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Dispersed cuticles and conducting tissue of *Sphenophyllum* BRONGNIART from the Westphalian D of Kalinovo, Donets Basin, Ukraine

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ABSTRACT

Upper Westphalian coals are usually rich in organic-matter of different plant taxa, including gymnosperms. The assemblage from Kalinovo (Eastern Ukraine) is exceptional in being dominated by *Sphenophyllum*, both cuticles and conducting tissues. *Sphenophyllum* cuticles are easily distinguished by their parallel oriented cells with sinuous anticlinal walls, and paracytic stomata on the abaxial cuticle. Tracheids with multiseriate bordered pits that occur in *Sphenophyllum* can be also found in the Calamitaceae and some pteridosperms. However, rectangular shaped remains of parenchyma cell strips along the radial wall of tracheids are only known in *Sphenophyllum*.

Keywords: *Sphenophyllum,* dispersed cuticles, Carboniferous – Westphalian, Donets Basin

1. INTRODUCTION

The genus *Sphenophyllum* BRONGNIART belongs to the sphenopsids and is characterized by linear, spatulate or fan-shaped leaves that extend up to several cm in length. The leaves are arranged along the axis in nodal whorls of six or nine. The name *Sphenophyllum* is used for both impression-compression and petrified Permo-Carboniferous samples.

Although more than 100 compression-impression and petrified *Sphenophyllum* species have been described in the world, cuticles are known only from 15 of those species. The cuticles known so far, have been prepared by maceration of coalified *Sphenophyllum* leaves; studied directly on fossils by means of optical techniques (BARTHEL, 1997); or studied in sections of coal balls (GOOD, 1973). This paper brings unique information on sphenophyllalean cuticles and conducting tissue obtained directly from the coal. Unfortunately, taxonomic affiliation was not possible because the leaf outline is not preserved. Similar cuticles have only been previously observed in *Sphenophyllum priveticense* LIBERTÍN et al., 2014. We presume that both species lived under similar conditions in a peat-swamp, however, they come from different geographical regions and stratigraphical horizons. *Sphenophyllum priveticense* is known from the lower Bolsovian (middle Westphalian) of Central Bohemia, whereas the *Sphenophyllum* sp. studied in this paper occurs in the uppermost Asturian (uppermost Westphalian) of the Kalinovo locality, Donets Basin, Ukraine.

2. GEOLOGICAL SETTING

The Carboniferous sequence in the research area transgressively overlies marine and younger terrestrial Devonian deposits. Carboniferous and Permian deposits in the southeastern part of the Donets Basin achieve a thickness of 12 km. Coal-bearing cyclothems consist of basinal marine to shallow marine claystones and limestones with marine fauna; and terrestrial sandstones, siltstones, claystones with roots, and coal (HAVLENA, 1965). Lithostratigraphic units are marked with letters and their subunits by letters with numbers; limestones with capital letters and coal seams above the limestone with corresponding small letters (Fig. 1).

