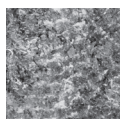


Lepidostrobus willardii sp. nov. and its spores from the Lower Pennsylvanian of the Illinois Basin, USA

JOSEF PŠENIČKA, JIŘÍ BEK & W. JOHN NELSON



This paper describes a Pennsylvanian lycopphyte cone collected from a highway cut along the southbound lanes of U.S. Interstate Highway 24 (I-24) north of Vienna, Illinois (USA) and stratigraphically belonging to the basal Tradewater Formation, under the Reynoldsburg Coal Bed (upper Bashkirian, lowermost Pennsylvanian). The cone is incomplete, more than 135 mm long and 26 mm wide, mainly representing the distal part with a missing base. The *in situ* spores from the cone represent trilete cingulizonate microspores belonging to the *Lycospora brevijuga* Group. Based on these spores together with morphological characters, the cone was compared with already existing species and differs sufficiently to warrant establishing a new species, here named *Lepidostrobus willardii* sp. nov. • Key words: *Lepidostrobus*, *Lycospora*, Tradewater Formation, Pennsylvanian, Illinois Basin.

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This contribution deals with a monosporangiate lycopphyte cone of the genus *Lepidostrobus* Brongniart emend. Brack-Hanes & Thomas from the Illinois Basin, USA. Generally, cones of the *Lepidostrobus* type belong to the most abundant elements of Pennsylvanian plant assemblages. Because cones are seldom found attached to vegetative correlatives, identification depends upon characters of the cones. Therefore, palaeobotanists have focused on morphological features of lycopphyte cones with less emphasis on *in situ* spores and their significance, which often has been overlooked. The specimen studied in this paper comes from the Illinois Basin (USA) where the majority of contributions on Pennsylvanian age lycopphyte cones come from coal balls with focus on detailed description of anatomical structures, sometimes including *in situ* spores (Felix 1954; Balbach 1966, 1967; Taylor & Eggert 1968; Brack 1970; Willard 1989a).

The most extensive study of compression *Lepidostrobus* with their *in situ* spores from the Pennsylvanian of the USA was published by Willard (1989b), who described *in situ* spores from more than 200 lycopphyte cones. However, the different preservational quality and type of morphological *versus* anatomical data found in coal balls *vs* adpressions makes it difficult to correlate species that may occur in both modes of preservation. In such cases, *in situ* spores can be an effective tool for connecting

species found in different types of preservational as was demonstrated by Bek & Opluštil (2004, 2006), Opluštil & Bek (2009), Thomas *et al.* (2009), Thomas & Bek (2014) and Bek (2012). The *Lepidostrobus* cone described here contains *in situ* spores assigned to the miospore genus *Lycospora* Schopf *et al.*, which is the most abundant and the most reported dispersed miospore genus of Pennsylvanian age (Bek & Opluštil 2006, Bek 2012). Brack-Hanes & Thomas (1983) re-defined *Lepidostrobus* cones as monosporangiate with *Lycospora* microspores. They segregated *Flemingites* Carruthers strobili as bisporangiate with *Microspinosporites* Bek microspores and *Lagenosporites* Potonié & Kremp/*Lagenicula* Zerdnd megaspores. An important palynological grouping of *Lycospora* (six morphological groups) and assignment to parent *Lepidostrobus* cones was proposed by Bek (2012).

Knowledge about European *in situ* spores isolated from adpressed Pennsylvanian *Lepidostrobus* species of the Euramerican Palaeoprovince (*e.g.* Thomas 1965, 1970; Drábek 1967; Bek 1998; Bek & Opluštil 2004, 2006; Libertin *et al.* 2005; Opluštil & Bek 2009; Thomas *et al.* 2009) is more comprehensive than such knowledge of *in situ* *Lycospora* described from petrified *Lepidostrobus* in the USA (Willard 1989b; Balbach 1966, 1967; Felix 1954). Each lycopphyte cone produced a huge number



Figure 1. Location map showing the collecting site.

of spores, therefore, the correlation of spores with their parent plants is of particular importance for investigation of Pennsylvanian lycophyte stratigraphical–regional occurrence due to wide distribution of dispersed spores in most fine-grained shales and coal.

The specimen studied herein was collected from a highway cut along the southbound lanes of Interstate 24 about 8 km north of Vienna, Illinois (USA) (Fig. 1). The specimen represents a partial cone more than 135 mm long with a preserved distal part. The cone was studied in detail under a binocular microscope, macerated from both ends, and observed under SEM. Based on the data obtained from these analyses, we establish here a new species, *Lepidostrobus willardii* sp. nov. Justification of the new species is described in detail in the discussion.

Geologic setting and stratigraphy

The collecting site lies near the southern margin of the Illinois Basin (Fig. 1), a Palaeozoic intracratonic basin that encompasses most of southern and central Illinois, southwestern Indiana, and part of western Kentucky.

The locality lies within the Shawnee Hills Section of the Interior Low Plateaus physiographic province, a short distance beyond the southernmost extent of Pleistocene continental glaciation in North America (Horberg 1950). We collected the cone from siltstone underlying the Reynoldsburg Coal Bed, which is just above the base of the Tradewater Formation (Fig. 2). The highway cuts north of Vienna provide one of the most complete sections in Illinois of the lower Tradewater and the underlying Caseyville Formation (Fig. 3A–D). These roadcuts were featured on field trips for the Ninth International Carboniferous Congress (Palmer & Dutcher 1979, p. 90) and the 28th International Geological Congress (Cecil & Eble 1989). They also have been designated as a reference section for the Caseyville Formation (Nelson *et al.* 2022).

Peppers (1996) placed the Morrowan–Atokan Stage boundary in the Illinois Basin above the Reynoldsburg Coal Bed and below the next younger coal, the Bell Coal Bed. Peppers further correlated the Langsetian–Duckmantian (Westphalian A to B) boundary of Western Europe with the Morrowan–Atokan Stage boundary. Peppers (1996, p. 36) based these placements on the boundary between the *Schultzospora rara* and *Laevigatosporites desmoinesensis* spore assemblage zone, found in the Reynoldsburg, and the *Microreticulatisporites nobilis*–*Florinites junior* palynozone assemblage found in the Bell Coal.

