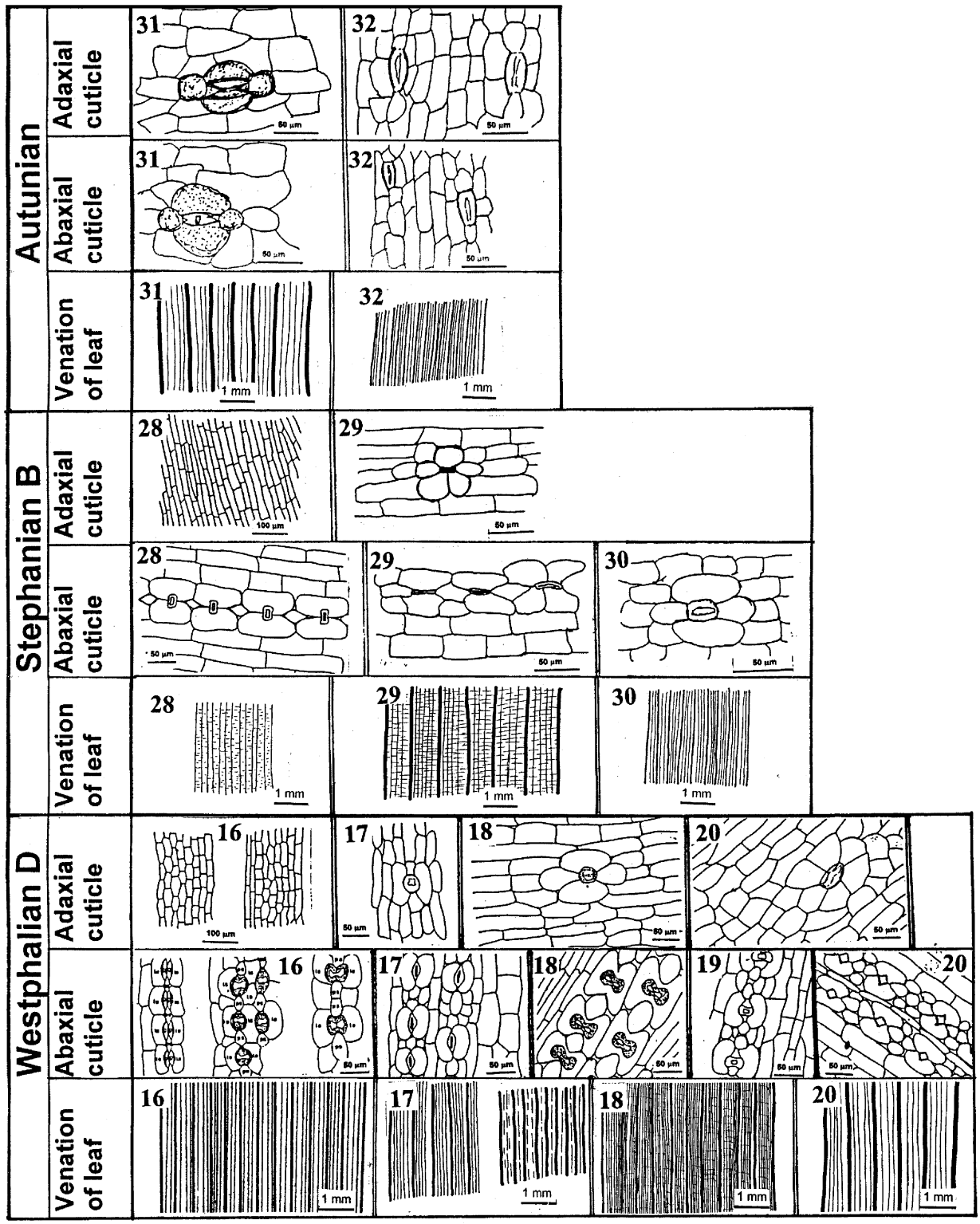

Fig. 4. Adaxial and abaxial cuticles and venation diagrams of *Cordaites* leaves from the Westphalian D, Stephanian B and Autunian of the Bohemian Massif. **16** – *Cordaites* cf. *principalis*, loc. Dobřany, Dobré štěstí mine, slide Nos. 241, 242, 243, Plzeň Basin, Nýřany Member, **17** – *Cordaites* sp., loc. Nýřany – Tesla, borehole HJ 3/4, depth 94 m, slide No. 166, Plzeň Basin, Nýřany Member, **18** – *Cordaites* cf. *principalis*, loc. Dobřany, Dobré štěstí mine, slide No. 163, Plzeň Basin, Nýřany Member, **19** – *Cordaites* cf. *principalis*, loc. Dlažkovice, borehole RPZ 30, depth 338 m, slide No. 188, Kladno Basin, Nýřany Member, **20** – *Cordaites* cf. *principalis*, loc. Dlažkovice, borehole RPZ 30, depth 351.3 m, slide No. 189, Kladno Basin, Nýřany Member, **28** – *Cordaites* sp., loc. Slaný, Slaný mine, slide No. 165, Kladno Basin, Slaný Formation, **29** – *Cordaites* sp., loc. Sušno, borehole Sš 1, 724,9 m, slide No. M9, Mšeno Basin, Slaný Formation, **30** – *Cordaites* sp., loc. Radvanice, Kateřina mine, slide No. 318, Intrasudetic Basin, Jívka Member, **31** – *Cordaites* cf. *principalis*, loc. Vrchlabí, roadcut W. from the town, 430 m. sect., 7th layer, slide Nos. M12, 205, Krkonoše Piedmont Basin, Vrchlabí Formation, Rudník Horizon, **32** – *Cordaites* cf. *palmaeformis*, loc. Vrchlabí, roadcut W. from the town, 110 m. sect., 1st layer, slide Nos. M11, 209, Krkonoše Piedmont Basin, Vrchlabí Formation, Rudník Horizon