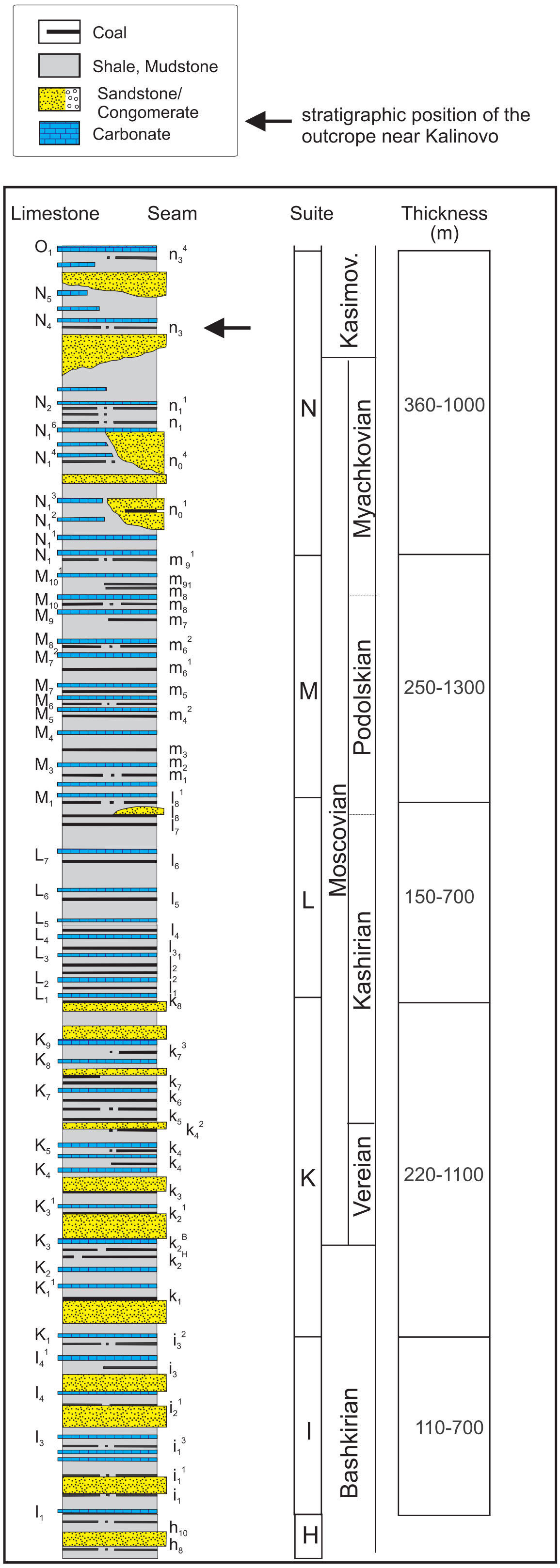

Figure 1: Stratigraphy of the Pennsylvanian of the Donets Basin. The coal sample was taken from the upper part of the section. Adapted from PRIVALOV et al. (2005).

Figure 2: Map of Ukraine with Kalinovo locality highlighted.

Limestone N_3 in the Isayevskaya Suite (Formation) is overlain by a 7 m thick sequence of unfossiliferous bluish-grey claystones and siltstones and about 30 m of fine-grained sandstones (AIZENVERG et al. 1975). Mudstones with roots and coal seam no. n_3 (0.3 m thick) are located above the sandstone. A sample from this coal seam from the Kalinovo locality, which is situated about 55 km W. from Luhansk in the Donets Basin (Fig. 2) was macerated for dispersed cuticles (sample position: N = 48° 35.355'; E = 38° 31,956'; H = 123 m). Above the coal seam, there are mudstones and claystones of lacustrine origin. *Stigmaria* occurs in the rooted horizon, while *Linopteris obliqua* (BUNBURY) ZEILLER, *Neuropteris ovata* HOFFMANN, *Laveineopteris rarinervis* (BUNBURY) CLEAL et al., *Alethopteris* sp., *Annularia sphenophylloides* (ZENKER) GUTBIER and *Pecopteris* sp. have been determined above the coal seam (AIZENVERG et al. 1975). This flora is of Asturian (Westphalian D) age and is the youngest Westphalian flora found in the Donets Basin.

3. MATERIAL AND METHODS

In order to obtain cuticles authors applied a new method. A 2.5 g sample of coal was macerated in Schulze's reagent: 35 ml concentrated (65%) nitric acid (HNO_3) and 1.5 g of potassium chlorate ($KClO_3$) for 2 days and 18 hours. The black residue was fully washed under running water in a sieve and then treated with 10% potassium hydroxide (KOH) for up to one hour. During this process, the "coal matter" was completely dissolved and only the cuticles and vascular tissue remained. The cuticles were stained in Safranin, Bismarck brown, Malachite green or Neutral red, and mounted in Glycerine Jelly, or were attached to an SEM stub for observation under a scanning electron microscope (SEM).

About 30 foliar fragments of cuticles and a similar number of conducting tissue fragments were mounted on six slides. About ten cuticular fragments are longer than 1 mm (up to 1.3 mm), and represent both the adaxial and abaxial leaf surfaces. Some fragments of conducting tissue were up to 3 (4) mm long.

The dispersed cuticles are stored in slides no. 595/1–6.

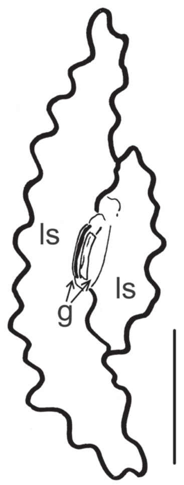

Figure 3: A paracytic stoma of *Sphenophyllum* sp. from Kalinovo locality. Note the uneven lateral subsidiary cells, ls = lateral subsidiary cells, g = guard cells. Scale bar = 50 μm.