Material and methods

As stated above, specimen F24016 (holotype) came from a roadcut along the southbound lanes of I-24 about 8 km north of Vienna, Illinois, USA (37° 29′ 46.3″ N, 88° 53′ 49.3″ W), in the basal Tradewater Formation, under the Reynoldsburg Coal Bed, Illinois Basin, USA (Fig. 3A–D). Additional specimens represented by association with holotype (F24009–F240012, F24014, F24015, F24018A, F24020, F24025, F24027) come from the same locality. The stratigraphical level of the studied cone is near the top of the Morrowan Stage which corresponds to uppermost Langsetian (former Westphalian A) in European subdivision (Peppers 1996). The specimen is preserved in light grey to ochre siltstones (Fig. 3D). The fossil plant remains have a low coalification grade that allows successful maceration. Samples for *in situ* maceration were taken from both the apical and the lower parts of the preserved cone. Only microspores and fragments of sporophyll were obtained. Measurements of spore diameters were taken from 20 spores from each part of the cone.

Sporangia were isolated from the rock matrix using 40% hydrochloric acid (HCl) for 48 hrs followed by washing in distilled water. Sporangia were subsequently

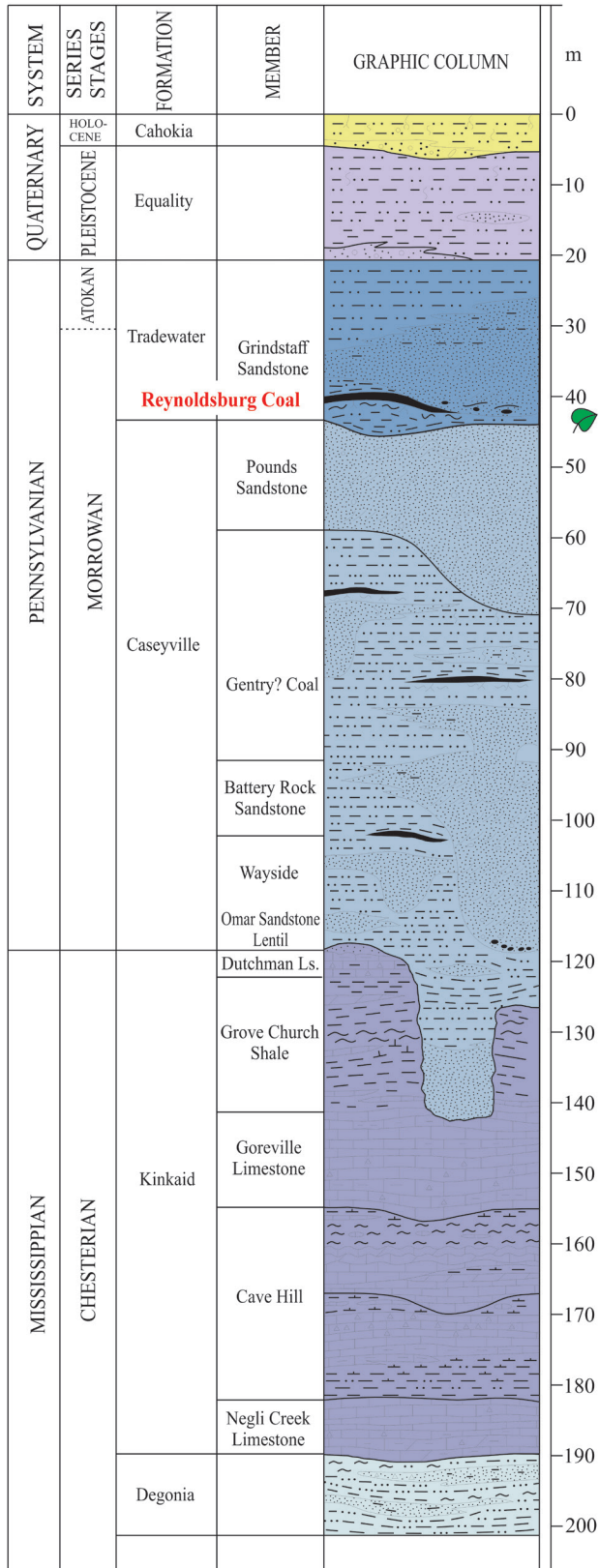


Figure 2. Stratigraphic column (modified from Nelson *et al.* 2004) showing position of the Reynoldsburg Coal and the collection of plant fossils (green leaf). For lithology see Nelson *et al.* (2004)

macerated in Schulze’s solution (saturated solution of potassium chlorate $KClO_3$ in 65% nitric acid HNO_3) for 30–40 min depending on the degree of coalification, washed in distilled water several times, treated with a 10% potassium hydroxide solution to remove oxidation products, and washed in distilled water again. Sporangia and *in situ* spores were examined under SEM JEOL 6380LV (Institute of Geology and Paleontology, Faculty of Sciences, Charles University in Prague).

The classification of *Lepidostrobus* cones follows the approach of Brack-Hanes & Thomas (1983); the terms used for the descriptions of *in situ* spores are obtained from the latest edition of the Glossary of Pollen and Spore Terminology (Punt *et al.* 2007). *In situ* spores are compared according to the system of classification of dispersed spores suggested by Potonié & Kremp (1954, 1955) and Smith & Butterworth (1967).

Specimens are housed in the Centre of Palaeobiodiversity, West Bohemian Museum in Pilsen, Czech Republic. They include holotype F24016, additional specimens and all SEM stubs (labeled: USAIL 14B2LepidostrobusSCH24hodslot11 and USAIL 14B2LepidostrobusSCH24hodslot10x) with *in situ* spores, sporangia and cuticles.

Systematic palaeontology

Class Lycopsidea Scott, 1909

Genus *Lepidostrobus* Brongniart emend. Brack-Hanes & Thomas, 1983

Type species. – *Lepidostrobus ornatus* Brongniart, 1828.

***Lepidostrobus willardii* sp. nov.**

Holotype. – Specimen F24016, Fig. 4A, stored in the Centre of Palaeobiodiversity, West Bohemian Museum in Pilsen, Czech Republic.

Type horizon and locality. – Basal Tradewater Formation, directly beneath the Reynoldsburg Coal, Illinois Basin, USA. Southbound lanes of I-24, NE¼, Sec. 8, T12S, R3E, Johnson County, Illinois, USA on the Vienna 7.5-minute topographic quadrangle (37° 29' 46.3" N, 88° 53' 49.3" W).

Material. – specimen F24016 (holotype); additional specimens represented by association with holotype: F24009–F240012, F24014, F24015, F24018A, F24020, F24025, F24027. All specimens stored in the Centre of Palaeobiodiversity, West Bohemian Museum in Pilsen, Czech Republic.