eral subsidiary cells and 2 smaller polar subsidiary cells. Others *Cordaites* cuticular types are quite different. Number 21 has stomata in dense stomatal rows, normal cells serve as subsidiary cells. Number 22 has two big polar subsidiary cells and 2 to 3 lateral subsidiary cells. Specimens numbers 24 and 25 are hypostomatic. Cells of adaxial cuticle in the intercostal field are randomly oriented. Specimen number 26 has stomata oriented in strongly cutinized stomatal rows. Stomatal density varies from 14 (numbers 17, 18 and 23) to 140 (number 26) stomata per mm^2. Stomatal index varies from 0.75 (numbers 17, 18 and 23) to 13 (number 26).

Stomatal complexes of abaxial cuticles are usually formed by 2 guard cells, 2 big oblong or kidney-shaped lateral subsidiary cells and 2 small polar subsidiary cells. They are organised in well-defined stomatal rows that form stomatiferous bands. This type (numbers 16 to 20 and 23) probably belong to *Cordaites principalis* (Germar) Geinitz deduced from venation. Cuticular type number 21 has 2 prominent lateral subsidiary cells, polar subsidiary cells are small. Specimens numbers 22, 24 to 27 have stomatal complexes also oriented into stomatal rows. They differ in shape of guard cells and subsidiary cells. Stomatal density is 40 (number 27) up to 270 (number 16) per mm^2. Stomatal index varies from 3 (number 27) to 25 (number 16).

Cordaites of the Stephanian B of the Central Bohemian region (Slaný Formation) and the Intrasudetic Basin (Odolov Formation, Jívka Member

Fig. 4: 28, 29, 30

Cuticles of *Cordaites* of the Stephanian B of the Bohemian Massif have been not very well known. Type number 28 is hypostomatic and is comparable with some *Cordaites* cuticular types from the Westphalian D. Number 29 is amphistomatic. Stomata of adaxial cuticle are dispersed in wide dark bands. Its stomatal density is 8 stomata per mm^2 and stomatal index is 1 to 1.4.