4. SYSTEMATICS

Systematics performed according to CLEAL & THOMAS (1995)

Class Equisetopsida ('horsetails')
Order Bowmanitales ('sphenophylls') MEYEN, 1978
Family Bowmanitaceae MEYEN, 1987
Genus *Sphenophyllum* BRONGNIART, 1828

***Sphenophyllum* sp. (Fig. 3, Pls. 1, 2, 3)**

Description:

Adaxial cuticle: The cells are elongate, more or less fusiform or elongate tetragonal in shape with coarsely sinuous anticlinal walls that affect the original cell shape. The cells are oriented parallel to the veins, and are 150–300 μm long and 25–50 μm wide. The costal (vein) areas are usually prominent with original black vascular tissue (Pl. 1, fig. 2), which is about 100 μm wide. When this tissue is not preserved (Pl. 1, fig. 1), the costal area is about 50 μm wide and shows narrow cells only 15–20 μm wide.

Abaxial cuticle: The cells have essentially the same shape and dimensions as the cells of the adaxial cuticle. The difference is in the presence of stomata (Pl. 1, figs. 3–4). The stomata tend to be concentrated in "bands" along the veins and they are oriented parallel to the veins. The guard cell pairs are fusiform or elliptical, 26–32 μm long and 10–14 μm wide (Pl. 1, figs. 4, 6, Pl. 2, fig. 4). Each stoma has two lateral subsidiary cells (paracytic stomatal type), one of which is shorter – 78–90 μm long; and the longer is 176–192 μm long. Both cells have approximately the same width – 20–35 μm.

The cuticles in scanning electron microscope have very fine striated periclinal walls in outer view (Pl. 2, fig. 1) and the anticlinal walls are prominent in the inner view (Pl. 2, figs. 2–4B).

Using the same approach as described by POOLE & KÜRSCHNER (1999) stomatal density and stomatal index were counted from several cuticle fragments; the area of each fragment was 0.1–0.15 mm^2. The stomatal density of *Sphenophyllum* sp. is 83–90 stomata per mm^2 and the stomatal index is 20.5–23.

Conducting tissue: Fourteen tracheids from slides 595/1, 2, 3 and 5 were studied. Fragments of tracheids have walls perforated mainly by multiseriate bordered pits (Pl. 3, figs. 1, 3), which locally become in reticulate cell wall thickening (Pl. 3, fig. 4). Bordered pits are free, and according to the number of their rows and tight configuration they belong to the alternate pitting surface type . The number of bordered pit rows on the tracheid wall is (2)–4–6. Bordered pits have a circular to elliptical shape and approximately the same dimension. The tracheids are 60–100–(125) μm wide. The thickening on some tracheids is interrupted by the walls of parenchyma cells that form a rectangular outline on the tracheid (Pl. 3, fig. 2). Due to the fragmentary size of the preserved tracheids, it was not possible to determine their original total length.

5. REMARKS

Fragments of the xylem – tracheids were found in association with the *Sphenophyllum* cuticles. According to TAYLOR et al. (2009, p. 206), annular or helical thickenings of tracheids are most often found in the earliest matured primary xylem. Secondary xylem is made up predominantly of pitted tracheids, although some plant groups also have secondary xylem tracheids. Bordered pits in tracheal elements are according to NĚMEJC (1963, p.76) very rare in many pteridophylls (Pteridophyta). It is common in equisetopsids (Equisetopsida) and in many pteridosperms and gymnosperms.

6. *SPHENOPHYLLUM* CUTICLES AND THEIR COMPARISON

Most species of *Sphenophyllum* BRONGNIART have irregularly isodiametric to elongate epidermal cells that usually posses sinuous anticlinal walls. Stomatal complexes occur on the abaxial surface of the leaf and consist of two guard cells with polar and circumpolar thickenings, and two paracytic lateral subsidiary cells. Subsidiary cells may have the same shape and size as normal epidermal cells, or they can differ. One subsidiary cell is usually distinctly larger than the other (TAYLOR et al. 2009).

These characteristics fit very well with the cuticles described above. Individual species differ in the distribution of the stomata, the orientation and size of the guard cells, and the shape, arrangement and size of the intercostal cells (Table 1). BARTHEL (1997) distinguished two groups among the *Sphenophyllum* species. Group 1 consists of *Sphenophyllum cuneifolium, S. emarginatum, S. majus* ABBOT (=*S. geinitzii* STORCH)*, S. thonii, S. speciosum. S. longifolium* and *S. saxonicum.* This group is hypostomatic, with sinuous anticlinal walls and larger cells. Group 2 consists of *Sphenophyllum oblongifolium* and the anatomically preserved species *S. quadrifidum* RENAULT and *S. reedae* GOOD. In this group, the epidermis has rectangular cells with straight anticlinal walls.