Figure 3. Photographs of the collecting locality. A – view of site from across highway. The people are standing at about the level where fossils were collected (green leaf). The Reynoldsburg Coal (R) is at waist level, and the Grindstaff Sandstone forms the vertical wall above their heads. The top of the Pounds Sandstone Member, Caseyville Formation, is just above road level. B – detail of section with well exposed Reynoldsburg Coal (R). The coal is approximately 50 cm thick (photo by W.A. DiMichele). C – detail of the section with cross bedded Pounds Sandstone, probably representing a fluvial/distributary channel. D – The place where the collection was taken. Abbreviations: PS – Pounds Sandstone; U – Underlying coal seam; Sh/ss – Shale and sandstone; R – Reynoldsburg Coal.

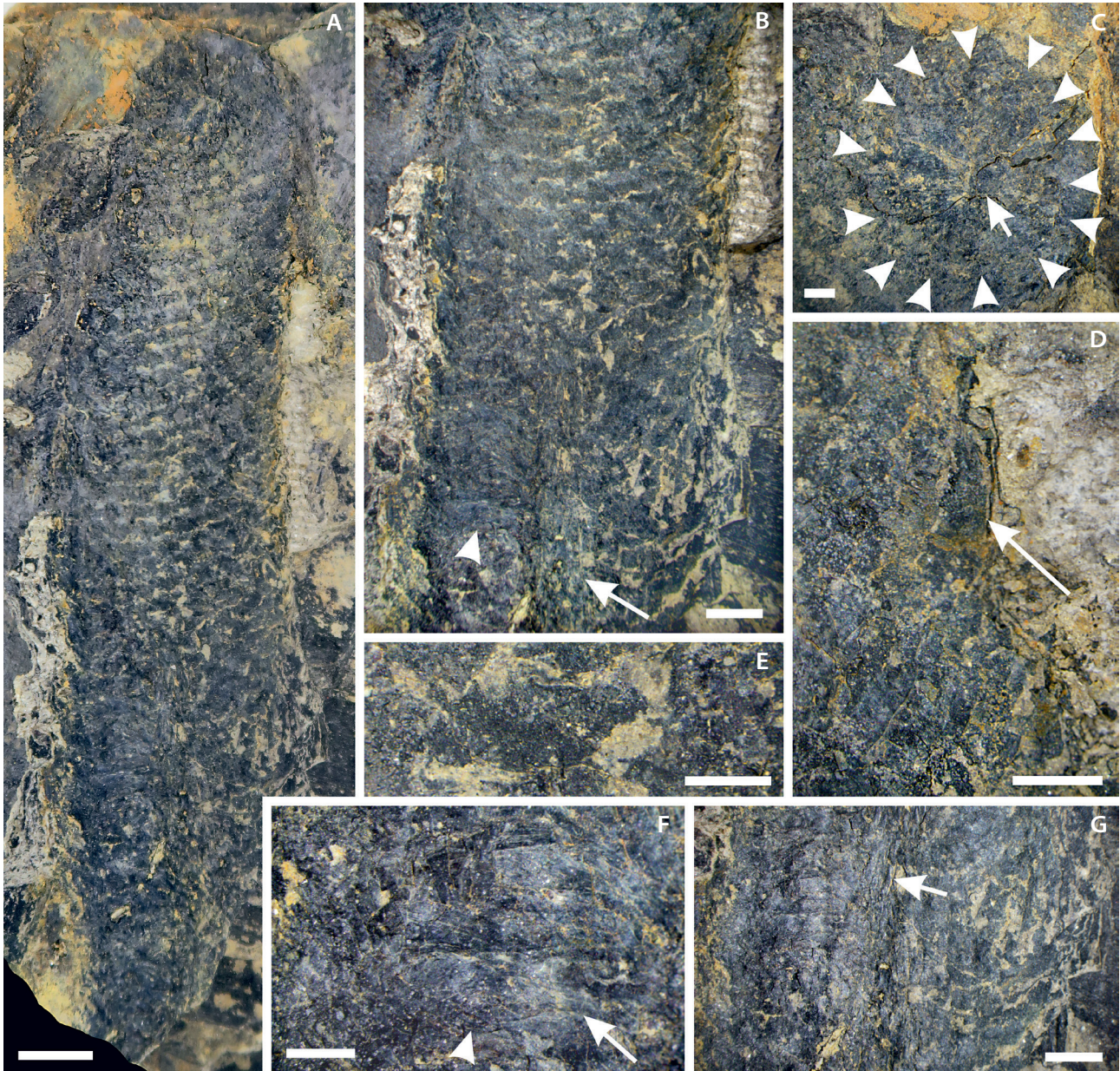


Figure 4. Holotype F24016 of *Lepidostrobus willardii* sp. nov., collected from the I-24 roadcut during this investigation. A – holotype F24016. B – detail of cone from lower part of the specimen. Arrow points to axis and arrowhead points to sporangium lying on pedicel of a sporophyll. C – detail organization of 14 sporophylls (arrowheads) in distal part of the cone. Arrow points to the axis. D – detail of poorly preserved distal lamina (arrow). E – detail of sporophyll at the junction of pedicel and distal lamina. F – detail of pedicel with sporangium (arrowhead) with small pedicel base (arrow). G – detail of cone with uncovered axis (arrow) and several, helically arranged pedicel bases. Scale bars: 2 mm (C–F), 5 mm (B, G), 10 mm (A).

Etymology. – In honor of D.A. Willard, famous palynologist and palaeobotanist (US Geological Survey, Reston, Virginia) who contributed to our knowledge of *Lepidostrobus* cones from the Illinois Basin.

Diagnosis. – Cone more than 135 mm long and 26 mm wide. Cone central axis ~5 mm wide. Sporophyll appendages have small heel, ~2 mm wide, up to 7–9 mm long. Distal laminae fully adpressed to the cone body.

Sporophyll pedicel ~6 mm long, with pedicel base ~3 mm long and 0.6 mm wide. Ellipsoid circles, sometimes grouped, preserved on cuticle above distal lamina midrib. Sporangia 4–5 mm long, 2 mm high. Trilete subtriangular to subcircular microspores, 25–37 μ m, rays of trilete mark reach spore margin. Proximal and distal surface sculpture microgranulate, granulate, microverrucate, verrucate, and rugulate. Proximal surface of zona laevigate, rarely perforated, distal surface of the cingulum and zona

sculptured. Cingulum 2 (3.2) 5 μm wide and zona 2 (3.1) 4 μm wide.

