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Acta Palaeobotanica 57(2): 153–163, 2017
DOI: 10.1515/acpa-2017-0014

e-ISSN 2082-0259
ISSN 0001-6594

Revision of Pennsylvanian genus *Sturia* Němejc and its spores (Duckmantian, Czech Republic)

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Received 20 August 2017; accepted for publication 30 October 2017

ABSTRACT. *Sturia amoena* (Stur) Němejc is a Pennsylvanian adpression true fern known from the Charbonnière de Belle et Bonne (Belgium) and from the Radnice and Kladno-Rakovník basins (Czech Republic). This revision includes a detailed study of pinna and pinnule morphology, aphlebiae and reproductive organs. Interesting details of sporangia and *in situ* spores are described for the first time. The sporangia of *Sturia amoena* have an equatorial bi-triseriate annulus and yielded *in situ* spores of the *Punctatisporites* and *Apiculatisporites* types.

KEY WORDS: *Sturia*, ferns, Carboniferous, aphlebiae, sporangia, *in situ* spores

INTRODUCTION

The paper represents a revision and emendation of the Pennsylvanian genus *Sturia* Němejc, which belongs to the compressed fossil ferns with a sphenopteroid type of pinnule. The genus was established by Němejc (1934, p. 2) for fossil ferns with sterile fronds bearing aphlebiae, and fertile specimens with oval, free, sessile, annulate sporangia that form irregular groups. Němejc (1934) erected *Sturia amoena* (Stur) Němejc (originally *Hapalopteris amoena* Stur) as the type species of the genus. Although Stur's (1885, pl. 41, fig. 7) specimen of *Sturia amoena* is sterile and comes from the Charbonnière de Belle et Bonne, Avaleresse Mine, Belgium (Langsettian-Duckmantian), its conformity with fertile specimens from the Duckmantian of Czech Republic is indisputable (see later in Discussion). Němejc (1934, 1936) described sporangia of *Sturia* with one row of cells of the annulus from the ventral side, which is different from our observation. Němejc (1934) stated that sporangia (based on his mistaken description) of Czech specimens show similarities with the genera *Oligocarpia* Goeppert or *Boweria* Kidston. Based on the occurrence of aphlebiae on antepenultimate rachises and sporangia of *Sturia amoena*, features differing from *Oligocarpia* and *Boweria*, he established the new genus *Sturia*. Later Němejc (1963) described sporangia of *Sturia* with an incomplete vertical annulus (Němejc 1963, pl. 52, figs 1–6) and pointed to their similarity with *Boweria* and *Dendraena* Němejc (p. 427).

Danzé (1956) and Brousmiche (1983) followed Němejc's (1934) concept and newly described Stur's (1885) sterile specimen of *Sturia amoena*, and included another sterile specimen from the Nord de la France Basin and Sarre-Lorrain Basin in this species. Neither Danzé (1956) nor Brousmiche (1983) studied fertile specimens from Němejc's (1934) type collection. Danzé (1956) officially established a generic diagnosis of *Sturia* according to ICBN rules. The diagnosis corresponds with Němejc's

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(1934) description. Later, Brousmiche (1983) illustrated Stur's types (Stur 1885, pl. 41, fig. 7) and slightly extended Danzé's (1956) diagnosis. Gothan (1941), Danzé (1956) and Brousmiche (1883) synonymized *Sturia* (*Hapalopteris*) *amoena* with *Hapalopteris bella* Stur.

This paper gives new detailed information about Stur's and Němejc's (1934) type specimens of *Sturia amoena*. Stur's specimen was redrawn using a camera lucida, and Němejc's fertile specimen was successfully macerated. Maceration enabled a more precise description of the sporangia, especially the character of the annulus or position of the stomium together with *in situ* spores. Based on this new information it was possible to emend the generic and species diagnoses.

MATERIAL AND METHODS

We studied specimens from Stur's (GBA 1885/001/0022) and Němejc's (E5083, E5065) type collections. Stur's type specimen (GBA 1885/001/0022) is stored in the Geologische Bundesanstalt (GBA), Vienna, Austria. Němejc's specimens (E5083, E5065) are stored in the National Museum, Prague, Czech Republic. All of them are preserved as compressions in greyish silty claystone, and all specimens come from the same stratigraphic position, Langsettian-Duckmantian. Stur (1885) did not determine the coal seam but the Charbonnière de Belle et Bonne locality in Belgium is of Langsettian-Duckmantian age (Peppers 1996). The Břasy locality in the Radnice Basin, and Motyčín, district of Kladno-Švermov, in the Kladno-Rakovník Basin, Czech Republic, are also of Duckmantian age (Opluštil et al. 2016).

Destructive and non-destructive methods were used to observe the specimens. Non-destructive methods included drawing the fossils (GBA 1885/001/0022) using a camera lucida attached to a binocular microscope (Olympus SZX12). Sporangia of specimen E5083 were isolated from the rock matrix using 38% hydrofluoric acid for 24 h, and then washed in distilled water several times. Sporangia and *in situ* spores were selected and examined using several SEMs, including a JEOL 6380LV (Institute of Geology and Palaeontology, Faculty of Sciences, Charles University, Prague), Tescan VEGA3 XMU (Institute of Geology of the Czech Academy of Sciences, v.v.i., Prague), and Hitachi S-3700N (National Museum, Prague). Other sporangia were macerated in Schulze's solution (Schulze 1855, Frojdová et al. 2017a), washed in distilled water several times, percolated with potassium hydroxide (10%) to remove oxidation products, and washed again in distilled water. Macerated sporangia and *in situ* spores were observed by SEM. *In situ* spores were recovered by dissolving sporangia taken from fertile fronds in Schulze's solution. Some *in situ* spores were mounted in glycerine jelly for direct light microscopic examination.