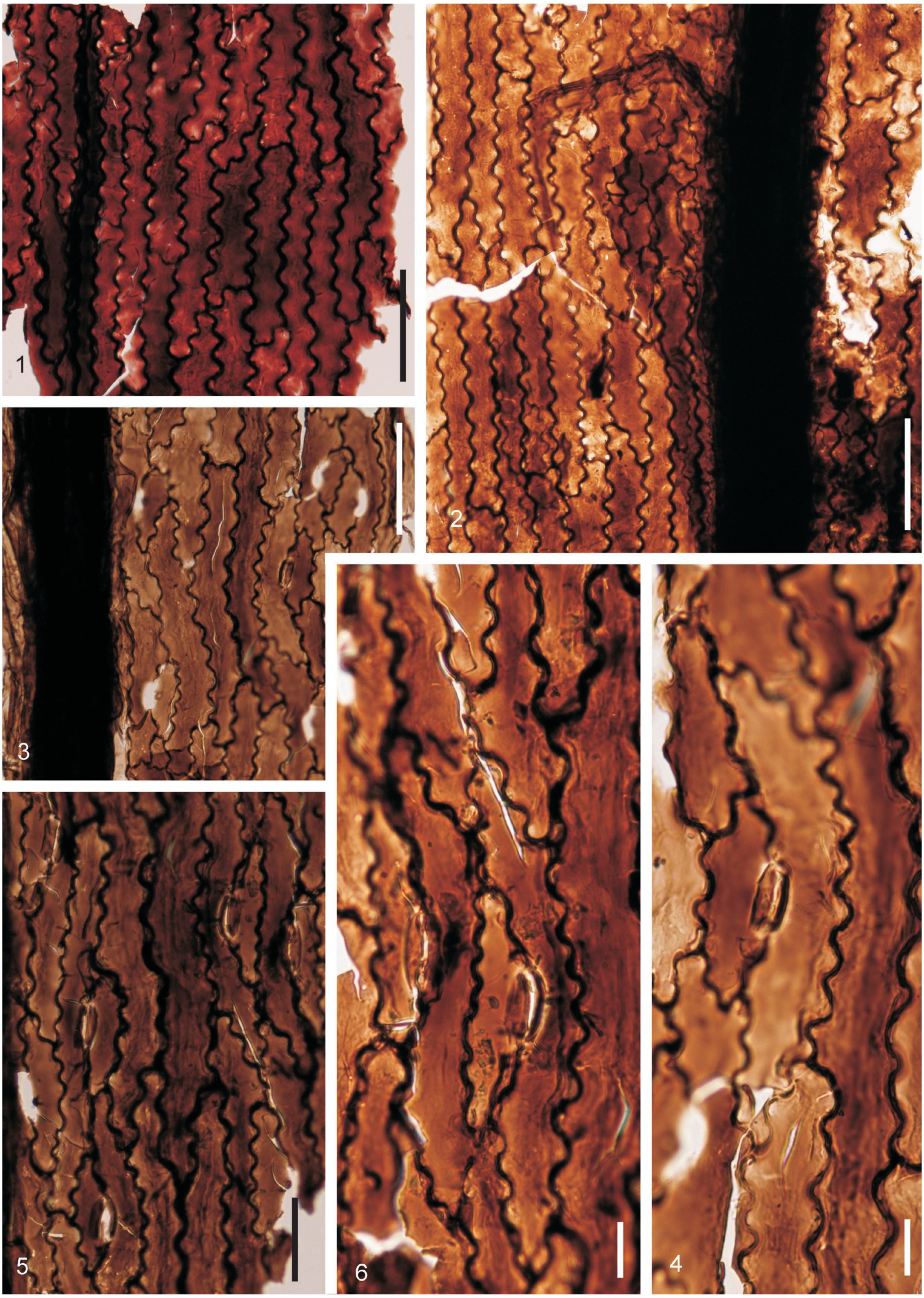

Plate 1 *Sphenophyllum* sp., locality Kalinovo, Donets Basin, coal seam n_3, Upper Asturian (Moscovian, Pennsylvanian)

1 and 2 – Adaxial cuticle, slide 595/3, scale bar = 100 µm;
2 – Note black costal area.
3–6 – Abaxial cuticle; Fig. 3 – Cuticle with black costal area and holes where guard cells, have fallen out, slide 595/3, scale bar = 100 µm;
4 – Detail of a stomatal complex with guard cells, scale bar = 20 µm;
5 – Cuticle with 5 stomatal complexes, slide 595/5, scale bar = 50 µm;
6 – Close up to two stomatal complexes from fig. 5 scale bar = 20 µm