Description. – The specimen is an incomplete cone with a preserved distal end. It is more than 135 mm long and 26 mm wide (Fig. 4A). Organic matter of the apex of the cone is not really preserved on the slab, although it appears as rounded in outline. In detail we can notice that the true apex is not preserved. In the top part, 14 sporophyll pedicels are preserved (Fig. 4C arrowhead) arranged concentrically around the axis (Fig. 4C arrow). The axis is ~ 5 mm wide (Fig. 4B arrow). The sporophylls (Fig. 5) are borne in tight helix, probably constantly 14 per one rotation cycle around axis. The pedicel is ~ 6 mm long (Figs 4B arrowhead, 4E). The distal part of the pedicel is rhomboidal in cross-section (Fig. 4E) with a ridge on upper side; it is 5–6 mm wide and 2 mm high in side view as preserved (Fig. 4F arrowhead). A small heel was observed abaxially at the distal end of the pedicel. Distal laminae are ~ 2 mm wide up to 7–9 mm long (Fig. 4D arrow). Distal laminae are fully adpressed to the cone body. The pedicel base is ~ 3 mm long and 0.6 mm wide (Fig. 4F arrow). Cuticle of the sporophyll shows long tetragonal epidermal cells 28–76 μm long and 4–12 μm wide, along the midrib (Fig. 6E). Anticlinal walls are straight. The lens-shaped structures are ~ 20 μm long and

7 μm wide with a central perforation present on the cuticle (Fig. 6E arrowheads). These structures are parallel with their longer axis to the midrib and probably represent the remains of sunken stomata apparatuses. The arrow in Fig. 6C points to thick-walled cells that were probably situated above the midrib. Ellipsoid structures are often preserved above the midrib (Fig. 6D arrow). They are ~ 30 μm long and 16 μm wide consist of a 5 μm thick rim. They are sometimes grouped where these structures are close together (Fig. 6D).

Sporangia are 4–5 mm long and 2 mm high. Figure 6B shows a fragment of a proximal part of a sporangium filled by microspores and surrounded by sporophyll pedicel remains (see Fig. 6A). Sporangia are club-like in shape viewed in longitudinal section (Fig. 4F). It is not clear how many sporangial wall layers comprise a sporangium. Nevertheless, after maceration we observed polygonal, or rectangular shaped cells 10–15 μm in diameter (Fig. 7A). Some cells have relatively thicker anticlinal walls (Fig. 7A). The sporangium on Fig. 6B, respectively 6A is open and it seems that dehiscence ran parallel to the long axis of the sporangium.

Trilete subtriangular to subcircular microspores (Fig. 7B) range in size from 25 to 37 μm . Rays of the trilete mark reach the margin (Fig. 7C, D). A labrum up to 3.5 μm wide and high is sometimes developed. The sculpture of proximal (Fig. 7C, D) and distal surfaces (Fig. 7E, F) is microgranulate, granulate, microverrucate, verrucate and rugulate. The proximal surface of the zona is laevigate, rarely perforated (Fig. 7D); the distal surface of the cingulum and zona is sculptured (Fig. 7E, F). The cingulum is 2 (3.2) 5 μm wide and the zona is 2 (3.1) 4 μm wide.

Remark. – *In situ* microspores belong to the cingulizonate *Lycospora brevijuga* Group.

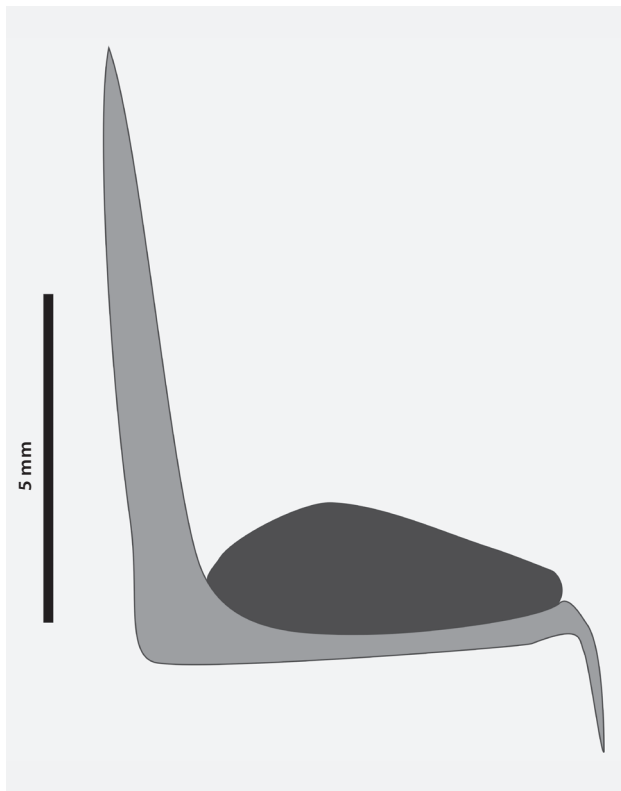


Figure 5. Suggested reconstruction of sporophyll.

Discussion

In the last twenty years, more extensive works are beginning to appear, devoted to correlating *Lepidostrobus* cones with their *in situ* spores. However, precise classification is still accompanied by many objective problems that create complications. In the first place, it is necessary to mention taphonomic factors, such as the type of preservation, completeness/incompleteness, the quality of preservation, the presence or absence of coaly matter, and the degree of charring, if present. Original factors, such as the morphological variability of cones/spores within the species, and the relationship of that variability to spore maturity, must also be taken into account in classification problems (e.g. Hagemann 1966, Balbach 1967, Willard 1989b). Due to the fact that in allochthonous associations there may be several biological species present that ori-