All digital photos of sporangia and *in situ* spores are housed in the National Museum, Prague, Czech Republic; Geologische Bundesanstalt, Vienna, Austria; and the Institute of Geology of the Czech Academy of Sciences, v.v.i., Prague, Czech Republic. SEM tubes with sporangia and slides of specimens from Němejc's collection are stored in the National Museum, Prague, Czech Republic.

Descriptive terms for the spores follow the latest edition of the *Glossary of Pollen and Spore Terminology* (Punt et al. 2007). Spores are classified according to the system of dispersed spores given by Potonié and Kremp (1954, 1955), and Smith and Butterworth (1967). *In situ* spores were compared directly with the original diagnoses, type specimens, descriptions, and illustrations of dispersed spore species. Species determinations are based only on the original diagnoses, and not on the interpretations of subsequent authors.

SYSTEMATICS

Class Filicopsida

Order Filicales

Family *Incertae sedis*

Genus: ***Sturia*** Němejc 1934

Emended diagnosis. Pinnae triangular-ovate; aphlebiae developed; pinnules sphenopteroid, deeply lobate; sporangia leptosporangiate, irregularly grouped, free, sessile, equatorial bi-triseriate annulus; septaseriate stomium; rounded apical cell; trilete circular to subcircular laevigate, microconate, microgranulate to laevigate microspores.

Type species. *Sturia amoena* (Stur 1885) Němejc (1934).

Sturia amoena (Stur) Němejc

1885 *Hapalopteris amoena* Stur, p. 52, pl. 41, figs 7, 7a.

1923 *Sphenopteris amoenaeformis* Kidston, p. 125, pl. 25, fig. 6, pl. 26, figs 1–3b.

1934 *Sturia amoena* Němejc, p. 2, pl. 1, figs 1–6.

1941 *Sphenopteris* (? *Renaultia*) *amoena* Gothan, p. 29, pl. 60, figs 1, 4.

1983 *Sturia amoena* (Stur) Němejc; Brousmiche, p. 273, pl. 73, figs 1, 3–6.

Lectotype. coll. No GBA 1885/001/0022, Geologische Bundesanstalt, Vienna, Austria.

Type locality. Charbonnière de Belle et Bonne, mine Avaleresse (Crépin).

Type horizon. Langsettian-Duckmantian.