Stomata of abaxial cuticles are oriented in stomatal rows, in the type 29 in stomatiferous bands. Stomatal density is from 150 to 286 per mm^2 and stomatal index is from 10 to 18.

Cordaites of the Autunian of the Krkonoše Piedmont Basin (Vrchlabí Formation, Rudník Horizon)

Fig. 4; 31 and 32

Only 2 cuticular types of *Cordaites* was distinguished in the Autunian of the Bohemian Massif. The venation of the first type (number 31) resembles to *Cordaites principalis* (Germar) Geinitz, (number 32) resembles to *Cordaites palmaeformis* (Goeppert) Weiss). Both are amphistomatic, subsidiary cells of the first type are very prominent. Normal cells of the second type serve as subsidiary cells. Stomatal density of the adaxial cuticle is 50 (number 32) and 123 (number 31). Stomatal index is 4 and 8.

Abaxial cuticle has cells and stomata of the similar shape. Stomatal density of the abaxial cuticle is 80–90 (number 32) and 130 (number 31). Stomatal index is 5 and 10.

CONCLUSION

26 or 27 cuticular types of *Cordaites* were described from the Carboniferous and Permian of the Bohemian Massif. The oldest known cuticles of *Cordaites* come from Langsettian of the Upper Silesian Basin, where 3 cuticular types of *Cordaites* were discovered. Three *Cordaites* cuticular types were recorded in the Duckmantian of the Intrasudetic Basin. The highest diversity of *Cordaites* cuticular structures is in Bolsovian of the Central Bohemian region, where 9 cuticular types were described. 6 or 7 cuticular types come from the Westphalian D of the Central Bohemian region. Cuticular structures of Stephanian and Autunian *Cordaites* are known only from several specimens. Therefore only 3 cuticular types of Stephanian and two cuticular types of Autunian *Cordaites* were described. Most *Cordaites* leaves are amphistomatic. *Cordaites* belong to the haplocheilic stomatal type.

Stomatal density and value of stomatal index vary in different abaxial cuticles of investigated *Cordaites*. It is interesting that these parameters change from one stratigraphical level to another. The lowest value of these parameters is in the Langsettian and Autunian, where stomatal density is approximately 80 to 130 stomata per mm^2 and stomatal index varies from 5 to 10. Value of stomatal density about 150 to 270 stomata per mm^2 is

in units from the Duckmantian to Stephanian B age (in the Bolsovian up to 400 stomata per mm^2). Stomatal index varies usually from 10 to 20 (up to 25 in the Westphalian D). Recently has been demonstrated (Van der Burgh et al. 1993) that plants of C^3 physiology respond developmentally to changing CO_2 pressures. An atmospheric increase of CO_2 over the past 200 years has resulted in a decrease in stomatal frequency on leaves of certain woody angiosperm (Woodward 1987). The stomatal resistance to CO_2 within the diffusion of the C3 plant leaf is mainly determined by frequency and size of stomata. Plants of C4 physiologies, first appearing in the Tertiary, have developed different metabolic pathways to compensate for changing atmospheric CO_2. It is believed that only plants of C3 physiologies existed in the Permo-Carboniferous. These preliminary data about stomatal density and stomatal index of *Cordaites* from the Bohemian Massif would be able to confirm the fluctuations in pCO_2 in the geological time that have wider relations to the greenhouse/icehouse changes during the Permo-Carboniferous (Wagner 1993).

This preliminary report only revealed large diversity of cuticular structures of *Cordaites* from the Carboniferous and Permian of the Bohemian Massif. The evaluation of cuticular structures, comparison of cuticles from the Bohemian Massif to that ones described by foreign authors (e.g. Harms and Leisman 1961, Barthel 1964, Pant and Verma 1964, Ledran 1966 and Rabitz 1966) and study of different *Cordaites* venation patterns will be subject for the future.

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