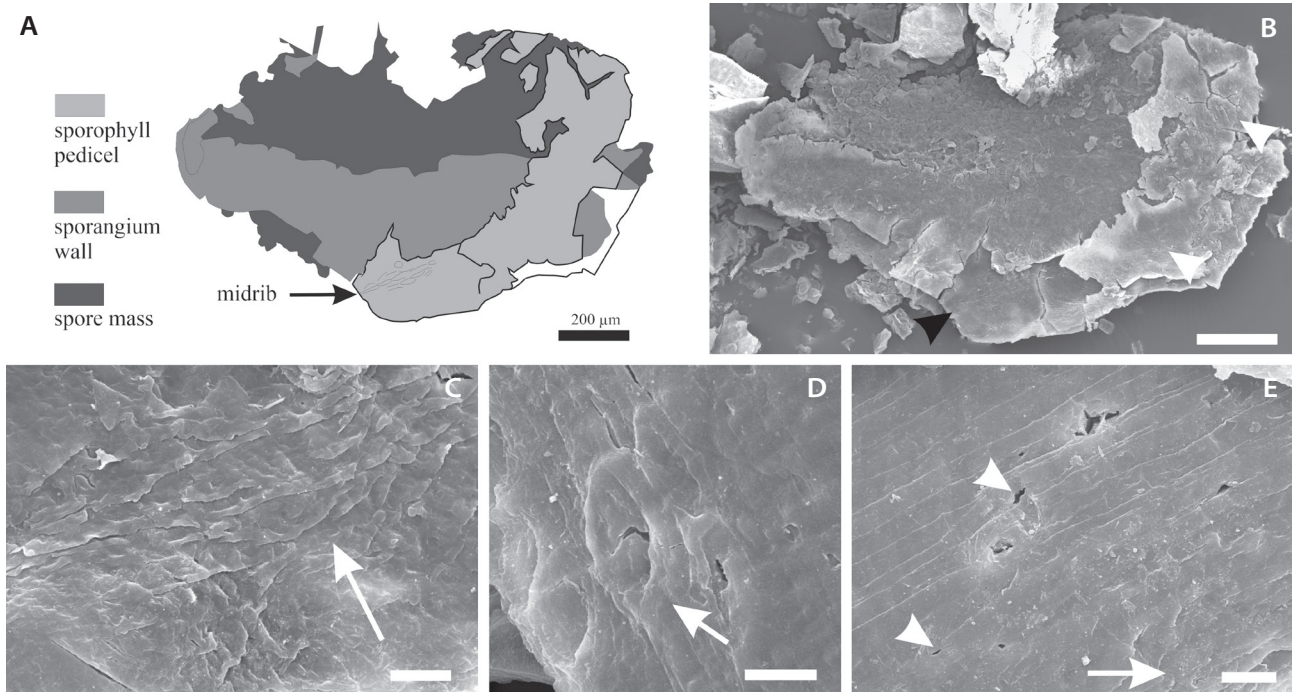


Figure 6. Cuticle and sporangium from Holotype F24016 of *Lepidostrobus willardii* sp. nov. A – schematic sketch from a photograph Figure 6B that shows open sporangium with sporophyll pedicel lamina, sporangium wall and spore mass. B – fragment of proximal part of sporangium filled by microspores and surrounded by sporophyll pedicel remains (arrowhead). SEM stub – USAIL14B2LepidostrobusSCH24hodslot10x. C – thick-walled cells (arrow) are situated above the midrib. SEM stub – USAIL14B2LepidostrobusSCH24hodslot11. D – ellipsoid circles preserved above the midrib. SEM stub – USAIL14B2LepidostrobusSCH24hodslot11. E – cuticle of the sporophyll shows long tetragonal epidermal cells with lens shaped structures (arrowheads) that probably represent the remains of sunken stomatal apparatuses. Arrow points to ellipsoid circles preserved above the midrib. SEM stub – USAIL14B2LepidostrobusSCH24hodslot11. Scale bars: 20 µm (C–E), 200 µm (B).

ginated from different plant communities, there may be a problem with clear species assignment of individual *Lepidostrobus* specimens, particularly if fragmentary. This is especially true for biological species that produced very similar cones. Confident assignment of *Lepidostrobus* specimens to one particular species is a condition for characterizing the intraspecific variability of cones within that species. The only environment that fulfills this condition are findings of autochthonous communities from T⁰ horizons (e.g. buried instantaneously in situ by volcanic tuff), which the studied material does not fulfill.

Herein, we tried to compare *Lepidostrobus* with already existing species, so as not to artificially increase the number of species. We focused mainly on *Lepidostrobus* species, with known *in situ* spores that belong to the *Lycospora brevijuga* Group (see Tab. 1). For an overall comparison, including morphological characters, species were selected from Tab. 2, which includes species that more or less correspond to a lower or middle Pennsylvanian stratigraphic position and were defined on the basis of compression preservation – see Tab. 3. Problems with correlating compression/adpression-preserved specimens with mineralized specimens have been mentioned in many works in the past (e.g. Abbott

1963, Galtier 1986, Pšenička *et al.* 2005). For this reason, the species described from mineralized samples are eliminated from the comparison. Based on the characters of the cones considered, we determined that the cone described here does not match any earlier described cones and therefore the establishment of a new species is justified (see Justification of *Lepidostrobus willardii* sp. nov. below).

Discussion of *Lycospora*

Dispersed *Lycospora* miospores are the most abundant among Lower and Middle Pennsylvanian dispersed spore genera. Due to its relatively long stratigraphical interval (Devonian–Tertiary, Somers *et al.* 1972) *Lycospora* has not been found to have stratigraphical significance at the species level. Nevertheless, the significant change of *Lycospora* abundance was recorded at the Middle–Late Pennsylvanian boundary (Desmoinesian–Missourian) in the American Pennsylvanian Basins, when lycosid dominance of (mostly peat) swamps changed to marattialean tree-fern and medullosan pteridosperm dominance, and biodiversity decreased as mentioned

Table 1. Measurements and stratigraphic occurrences of *in situ* lycospores assigned to the *Lycospora brevijuga* Group. Legend: N – not measured; white – compression; grey – coal-ball permineralization.