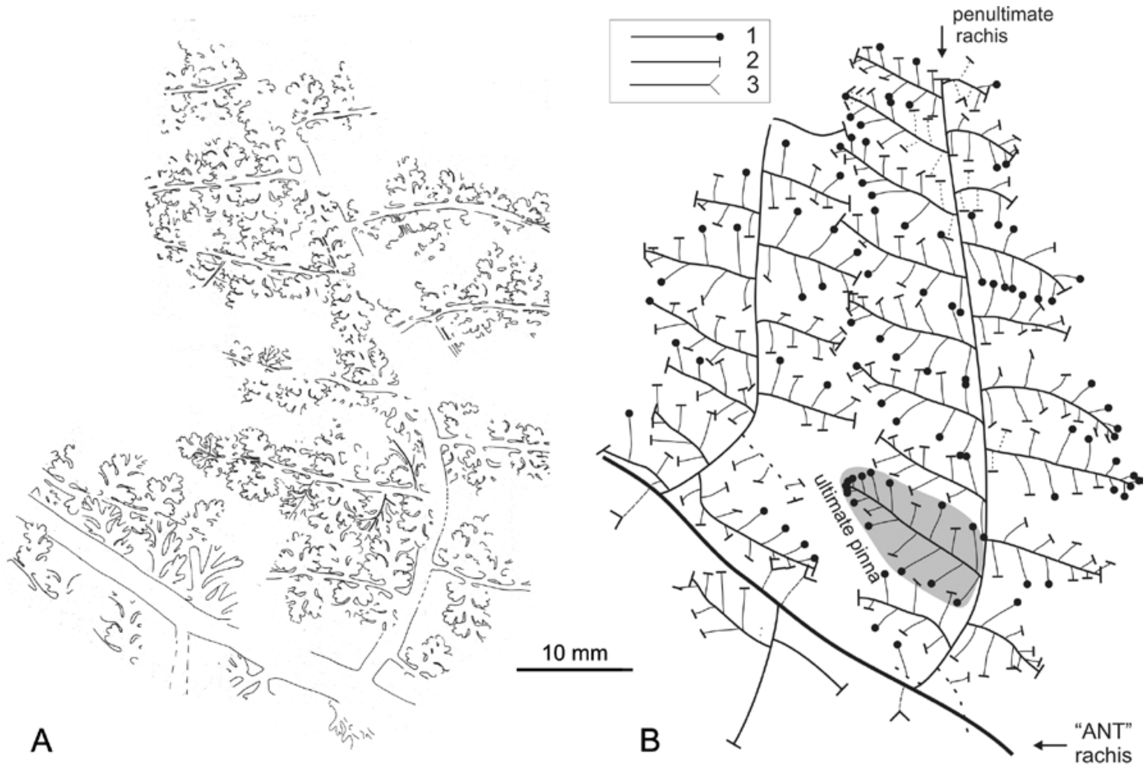


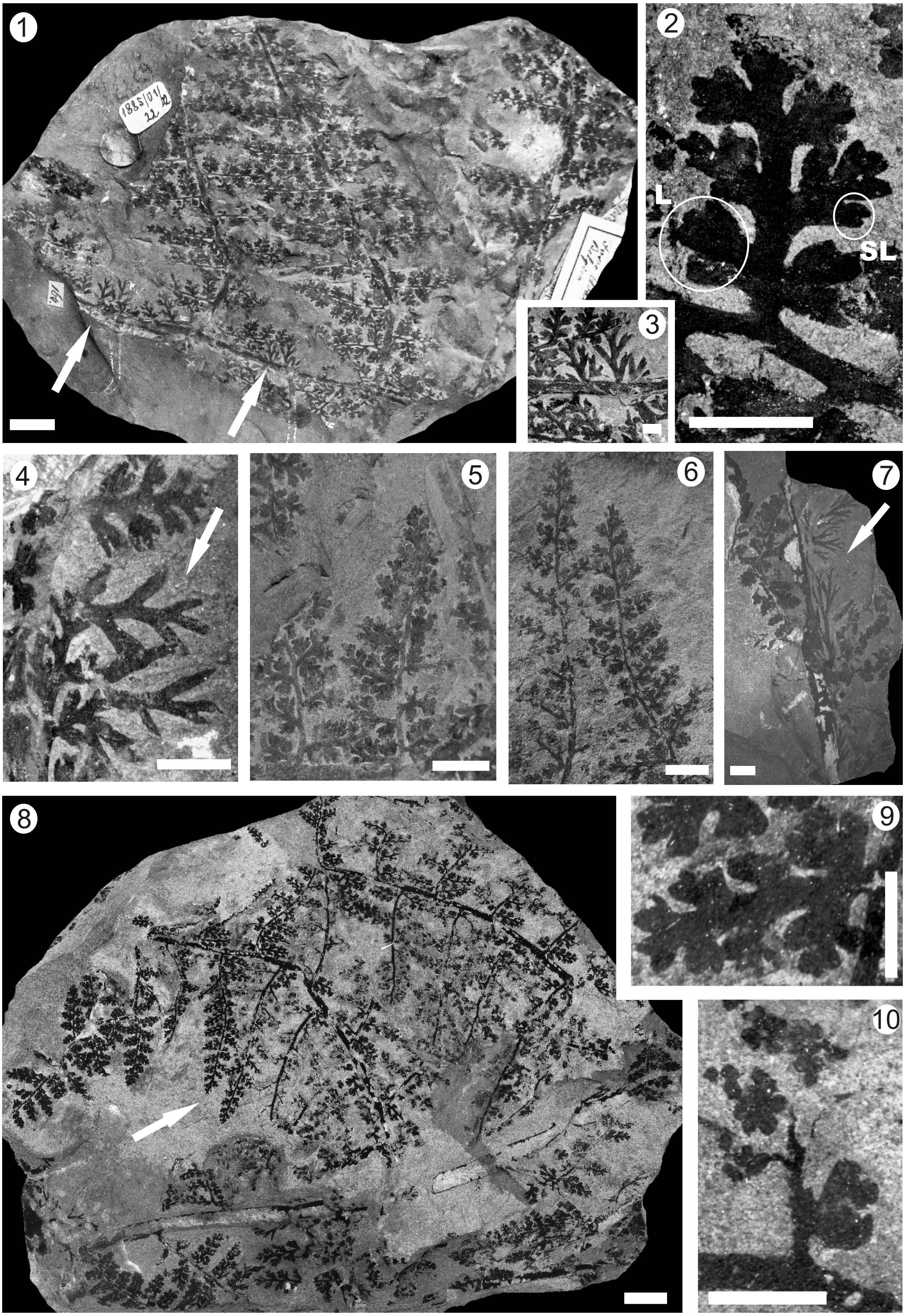
Fig. 1. **A**. *Sturia amoena* (Stur) Němejc, lectotype GBA 1885/001/0022, selected best-preserved part of penultimate pinna attached to antepenultimate rachis with aphlebiae, camera lucida drawing; **B**. Rachis diagram of *Sturia amoena* (Stur) Němejc, lectotype GBA 1885/001/0022, **1** – complete pinna/rachis, **2** – incomplete pinna/rachis, **3** – aphlebiae, **ANT** – antepenultimate

Emended diagnosis. Frond segments at least tripinnate, antepenultimate rachis with aphlebiae, winged; aphlebiae horn-fork-shaped, divided into several laminar segments; penultimate rachises winged; ultimate pinnae triangular-ovate; pinnules ovoid to elongated-ovoid; rounded deeply lobed; U-shaped gap between two adjacent lobes; lateral veins bifurcated three times; sporangia irregularly grouped 12–32 per group, ovoid-shaped, annulate; two-three irregular rows of cells forming equatorial annulus occupying half to three-quarters of sporangium circumference; stomium of seven to eight rows of elongated, thick-walled cells; apical cell at top of sporangium; trilete circular to subcircular laevigate, microconate, microgranulate to laevigate microspores.

Description. The lectotype (specimen GBA 1885/001/0022) from Stur's collection and a specimen (E5065) from Němejc's collection show pinnae attached to antepenultimate rachises (for all measurements see Tab. 1). The antepenultimate rachises are very slightly sinusoidal, winged, and have longitudinal striation (Pl. 1, figs 1, 7). Horn-fork-shaped aphlebiae (Pl. 1, figs 3, 4, 7 arrows) are attached to the antepenultimate rachises (E5065 and GBA 1885/001/0022). The aphlebiae are more than 20 mm long and 7.75 mm wide at the base, divided into several laminar segments (Pl. 1, figs 3, 4, 7 arrows). Penultimate rachises are preserved on all specimens (GBA 1885/001/0022, E5083, E5065) from both collections. The penultimate rachises are winged (for all measurements see Tab. 1), almost straight (Fig. 1A; Pl. 1, figs 1, 8), alternating on the antepenultimate rachis (Fig. 1A, B; Pl. 1, figs 1, 8) and inserted at 80°–90° (Pl. 1, figs 1, 8). It is not possible to determine the general shape of the penultimate