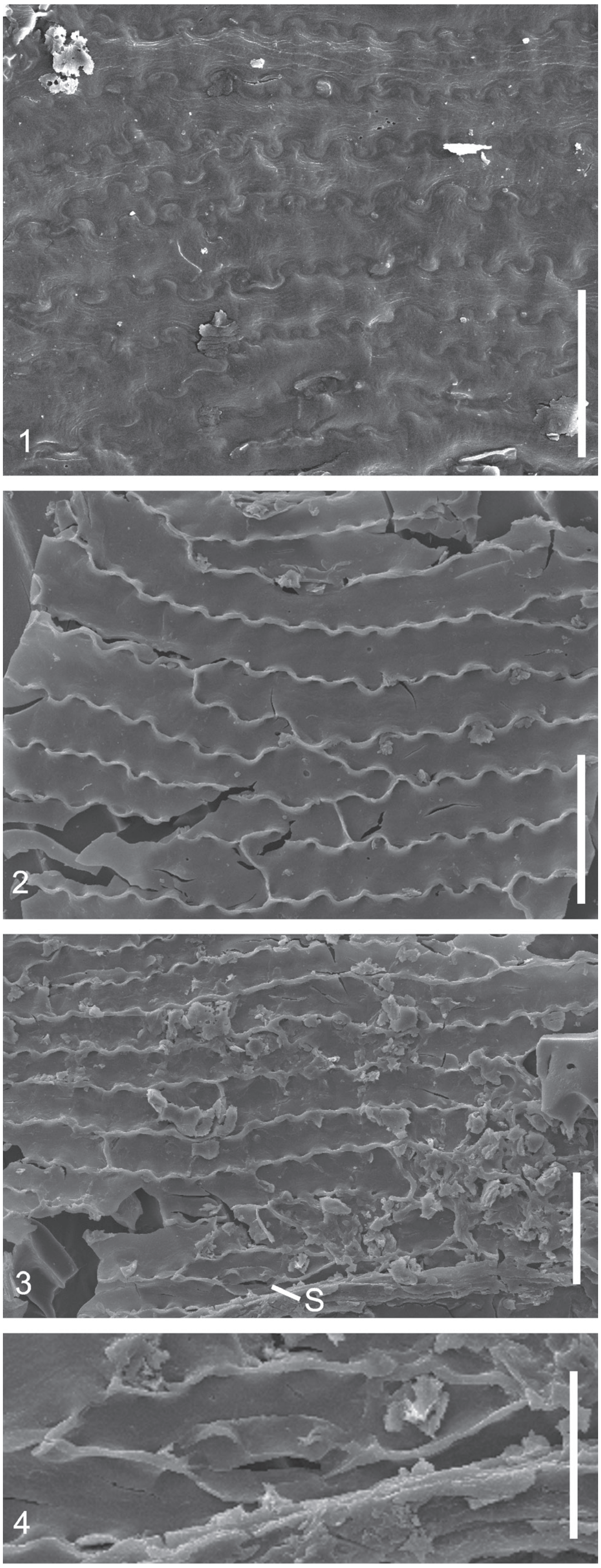

Plate 2 *Sphenophyllum* sp., loc. Kalinovo, Donets Basin, coal seam n_3, Upper Asturian (Moscovian, Pennsylvanian) cuticles in scanning electron microscope. SEM stub no. 84.

1 – Adaxial or abaxial cuticle in outer view. Note the periclinal walls with very fine longitudinal striations and sinuous anticlinal walls, scale bar = 50 µm.
2 – Adaxial or abaxial cuticle in inner view. Note prominent sinuous anticlinal walls, scale bar = 50 µm.
3 – Abaxial cuticle with a stoma (S) in inner view, scale bar = 50 µm.
4 – Close up of the stomatal complex from fig. 3, scale bar = 20 µm.