<i>In situ</i> lycospores					
Parent plant	Diameter (µm)	Width of cingulum (µm)	Width of zona (µm)	Stratigraphic level	Reference
<i>Lepidostrabus xinjiangensis</i>	22–27	1.5	2–3	Upper Devonian	Wang <i>et al.</i> (2003)
<i>Lepidostrabus comosus</i>	21–39	4–5	2–3	Holkerian	Thomas (1965)
<i>Lepidostrabus ornatus</i>	25	2.5	3	Westphalian	Brack-Hanes & Thomas (1983)
<i>Lepidostrabus spinosus</i>	29–35	2–3.9	1.3–3.3	Westphalian	Opluštil & Bek (2009)
<i>Lepidostrabus boltonensis</i>	29–35	2.6–4.2	1.2–2.5	Langsettian	Opluštil & Bek (2009)
<i>Lepidostrabus willardii</i> sp. nov.	25–37	2–5	2–4	Langsettian	herein
<i>Lepidostrabus</i> sp. D	24–43	1.4–3	1.5–3	Langsettian–Bolsovian	Hagemann (1966)
<i>Lepidostrabus variabilis</i> sensu Willard (1989b)	27–35	3.7	3.8	Asturian?	Willard (1989b)
<i>Lepidostrabus nemejcii</i>	28–42	1.5–3.5	1.5–3	Bolsovian–Asturian	Bek & Opluštil (2004)
<i>Lepidostrabus huttonii</i>	28–35	2.5–3.8	1–2.5	Langsettian–Duckmantian	Opluštil & Bek (2009)
<i>Lepidostrabus oldhamius</i> (associated with <i>Lepidodendron hickii</i>)	21–34.9	1–5	1–6	Langsettian–Asturian	Willard (1989a)
<i>Lepidostrabus jacksoni</i>	30–46	2–3	2–3	Duckmantian	Thomas (1965)
<i>Lepidostrabus</i> sp. B	35–48	2–3.5	2–4	Bolsovian	Bek & Opluštil (2006)
<i>Lepidostrabus</i> sp. C	26–36	2–3.5	1.4–3.6	Bolsovian	Bek & Opluštil (2006)
<i>Lepidostrabus</i> sp. D	28–41	2–3.5	1–2.8	Bolsovian	Bek & Opluštil (2006)
<i>Lepidostrabus oldhamius</i>	20–30	N	N	Bolsovian	Balbach (1967)
<i>Lepidostrabus oldhamius</i> f. γ	23	N	N	Bolsovian	Balbach (1967)
<i>Lepidostrabus coulteri</i>	27	N	N	Bolsovian	Balbach (1967)
<i>Lepidostrabus pulvinatus</i>	15–33	N	N	Bolsovian	Balbach (1967)
<i>Lepidostrabus obovatus</i>	24–44	1.2–5	1–4.5	Bolsovian	Bek & Opluštil (2004)
<i>Lepidostrabus praelongus</i>	27–35	3.7	3.8	Asturian	Willard (1989b)
<i>Lepidostrabus</i> cf. <i>squarrosus</i>	26–36	3.4	3.4	Asturian	Willard (1989b)
<i>Lepidostrabus stephanicus</i>	28–40.5	1.6–3	1.4–3.6	Asturian–Kasimovian	Bek & Opluštil (2004)
<i>Lepidostrabus</i> sp. A	32–42	1.4–3.5	1.5–3.5	Kasimovian	Bek & Opluštil (2006)

e.g. by DiMichele & Phillips (1996), Elrick *et al.* (2017), DiMichele *et al.* (2023), Schachat *et al.* (2023). Thus, *Lycospora* is important from a palaeoecological viewpoint (Smith & Butterworth 1967) and its occurrence is typical for rheotrophic swamp (Opluštil *et al.* 1999). This type of the swamp is typified by increasing ions in

the water column, increased pH, a rich nutrient supply, and a planar surface. The most abundant plants in such environments during the Late Mississippian through Middle Pennsylvanian were arborescent lycophytes of the *Lepidophloios* and *Lepidodendron* type, *i.e.* *Lycospora*-producers (Tab. 2).