Table 1. Measurement of rachises and pinnules of *Sturia amoena* (mm) from Stur's specimen (1885/01/22) and Němejc's specimens (E5083 and E5065). Numbers in brackets show size with winged lamina. * – incomplete pinnules

Specimen No.	Antepenultimate rachis	Penultimate rachis	Ultimate rachis	Pinnules		Lobes
				Lenght	Width	
GBA 1885/01/22	2 (4)	0.9 (1.9)	0.5–0.6	4.2–7.0	4.0–4.5	2.0–2.2
E 5083	xxx	1.1 (1.9)	0.5–0.7	7.0–8.0	4.0–4.5	2.0–2.2
E 5065	1.9 (4)	0.8 (2.1)	0.5	4.0–4.5*	3.0–3.4*	1.1–1.6*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pinnae because they are not preserved as whole pinnae. From the size of the pinna fragments it can be inferred that penultimate pinnae could reach up to 95 mm in length (Pl. 1, figs 1, 8). The ultimate rachises (for all measurements see Tab. 1) are very slightly sinusoidal (Fig. 1A, B; Pl. 1, figs 1, 5, 6, 8), alternating on the penultimate rachis (Fig. 1A, B; Pl. 1, figs 1, 8), inserted at 58°–75° (Pl. 1, figs 1, 8). The ultimate pinnae are triangular-ovate (Fig. 1A, B; Pl. 1, figs 1, 5, 6, 8), 20–47 mm long and 8–15 mm wide at the broadest (proximal) part of the pinna. The ultimate pinnae situated in the upper part of penultimate pinnae merge into pinnatified pinnules (Pl. 1, figs 5, 6). The largest and most complete ultimate rachis bears up to 23 pinnules (Pl.1, fig. 8 arrow). The pinnatified pinnules (for all measurements see Tab. 1) alternate on ultimate rachises (Pl. 1, figs 2, 5, 6, 8), and are ovoid to elongated-ovoid (Fig. 1A, Pl. 1, figs 2, 9, 10), with a deeply lobate smooth margin (Fig. 1A; Pl. 1, figs 2, 9, 10). Each pinnule bears up to 9 rounded lobes (Fig. 1A, B; Pl. 1, figs 2 "L", 9, 10). The area between two adjacent lobes is U-shaped (Pl. 1, figs 2, 9, 10; Pl. 2, fig. 1). Each lobe of a pinnule is additionally divided into 4–6 small sub-lobes (Plate 1, 2 "SL"). The midvein is almost straight (Pl. 1, figs 2, 9, 10; Pl. 2, fig. 1) and divided at the distal end of the pinnules (Fig. 1A). The lateral veins are bifurcated up to three times and end in sub-lobes (Fig. 1A).

Fertile pinnule are identical with sterile ones (Pl. 1, figs 2, 9). Sporangia are situated at the end of sub-lobes (Pl. 1, figs 8, 10; Pl. 2, fig. 1). The sporangia are irregularly grouped in a sorus (Pl. 1, fig. 10; Pl. 2, fig. 1) often overlapped by whole pinnule lobe lamina (Pl. 2, fig. 1 arrows). It is not possible to determine if the sporangia arise from the pinnule lamina or from lateral veins. Each pinnule lobe contains an irregular group of 12–32 sporangia (Pl. 2, figs 1, 2). The sporangia are free, sessile on the pinnule, ovoid in shape and annulate, with their longer axis 340–375 µm and their shorter axis 300–325 µm (Pl. 2, figs 2–4). The sporangial wall consists of one sporangial cell layer differentiated into three types of sporangial cells: cells of the annulus, stomium, and apical cell.

The cells of the annulus are located in the equatorial region of the sporangium (Pl. 2, figs 2–5) and occupy a half to three-quarters of the sporangium circumference (Pl. 2, figs 2–5). The annulus consists of 2–3 irregular rows of thick-walled elongated tetragonal/polygonal cells (Pl. 2, figs 2–5) which are 67–96 µm long and 22–46 µm wide. The anticlinal walls of cells are straight. The annulus can be classified as an equatorial type and is located approximately at the equatorial area of the sporangium, with an oblique shape and occupying a half to three-quarters of the sporangium.

The stomium (Pl. 2, fig. 4 "SC") consist of 7–8 rows of thick-walled elongated cells, 51–60 µm long and 8–13 µm wide. The anticlinal walls are straight. The stomium comes from the apical cell, interrupts the annulus ring in the equatorial region and ends near the sporangial base.

The apical sporangial cell (Pl. 2, fig. 4 "APC") is tetragonal, thick-walled and located between annulus cells and stomium cells (Pl. 2, fig. 4). The apical cell is 31 µm long and 19 µm wide.

In situ spores. Trilete circular to subtriangular microspores 30 (37) 42 µm in diameter. Rays of the trilete mark reach a half to two-thirds of the radius. The sculpture is microgranulate, and microconate (Pl. 2, fig. 6) to laevigate (Pl. 2, figs 7, 8).