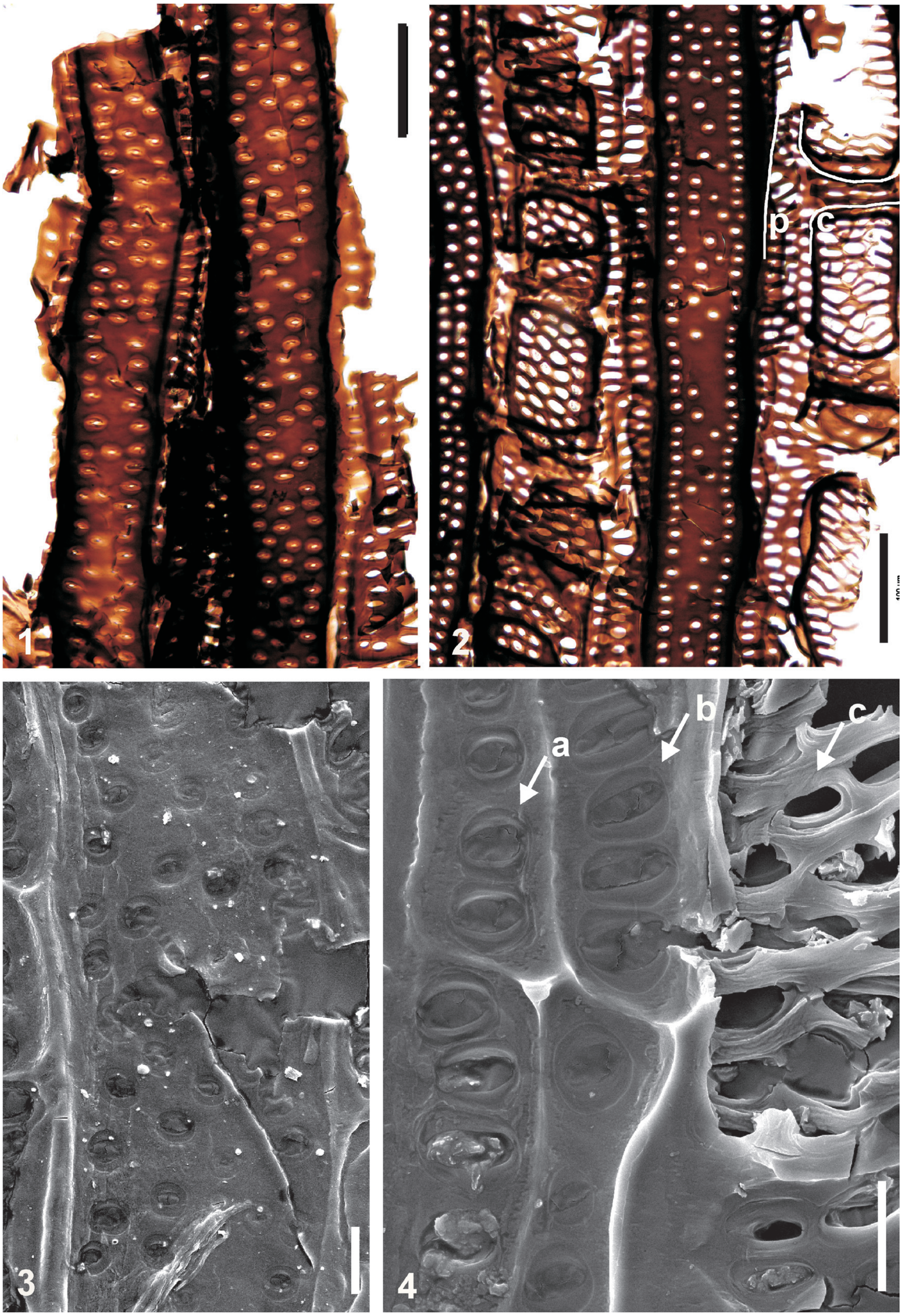

Plate 3 Typical structure of secondary xylem tracheids in the studied specimens resembling the tracheid structure of *Sphenophyllum* sp.

1 – Secondary xylem tracheids with multiseriate bordered pits, the shape of the bordered pits is circular – elliptical, slide 595/3. Scale bar = 100 µm.

2 – View of the tracheid walls in places where strips of parenchyma cells were attached. p – tracheid surface (? wall) in the place where parenchyma cells were attached. c – Contiguous tracheid wall is demarcated and perforated. The tracheid has reticulate cell wall thickening. Slide 595/3, scale bar = 100 µm.

3 – A close up of tracheidal wall with pentastichous pitting of a circular shape. SEM stub 84. Scale bar = 20 µm.

4 – A close up of a tracheidal wall, a – circular bordered pits, b – elliptical bordered pits, c – reticulate cell wall thickening, the tracheid wall is partly sagging. SEM stub 84, scale bar = 20 µm.

Table 1: Epidermal structures of *Sphenophyllum* species.