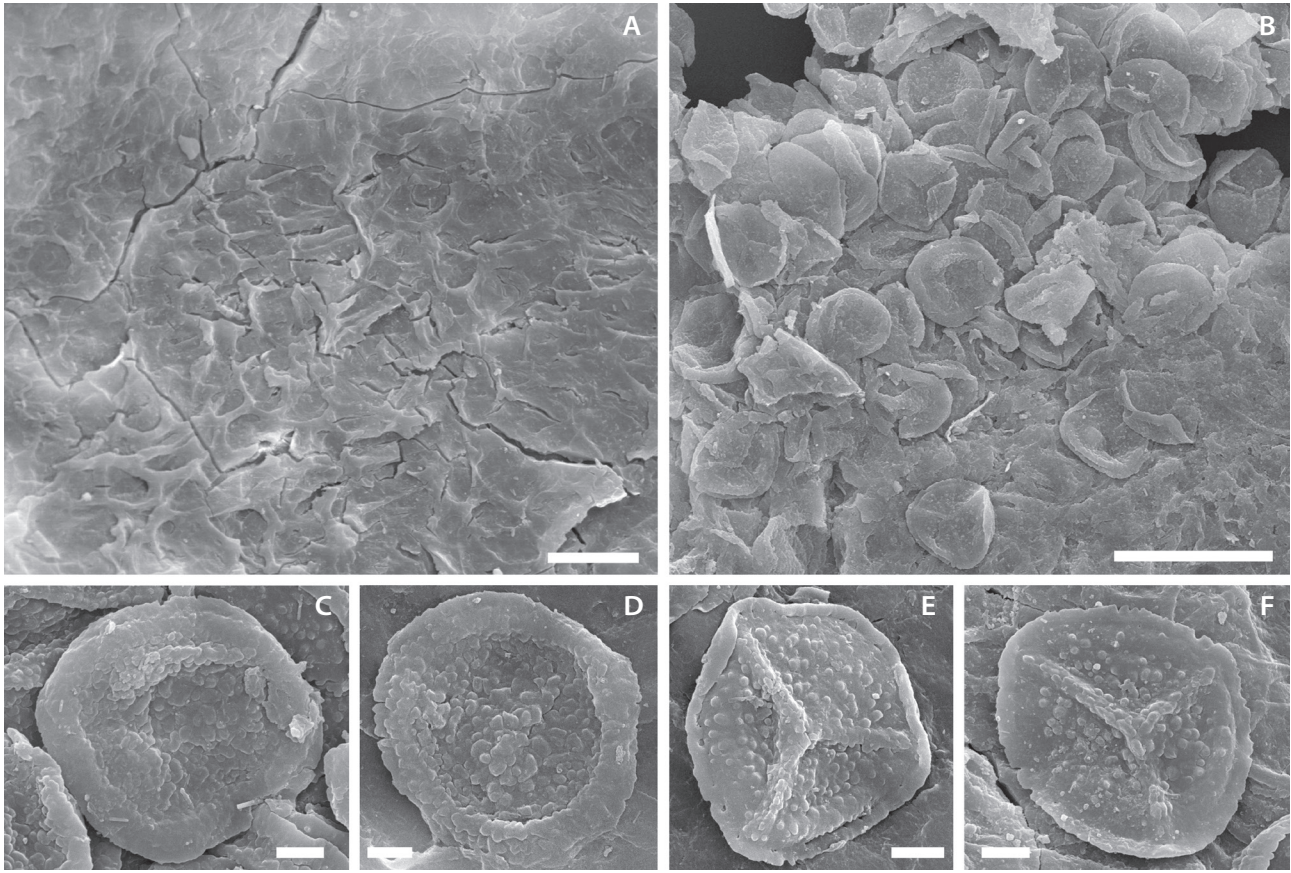


Figure 7. Sporangium wall structures and *in situ* microspores from holotype F24016 of *Lepidostrobus willardii* sp. nov. A – polygonal or rectangular shaped cells of the sporangial wall. SEM stub – USAIL14B2LepidostrobusSCH24hodslot10x. B – sporangium filled by *in situ* spores of the *Lycospora brevijuga* type. SEM stub – USAIL14B2LepidostrobusSCH24hodslot10x. C, D – proximal surfaces of *in situ* spores of the *Lycospora brevijuga* type. Note labrum and microgranulate to microverrucate sculpture elements. SEM stub – USAIL14B2LepidostrobusSCH24hodslot11. E, F – distal surfaces of *in situ* spores of the *Lycospora brevijuga* type. Note that microgranulate to microverrucate sculpture elements on proximal and distal surfaces are the same. SEM stub – USAIL14B2LepidostrobusSCH24hodslot11. Scale bars: 5 μ m, (C–F), 20 μ m (A), 50 μ m (B).

We know of many dispersed *Lycospora* species, all summarized and re-examined by Somers *et al.* (1972). Bek (2012) reported seventy-one occurrences of *in situ* *Lycospora* and mentioned twenty-nine dispersed *Lycospora* species. Bek (2012) divided *Lycospora* species into six morphological groups and described all of the parent plants that produced the spores of each group. *In situ* spores isolated from *Lepidostrobus willardii* sp. nov. were sampled from both the apical and lower parts of the cone and are identical in size and character, with a relatively narrow cingulum and narrow zona. They belong to the *Lycospora brevijuga* Group. It means that we did not observe any morphological differences among spores isolated from apical and more basally located sporangia. Table 1 shows dispersed *Lycospora* species belonging to this group and all *in situ* records of spores of this morphological type and their parent plants. It means that cones described herein can be compared with lycophyte species that produced the same morphological type of *Lycospora*.

Justification of the *Lepidostrobus willardii* sp. nov.

Comparison with already published species can be problematic (see introduction). We selected species that approximately correspond to the stratigraphic level (except for *Lepidostrobus variabilis sensu* Willard, 1989b, which, although stratigraphically belonging to the Asturian, has the characters that more or less correspond to the studied specimen), the same type of preservation, and yielded *in situ* spores belonging to the *Lycospora brevijuga* Group (see Tab. 3).

Table 3 shows that the species *Lepidostrobus jacksoni* Arber, *L. obovatus* (Rénier) Bek & Opluštil or *L. huttonii* Opluštil & Bek are significantly shorter and wider with a narrower axis than the studied specimen. The species *Lepidostrobus* sp. B (*sensu* Bek & Opluštil 2006), *L. comosus* and *L. sp. C* (*sensu* Bek & Opluštil 2006) are wider, sometimes almost twice as wide, with a significantly longer pedicel than that of the studied cone.

The comparison with *Lepidostrobus* sp. D (*sensu* Bek & Opluštil 2006, pl. 2, Fig. 25) is problematic. *Lepidostrobus* sp. D shows a 125 mm adpression fragment with detached distal laminae that are not preserved and internal morphology, including the axis, that also is not preserved. Due to this fact, comparison with the new species is impossible. *Lepidostrobus spinosus* Kidston is similar in the width of the cone, cone axis, and distal lamina, but the cone is markedly shorter (up to half) when compared to the studied cone. Based on the limited knowledge about the size variability of the species *L. spinosus*, the assignment to the studied species would be based more on speculation than on empirical data.

We included the species *Lepidostrobus imbricatus* Hoskins & Cross in the comparison species list because *L. imbricatus* is similar to the studied specimen, including some morphological characters, stratigraphical position (Langsettian), and origin from the Illinois Basin. Nevertheless, the comparison is made difficult by the fact that the holotype of *L. imbricatus* is preserved as a cast in fine grained sandstone (Hoskins & Cross 1940, p. 429, figs 1, 2), whereas our specimen is an adpression. Hoskins & Cross (1940) described *in situ* spores, however figured them only as *camera lucida* drawings (Hoskins & Cross 1940, figs 17, 18.). Later, Felix (1954) followed and adopted a spore description from Hoskins & Cross (1940). Due to this fact, it is problematic to compare these drawings with *in situ* spores from the study specimen. From the macromorphological view, the sporophyll including pedicel and distal lamina are significantly larger (see Tab. 3) in *L. imbricatus* compared to *L. willardii*. *Lepidostrobus imbricatus* also has almost twice the length of sporangia than the studied cone.

Lepidostrobus willardii can be compared with *Lepidostrobus* sp. D *sensu* Hagemann (1966), which was found in the Zwartberg Mine (Belgium), stratigraphically from the Langsettian–Bolsovian. Like the new species here, *Lepidostrobus* sp. D is incomplete and the base and apex area are missing (Hagemann 1966, pl. 3, fig. 1). If we look at Table 3, we see that the width of the cone, the axis width, and the size of the sporangium are approximately the same in both species. However, the pedicel is slightly larger in *Lepidostrobus* sp. D (max. 7.3 mm) whereas in the studied cone its maximum is 6 mm. All these differences could fall under intraspecific variability. However, Hagemann (1966) mentions the important fact that approximately the entire lower half of the *Lepidostrobus* sp. D cone is without sporangia, and Hagemann (1966) believes that it is possible that megasporangia were originally present here. If there really were megasporangia, then according to Brack-Hanes & Thomas (1983) it would be *Flemingites*. However, *Lepidostrobus* sp. D *sensu* Hagemann (1966) has *in situ* microspores assigned to the *Lycospora brevijuga* Group but generally

Flemingites has *Microspinosporites* type of microspores (Bek 2013). However, it must be noted that the division into *Lepidostrobus* and *Flemingites* is rather artificial, for the needs of identifying isolated lycopsid cones, rather than corresponding to natural genera/species (*e.g.* Phillips 1979). But the facts so far are that species with microspores of the *Lycospora brevijuga* Group have never been found in combination with megasporangia. For this reason, missing sporangia may be rather a taphonomic problem when the sporangia in the lower part are not preserved. Due to this fact that problem cannot be solved in this work. Therefore, we do not include *Lepidostrobus* sp. D *sensu* Hagemann (1966) among synonyms and the question of its relationship to the studied cone is open.