Remarks. Two sets of microspores were macerated. The first group is represented by laevigate forms that can be assigned to the dispersed miospore genus *Punctatisporites* Ibrahim. The second type of microspore has microgranulate

←

Plate 1. **1**. *Sturia amoena* (Stur) Němejc, specimen GBA 1885/001/0022 (lectotype), stored in the Geologische Bundesanstalt, Vienna, Austria. Sterile specimen with antepenultimate rachis with aphlebiae (arrows) and several incomplete penultimate pinnae; scale bar 10 mm; **2**. *Sturia amoena* (Stur) Němejc, specimen GBA 1885/001/0022 (lectotype). Detail of sterile pinnule with seven incomplete lobes; scale bar 2 mm **3**. *Sturia amoena* (Stur) Němejc, specimen GBA 1885/001/0022 (lectotype). Detail of antepenultimate rachis with first preserved aphlebiae, scale bar 2 mm; **4**. *Sturia amoena* (Stur) Němejc, specimen GBA 1885/001/0022 (lectotype). Detail of second preserved aphlebiae (arrow), antepenultimate rachis is covered by pinnules, scale bar 3 mm; **5**. *Sturia amoena* (Stur) Němejc, specimen GBA 1885/001/0022 (lectotype). Detail of penultimate pinnae, scale bar 5 mm; **6**. *Sturia amoena* (Stur) Němejc, fertile specimen E5083, stored in National Museum, Prague, Czech Republic. Fertile specimen with the best-preserved ultimate pinnae, scale bar 5 mm; **7**. *Sturia amoena* (Stur) Němejc, specimen E5065, stored in National Museum, Prague, Czech Republic. Sterile specimen with antepenultimate rachis with aphlebiae (arrow), scale bar 4 mm; **8**. *Sturia amoena* (Stur) Němejc, fertile specimen E5083, stored in National Museum, Prague, Czech Republic. Fertile specimen with several incomplete penultimate pinnae, ultimate pinnae with the largest number of pinnules (arrow), scale bar 10 mm; **9**. *Sturia amoena* (Stur) Němejc, fertile specimen E5083. Detail of pinnule with eight lobes, scale bar 2 mm; **10**. *Sturia amoena* (Stur) Němejc, fertile specimen E5083. Detail of pinnule showing lobes covered by groups of sporangia, scale bar 2 mm