Species (C-compression; P-petrification)	Distribution of stomata	Orientation of guard cells	Guard cell size [mm]	Subsidiary cells no./specialised in shape and size	Shape and arrangement of intercostal cells	Intercostal cell size [mm]	Shape of anticlinal walls	References
S. emarginatum BRONGNIART [C]	random	usually parallel to veins	31-57x5-18	2/no	long, irregular	79-179x26-50	coarsely sinuous	BATENBURG (1977), (1981)
S. cuneifolium (STERNBERG) ZEILLER [C]	random	parallel to veins	25x15	2/few	long, irregular	80-200x30-60	coarsely sinuous	BARTHEL (1997)
S. thonii MAHR [C]	random to stripped	parallel to veins	30x20	2/yes	long, irregular	100-200x20-30	coarsely sinuous	MEYEN (1970)
S. majus ABBOT non BRONN (=*S. geinitzii* STORCH) [C]	random	random	30x20	5-6/few	long, irregular	40-60-10-15	coarsely sinuous	ABBOT (1958)
S. speciosum (ROYLE) ZEILLER [C]	random	random	25x15	2/no	long, irregular	100-200x30-70	sinuous	PANT & MEHRA (1963)
S. longifolium (GERMAR) GUTBIER[C]	random	parallel to veins	20-28x12-15	2/no	longitudinal rows	140-200x40-55	finely sinuous	BARTHEL (1997)
S. saxonicum REMY & REMY [C]	random	parallel to veins	25x15	2/few	longitudinal rows	100-200x35-40	finely sinuous	BARTHEL (1997)
S. oblongifolium (GERMAR & KAULFUSS) UNGER [C]	?	?	?	?	rectangular in rows	100-180x15-25	straight	BARTHEL (1997)
S. multirame DARRAH (P)	in 2 sunken rows or furrows	random	15x10	2-4/yes	long, irregular	100-150x15-25	finely sinuous	GOOD (1973)
S. reedae GOOD (P)	random	parallel to veins	25x18	3-5/few	rectangular in rows	70-150x20-30	straight	GOOD (1973)
S. apiciseratum YAO et al. [C]	random	random	34-54x14-24	2/no	irregular	65-147x 41-112	coarsely sinuous	YAO et al. (2000)
S. koboense KOBATAKE [C]	random (near veins)	random	27-54x10-24	2/no	long, irregular	81-189x20-41	finely to coarsely sinuous	YAO et al. (2000)
S. zwickauvense STORCH [C]	?	?	?	?	longitudinal rows	60-177x14-52	sinuous	BATENBURG (1981)
S. priveticense LIBERTÍN, BEK & DRÁBKOVÁ [C]	In rows	parallel to veins	45x15	2/few	longitudinal rows	125-350x50-60	sinuous	LIBERTÍN et al. (2014)
S. sp. [dispersed]	near veins	parallel to veins	26-32x10-14	2/no	longitudinal rows	150-300x25-50	coarsely sinuous	present study

Only well preserved compression [C] species, and petrifaction (P) species whose foliar grooss morphology is known, have been included. Other compression species are known only by fragments without stomata (see BATEN BURG, 1981).

The *Sphenophyllum* sp. described in the present paper belongs to Group 1. The elongate cells with coarsely sinuous anticlinal walls occur in many species: e.g. *Sphenophyllum emarginatum*, *S. cuneifolium*, *S. thonii*, *S. majus* ABBOT (non BRONN) (=*S. geinitzii*), *S. kobatake* and *S. zwickawense.* However, the cell size in the present species (150–300 µm) is rather large compared to all the species mentioned above, where it is usually only up to 200 µm. The exception is the newly described *Sphenophyllum priveticense* LIBERTÍN, BEK et DRÁBKOVÁ, 2014, in which the cells are 125–350 µm long and so more comparable to our samples of *Sphenophyllum* sp. However, they differ in other characteristics (see Tab. 1) and it is unlikely that they belong to the same species, especially as *Sphenophyllum priveticense* is of early Bolsovian age whereas the present *Sphenophyllum* sp. is of latest Asturian age.