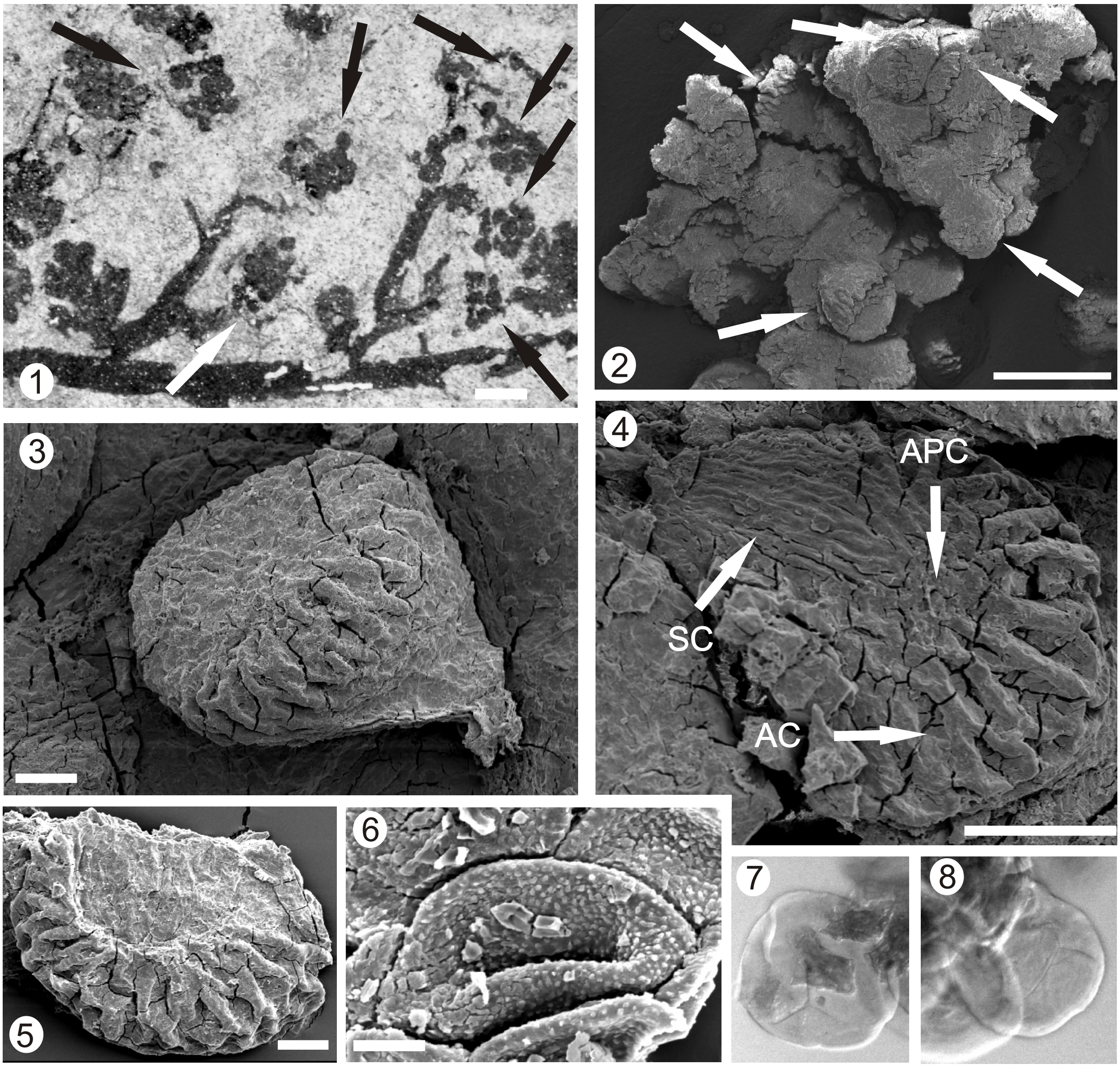

Plate 2. **1**. *Sturia amoena* (Stur) Němejc, fertile specimen E5083. Detail of pinnule showing lobes covered by groups of sporangia (arrows), scale bar 1 mm; **2**. *Sturia amoena* (Stur) Němejc, specimen E5083. Detail of irregularly grouped sporangia with annuli (arrows), SEM, scale bar 500 µm; **3**. *Sturia amoena* (Stur) Němejc, specimen E5083. Detail of sporangium with preserved equatorial annulus, SEM, scale bar 50 µm; **4**. *Sturia amoena* (Stur) Němejc, specimen E5083. Detail of sporangium with cells of annulus (AC), cells of stomium (SC) and apical cell (APC), SEM, scale bar 100 µm; **5**. *Sturia amoena* (Stur) Němejc, specimen E5083. Detail of annulus having three irregularly rows of thick-walled cells, SEM, scale bar 50 µm; **6**. *Sturia amoena* (Stur) Němejc, specimen E5083. *In situ* microspores of the *Punctatisporites* type. Note finely microgranulate to microconate sculpture of distal surface. SEM, scale bar 10 µm; **7**, **8**. *Sturia amoena* (Stur) Němejc, specimen E5083. *In situ* microspores of the *Apiculatisporites* type. Note the rays of trilete mark and laevigate sculpture ×500

to microconate sculpture elements and can be referred to the dispersed miospore genus *Apiculatisporites* (Ibrahim) Potonié and Kremp.

DISCUSSION

The results of our new research confirm Němejc's (1934) opinion that his fertile specimen represents a new genus different from *Boweria*, *Oligocarpia* and *Dendraena*. The problem arises from the fact that Němejc (1934) (and later Brousmiche in 1983) established a sterile specimen of *Sturia amoena* as the type of the genus. The main question is whether Stur's specimen (lectotype) is identical with Němejc's fertile specimens. It needs to be stressed that Němejc (1934) never saw Stur's specimen. This is why we studied both Stur's sterile and Němejc's sterile and fertile specimens. All specimens have the same measurements of all rachises (Tab. 1) and the same shape of ultimate pinnae

Table 2. List of plants producing miospores of the *Punctatisporites* and *Apiculatisporites* type; **A** – annulus, **Eq** – equatorial annulus, **O** – oblique annulus, **L** – different forms of lateral annulus, **O/L** – incomplete oblique annulus, **Z** – zygopterid fern, **E** – eusporangiate fern, **S** – seed ferns, **G** – gymnospermopsida

Parent plants	A	Diameter of *in situ* microspores (µm)	Classification of *in situ* microspores	References
Sturia amoena	Eq	35–53	*Punctatisporites* spp., *Apiculatisporites* spp.	Herein
Corynepteris scottii	Z	50	*Apiculatisporites aculeatus*	Galtier & Holmes 1976
Corynepteris sp. cf. *C. erosa*	Z	38–80	*Apiculatisporites* spp.	Pfefferkorn et al. 1971
Corynepteris sp.	Z	39–54	*Apiculatisporites* spp.	Trivett 1974
Corynepteris (?) sp.	Z	40–50	*Apiculatisporites* spp.	
Corynepteris involucrata	Z	50	*Punctatisporites* spp.	Balme 1995
Stauropteris oldhamia	Z	32–42	*Punctatisporites* spp.	Scott 1920, Potonié 1962
Pecopteris aspidoides	E	100–140	*Punctatisporites* spp.	Brousmiche et al. 1985
P. sp. (?) *P. densifolia*	E	56–124	*Punctatisporites* spp.	Laveine 1970, Barthel 1967
Radstockia kidstonii	E	40–60	*Punctatisporites* spp.	Taylor 1967, 1981
R. sphenopteroides	E	20–22	*Punctatisporites* spp.	Brousmiche 1983
Scolecopteris latifolia	E	32–42	*Punctatisporites obliquus*	Millay 1979, Mamay 1950, Millay & Taylor 1984
S. majopsis	E	64–115	*Punctatisporites* spp.	Millay 1979
S. major	E	45–55	*Punctatisporites* spp. ?	Mamay 1950, Taylor 1981
S. charma	E	49–64	*Apiculatisporites* spp.	Lesnikowska & Millay 1985
S. iowensis	E	57–83	*Punctatisporites* spp.	Millay 1979
S. mamayi	E	14–21	*Punctatisporites* spp.-*Leschikisporites* spp.-*Latosporites globosus*	Millay 1979, Millay & Taylor 1984
S. nigra	E	37–50	*Punctatisporites nahannensis*	Millay & Taylor 1984
S. revoluta	E	11–16	*Punctatisporites* spp. ?	Millay 1979
S. saharaensis	E	14–19	*Punctatisporites* spp.	Millay & Taylor 1984, Millay 1979, Taylor 1981
S. (?) sp. 1	E	16–23	*Punctatisporites* spp.	Pfefferkorn et al. 1971
Conostoma villosum	S	65	*Punctatisporites* spp.	Rothwell & Eggert 1970
Eccroustosperma langtonense	G	42–50	*Punctatisporites* spp.	Balme 1995
Kidstoniopteris minor	L	39–50		
		27–44	*Leiotriletes*, *Granulatisporites*, *Punctatisporites*	Frojdová et al. 2017a
Boweria schatzlarensis	L	32–58	*Leiotriletes gulaferus*	Brousmiche 1983
		32–58		
		27–44	*Granulatisporites*-type	Frojdová et al. 2017a
Oligocarpia gutbieri	O	20–35	*Leiotriletes gulaferus*, *Granulatisporites*	Brousmiche 1983, Remy & Remy 1957
Oligocarpia sp. cf. *O. mixta*		21–26	*Leiotriletes-Granulatisporites*	Brousmiche 1983
Oligocarpia lindsaeoides		20–39	*Leiotriletes subadnatoides*	Pšenička & Bek 2001
Oligocarpia brongniartii		35–36	*Leiotriletes-Apiculatisporitess*	Brousmiche 1983
		21–30	*Granulatisporites* sp.	
Oligocarpia cliveri		30–35	*Leiotriletes sphaerotriangulus*, *L. levis*	Remy & Remy 1957
Oligocarpia mixta		31	*Leiotriletes* sp.	Abbott 1954
Oligocarpia leptophylla		32–49	*Granulatisporites parvus*	Grauvogel-Stamm & Doubinger 1975
Oligocarpia bellii		19–31	*Granulatisporites* sp.	Zodrow et al. 2005
Sonapteris bathelii	L		*Leiotriletes* sp., *Granulatisporites* sp.	Pšenička et al. 2005
Renaultia sp.	x	25	*Leiotriletes* sp.	Remy & Remy 1957
Renaultia germanica		27–33	*Leiotriletes* sp.	Brousmiche 1986
Renaultia villosa		25	*Granulatisporites-Leiotriletes*	Brousmiche 1983
Renaultia crepini			*Leiotriletes* sp.	Brousmiche 1983, 1986
?*N. gen.* et sp.	?	30–35	*Leiotriletes gulaferus*	Remy & Remy 1957
Tenchovia bulgarensis	L	17–23	*Granulatisporites minutus*	Pšenička & Bek 2004
Discopteris occidentalis	L	15–23	*Leiotriletes* sp.	Brousmiche 1986
Discopteris karwinensis		21–57	*Leiotriletes parvus*	Balme 1995
		21–57	*Leiotriletes-Punctatisporites-Granulatisporites*	Brousmiche 1983
Discopteris schumannii		40–15	*Leiotriletes* sp.	Brousmiche 1986
Discopteris opulenta		36–61	*Leiotriletes* sp.	Brousmiche 1979

Table 2. Continued

Parent plants	A	Diameter of *in situ* microspores (μm)	Classification of *in situ* microspores	References
Myriotheca sp. cf. *M. scaberrima*	E		*Leiotriletes* sp. (immature)	Balme 1995
Grambastia goldenbergii	O	24–42	*Leiotriletes* sp.	Brousmiche 1986
Musatea duplex	Z	37–52	*Leiotriletes* spp. – *Punctatisporites* spp.	Chaphekar & Alvin 1972, Taylor 1981
Doneggia complura	O		*Leiotriletes* sp.	Rothwell 1978
Doneggia complura			*Leiotriletes levis*	Balme 1995
Norwoodia angustum	L	16–25	*Leiotriletes* sp.	Rothwell 1976
Sermaya biseriata	O		*Leiotriletes* sp.	Eggert & Delevoryas 1967
			Leiotriletes sp.	Balme 1995
Dendraena pinnatilobata	L	21 (27.4) 48	*Microreticulatisporites harrisonii*	Němejc 1934, Frojdová et al. 2017b
Kidstonia	O/L		unknown	Zeiller 1897, 1899

(triangular-ovate) with deeply lobate pinnules, and individual lobes have other sub-lobes (Pl. 1, figs 1, 2, 5, 6, 8, 9).

In situ microspores isolated from *Sturia amoena* belong to the morphologically simplest spore types: they possess a simple trilete mark, thin exine, no thickening, zona, pseudosaccus, etc., and laevigate (*Punctatisporites* type) and micrognulate to microconate (*Apiculatisporites* type) sculpture of both surfaces (Pl. 2, figs 6–8). Both sets of microspores differ only in their sculpture; all other morphological features including diameter are the same. Two types of *in situ* microspores of the *Punctatisporites* and *Apiculatisporites* types are interpreted as relatively mature, while the laevigate specimens correspond to immature microspores. This feature is described from several fertile Carboniferous ferns (e.g. Pšenička et al. 2005, Bek & Pšenička 2001, Pšenička & Bek 2003, 2008, Frojdová et al. 2017a, b, Zodrow et al. 2006).

Microspores assigned to the same miospore genera are known mainly from zygopterid and marattialean ferns (Tab. 2), including the genera *Corynepteris* Baily, *Musatea* Galtier, *Stauropteris* Binney, *Pecopteris* Brongniart, *Radstockia* Kidston, *Scolecopteris* Zenker, *Conostoma* Williamson and *Eccroustosperma* Long (Balme 1995). However, *Sturia* is a leptosporangiate fern. That is the main difference from all the afore mentioned genera. It means that palynologically all these taxa are similar but that there are crucial differences in the morphology of their reproductive organs. The reason for that is that these microspores represent morphologically simple spore types; all such simple types could be produced by more than one parent plant genus, often of different groups (Balme 1995).