Sphenophyllum guard cells are usually reniform and the outline of the pair is elliptical. Their size differs according to species, however some overlap exists. Our *Sphenophyllum* sp. has medium sized guard cells among the sphenophylls, 28–32 µm in length. The smallest ones are known from permineralised *S. multirame* (only 15 µm long) and the largest ones are known in four species *S. emarginatum* (31–57 µm), *S. apiciseratum* (34–54 µm), *S. koboense* (27–54 µm) and *S. priveticense* (45 µm). An important feature is also the shape of the subsidiary cells. Many species have two lateral subsidiary cells per stoma (usually one of them is larger than the other); they are of the same shape as normal epidermal cells in *Sphenophyllum* sp., *S. emarginatum, S. thonii, S. speciosum, S. longifolium, S. apiciseratum, S. koboense* and *S. priveticense.* According to LIBERTIN et al. (2014), the stomatal complex of *S. priveticense* is anomocytic, but it seems that all those mentioned above have paracytic stomata. In other species, the subsidiary cells differ significantly from the ordinary epidermal cells: *Sphenophyllum cuneifolium, S. thonii, S. geinitzii* (*S. majus* ABBOT), *S. saxonicum, S. multirame* and *S. reedae.* Some species have trichomes and papillae on the adaxial surface of the leaves: *Sphenophyllum majus, S. speciosum, S. saarensis, S. trichomatosum* STUR and probably also *S. sewardii* BATENBURG (LIBERTÍN et al. 2014). No trichomes or emergences have been observed on cuticles from *Sphenophyllum* sp. from Kalinovo.

7. COMPARISON OF CONDUCTING ELEMENTS

The characteristic pitting of the tracheid walls in the studied samples corresponds to the description of secondary xylem anatomy of the *Sphenophyllum* plant as mentioned in

BOUREAU (1964, p. 98, 99), who figured *Sphenophyllum* with multiseriate bordered pits. He also figured the distribution of parenchyma cell strips along the radial walls of a tracheid. It has been shown that strips of parenchyma cells created a rectangular contour on the radial wall of the tracheids. These contours are the only remnants of parenchyma cells. TAYLOR et al. (2009) also described tracheids of secondary xylem with circular–eliptical bordered pits on the lateral walls in *Sphenophyllum plurifoliatum* WILLIAMSON et SCOTT. Similarly, BUREŠ et al. (2013) described tracheids with circular–elliptical bordered pits in *Sphenophyllum* cf. *myriophyllum* CRÉPIN. BATENBURG (1982) described xylem with scalariform thickenings and elements with uni- or multiseriate bordered pits in *Sphenophylllum speciosum* ZEILLER (PANT & MEHRA). RÖSSLER & NOLL (2007 p. 174) described a similar structure in the secondary xylem of *Calamitea striata* COTTA (Calamitaceae). Cell walls show simple to bifurcate scalariform to reticulate thickening with elongate oval pits in radial and tangential sections. Multiseriated bordered pits of tracheids are common in pteridosperms as noted by ANDREWS (1940), NĚMEJC (1968), and TAYLOR et al. (2009).

8. CONCLUSION

Cuticles and conducting tissue of *Sphenophyllum* BRONGNIART have for the first time been identified in the dispersed cuticle spectrum. Many *Sphenophyllum* species have the same cuticular pattern, so it is difficult to identify *Sphenophyllum* species only using cuticles, as noted by BARTHEL (1997). Nevertheless, as it has paracytic stomata and elongate cells with sinuous anticlinal walls, the *Sphenophyllum* from Kalinovo clearly belongs to group 1 (sensu BARTHEL 1997) together with *Sphenophyllum cuneifolium, S. emarginatum, S. thonii, S. speciosum. S. longifolium*, *S. saxonicum* and *S. priveticense*. Although the Kalinovo species has medium-sized guard cells that fit with several species, together with *Sphenophyllum priveticense* LIBERTÍN, BEK et DRÁBKOVÁ, 2014, it has the longest cells that have been reported so far in a *Sphenophyllum* species, 300 – 350 μm long, in contrast to usually no more than 200 μm long seen in other species. Despite the similarity of their cuticles, the *Sphenophyllum* sp. from Kalinovo and *Sphenophyllum priveticense* cannot be regarded as conspecific as the former is stratigraphically much younger.

Sphenophyllum sp. was discovered in Kalinovo coal, and *S. priveticense* was found in a tuff that buried the peat-swamp "in situ" and also contained many peat-forming floral elements. It is likely, therefore, that both *Sphenophyllum* sp. and *S. priveticense* lived in similar habitats. LIBERTÍN et al. (2014) supposed that *Sphenophyllum priveticense* lived in peat-swamps with a high water table and also in slightly drier habitats with a transition to an *Omphalophloios*-phase. Maybe the larger cell dimension is caused by living in such an environment.

It is not possible to systematically classify the studied tracheid fragments of the genus *Sphenophyllum* sp. based on tracheid thickening. A similar structure of tracheids is also common in the other plant groups from the Pennsylvanian (Calamitaceae, pteridosperms). Any palaeoecological interpretation based on the tracheids is not possible, as their width depends on vegetation conditions, and we are not sure if all the studied tracheids in fact belong to this *Sphenophyllum*.

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