We compared genera with sphenopteroid-type pinnules, grouped sporangia and/or the same type of *in situ* spores (Tab. 2). We excluded genera with sporangia grouped into sori, such as *Discopteris* Stur, *Chansitheca* Halle, *Grambastia* Brousmiche, *Tenchovia* Pšenička & Bek, *Oligocarpia* Goeppert, *Sermaya* Eggert & Delevoryas and *Doneggia* Rothwell. *Renaultia* Zeiller has exannulate sporangia (e.g. Zeiller 1883, Danzé 1956, Brousmiche 1983). *Myriotheca* Zeiller is interpreted as an eusporangiate fern (Brousmiche 1983). *Sonapteris* Pšenička et al. belongs to the botryopterid ferns with sporangia solitary or in clusters, with a pedicel and bi-triseriate lateral annulus (Pšenička et al. 2005). This type of sporangia differs from those of *Sturia*. *Norwoodia* Good & Rothwell was designated a fern belonging to *Psalixochlaneaceae*, a group characterized by having sporangia with an oblique-horizontal-lateral and bi-triseriate annulus and multiseriated stalk. The main difference is that *Sturia* does not have a stalked sporangia. The other genera are *Boweria* Kidston, *Dendraena* Němejc, *Kidstonia* Zeiller and *Kidstoniopteris* Frojdová et al., which are discussed in detail. The main difference between *Sturia* and *Kidstonia* is that *Kidstonia* has sporangia on the lower side of the pinnules close to the pinnule base, and *Sturia* has sporangia placed at the end of the pinnule lobes. The other genus, *Kidstoniopteris*, has very similar characteristics, including aphlebiae and irregularly grouped or solitary sporangia attached to the pinnule lamina, placed on the pinnule lobe margin. It corresponds to *Sturia*, but *Kidstoniopteris* sporangia are stalked with a lateral annulus of semi-equatorial type and laminar or deeply laminar lobate pinnules, while the sporangia of *Sturia* are sessile with an equatorial type of annulus and pinnules with a deeply lobate margin (Frojdová et al. 2017a). The genus *Boweria* has pinnules with a deeply lobate margin and rounded lobes. The sporangia of *Boweria* are free, stalked marginal sporangia and have a lateral shield-like annulus (Frojdová et al. 2017a). The ungrouped and stalked sporangia do not correspond to *Sturia*. Although the genus *Dendraena* also has irregular groups of sporangia (7–18 sporangia per group) with a band-lateral-upper annulus, the type of *in situ* spore (*Microreticulatisporites* type) is very different (Tab. 2), as is the type of pinnule. *Dendraena* has a more laminar lobate pinnule but *Sturia* has a more deeply lobate pinnule (12–32 sporangia per group) with an equatorial annulus.

Němejc (1934) assigned this genus to the leptosporangiate ferns but did not macerate and did not see Stur's specimen. Němejc's observation was based only on Stur's illustrations (Stur 1885, pl. 41, figs 7, 7a). According to our observations, the fertile and sterile specimens agree in all morphological details. However, the anatomy of the plant is unknown, so *Sturia amoena* cannot be clearly classified within the plant system. Nevertheless, the sporangia of *Sturia* show great similarity with *Kidstoniopteris* or *Dendraena*, which appeared in approximately the same stratigraphic position (Duckmantian). All of these genera have irregularly grouped sporangia with an equatorial or oblique or band-lateral annulus, and *Kidstoniopteris* produced similar types of microspores (Tab. 2).

Němejc (1934) stated that *Sturia*, *Dendraena* and *Boweria* are close to the *Gleicheniaceae*, *Schizaeaceae* or *Hymenophyllaceae*, but the correct systematic positions of *Boweria* and *Sturia* genera are still unknown due to the absence of specimens showing anatomical preservation, in contrast with *Dendraena*. *Dendraena* pinnae were borne on the rachides of the *Anachoropteris robusta*-type and therefore falls in the family *Anachoropteridaceae* (Frojdová et al. 2017b). The anatomy of *Sturia* is unknown but the *in situ* spores are very different, and we can exclude a relationship with *Dendraena*. Němejc (1934) also noted similarity with *Schizaeaceae*, but this family has solitary, stalked sporangia with an apical annulus (Bower 1923), so it is not possible to place the genus *Sturia* in the *Schizaeaceae*.

The family *Sermayaceae* includes two genera, *Sermaya* and *Doneggia* (Taylor et al. 2009), which have sphenopterid pinnules and a similar type of annulus (oblique) but a different type of *in situ* spores (Tab. 2). The Pennsylvanian species *Oligocarpia lindsaeoides* (Pšenička & Bek 2001) probably also belongs to *Sermayaceae*, but the genus *Oligocarpia* has regularly grouped sporangia, as does *Discopteris*, unlike *Sturia*. Although some species of *Discopteris* or *Oligocarpia* have the same type of *in situ* spores (Tab. 2), *Sturia* has irregularly grouped sporangia; this is an important character.

Whereas the gleicheniaceous fossil remains are probably from the Carboniferous-Permian boundary (Yao & Taylor 1988, He et al. 2016), and these fossil records of the genera *Chansitheca* or *Szea* [*Leiotriletes* type (He et al. 2016) or *Triquitrites* type (Yao & Taylor 1988)] have sporangia regularly grouped into sori and a different type of *in situ* spores, in comparison with *Sturia* which have irregularly grouped sporangia, it is not possible to place this genus in *Gleicheniaceae*. We note that sporangia with *in situ* spores of *Sturia* are most similar to those of the genus *Kidstoniopteris* but that their systematic position is unknown due to the absence of anatomy.

ACKNOWLEDGEMENTS

We are grateful to I. Zorn (Geologisches Bundesanstalt, Vienna) and M. Libertín (National Museum, Prague) for providing access to the specimens in the collections of their institutions, to S. Opluštil for discussions about stratigraphy, and to H. Pfefferkorn and Z. Šimůnek for checking the English and for their comments. SEM observations were made in the Institute of Geology of the Czech Academy of Sciences, v.v.i., Prague, by N. Mészárosová; in the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague, by M. Mazuch; and in the National Museum, Prague, by L. Váchová. This paper was prepared with financial support from the Grant Agency of Charles University (GAUK 704216) and from the Research Plan of the Institute of Geology of the Czech Academy of Sciences, v.v.i., RVO67985831.

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