The basic characters (total width, axis width, length of pedicels – see Tab. 3) of the studied cone are similar to the type species of the genus *Lepidostrobus*, namely *L. ornatus* Brongniart that comes from the Coal Measures of Derbyshire (UK). The original type specimen of this species is partially preserved in a clay ironstone nodule (Brack-Hanes & Thomas 1983, p. 127, fig. 2), so the specimen is 3D preserved. Unfortunately, this fact is limiting for a serious comparison of both species – 3D versus adpression. For example, there is a complete lack of information about sporophylls, which have not been fully preserved in *L. ornatus*. However, one important parameter separates both species, namely the size of the sporangia (see Tab. 3) where the sporangia of *L. ornatus* are almost twice as long in comparison to the studied cone.

A certain similarity with the studied species can also be found with the species *Lepidostrobus boltonensis* Opluštil & Bek from the Lower Coal Measures of Chequerbent Pit, Bolton, South Lancashire Coalfield (UK). Although the length of the *L. boltonensis* cone is not known, due to the smaller width and especially the very narrow axis, the cone will be smaller overall (see Tab. 3) than our studied cone. This assumption is supported by the most complete specimen from Opluštil & Bek (2009, fig. 2a, d) that is 72 mm long and lacks only the base.

The studied specimen also more or less corresponds to the dimensions of *Lepidostrobus variabilis* in the sense that species name was used by Willard (1989b) for material from the Lower Kittanning Coal (probably Asturian age), Cannelton, Luzerne County, Pennsylvania, USA (Appalachian Basin). According to Chaloner (1967), however, *L. variabilis*, as originally described, is conspecific with *L. ornatus* and *L. ornatus* has nomenclature priority. Willard (1989b) stated the figures of microspores (Brack-Hanes & Thomas 1983, p. 128, figs 5, 6) from the type specimen of *L. ornatus* are not the same as spores isolated from specimens she studied and attributed to *L. variabilis* (Willard 1989b) and therefore she used the name *L. variabilis* as a separate species from *L. ornatus*.

Table 2. Measurements and stratigraphic occurrences of dispersed lycospores assigned to the *Lycospora brevijuga* Group. Abbreviation: N – not measured.

Dispersed lycospores (holotypes)				
Dispersed species	Diameter (µm)	Width of zona (µm)	Width of cingulum (µm)	Stratigraphic level of holotype
<i>Lycospora micrograna</i>	38 × 35	2	2	Viséan
<i>Lycospora brevijuga</i>	33 × 35	1.5–2	1.5–2	Bolsovia
<i>Lycospora brevis</i>	25 × 22	2–3	1–2	Bolsovia
<i>Lycospora denticulata</i>	24 × 23	1.5–2	2	Bolsovia
<i>Lycospora punctata</i>	35 × 32	2	2	Bolsovia
<i>Lycospora contacta</i>	32 × 32	2	2	Bolsovia
<i>Lycospora subjuga</i>	29 × 27	1–2	2	Asturian
<i>Lycospora microgranulata</i>	34	N	N	Stephanian
<i>Lycospora triangulata</i>	29 × 27	1.5–2	1.5–2	Stephanian
<i>Lycospora clavata</i>	27 × 30	2	2	Stephanian
<i>Lycospora perforata</i>	26 × 28	2	2	Stephanian C

Table 3. Measurements of *Lepidostrobus* species which were selected for comparison with a new species *Lepidostrobus willardii* sp. nov. belonging into *Lycospora brevijuga* Group.

Parent plant	Length (mm)	Width (mm)	Axis (mm)	Pedicel (mm)	Distal lamina (mm)	Sporang. (mm)	Reference
<i>Lepidostrobus comosus</i>	> 160	30–35	3–3.5	?	40	8–11 × 2 × 4	Thomas (1965)
<i>Lepidostrobus</i> sp. D	> 84	18–25	3.3–7.3	6.6–9.3	?	4–7.3 × 0.6–1.5	Hagemann (1966)
<i>Lepidostrobus ornatus</i>	> 140	22	6	8	?	8 × 3	Brack-Hanes & Thomas (1983)
<i>Lepidostrobus imbricatus</i>	> 135	18–25	4–5	8	15–20	6–8	Felix (1954)
<i>Lepidostrobus variabilis</i>	185	17–32	3–7	?	5–11.5	?	Willard (1989b)
<i>Lepidostrobus jacksoni</i>	60	17–20	3–4	?	6	1.5–2 × 3	Thomas (1965)
<i>Lepidostrobus obovatus</i>	65–100	18–22	1.5–2	<10	13	?	Bek & Opluštil (2004)
<i>Lepidostrobus</i> sp. B	?	43	2.5–3	9	12–13	?	Bek & Opluštil (2006)
<i>Lepidostrobus</i> sp. C	?	38–48	8.5	19	?	?	Bek & Opluštil (2006)
<i>Lepidostrobus</i> sp. D	> 125	20	?	?	?	?	Bek & Opluštil (2006)
<i>Lepidostrobus boltonensis</i>	> 72	21–22	2–2.2	4–9	5–6	4–9 × 1.5–2	Opluštil & Bek (2009)
<i>Lepidostrobus spinosus</i>	78	26	4	7–8	10	?	Opluštil & Bek (2009)
<i>Lepidostrobus huttonii</i>	68	20	1.5	?	8–9	?	Opluštil & Bek (2009)
<i>Lepidostrobus willardii</i>	> 135	26	4–5	5–6	7–9	4–5 × 2	herein

However, this creates nomenclatural confusion because Willard (1989b) misidentifying her specimens as *L. variabilis* name that already had been made synonymous with another species *L. ornatus*. Unfortunately, Willard (1989b) does not provide more detailed morphological characteristics of the cone, and it cannot be compared in detail with the studied species from this work. For this reason, we will not synonymize Willard's (1989b) *L. variabilis* with the studied cone yet, so as not to increase nomenclatural confusion. Our opinion is also supported by the fact that Willard's (1989b) specimen comes from younger strata (probably Asturian). A similar cone, but shorter and narrower than *Lepidostrobus variabilis sensu* Willard (1989b) and shorter than the studied cone, has been described from the Upper Mississippian–Lower Pennsylvanian Surprise Canyon Formation in the Grand Canyon, Arizona (USA), and was named *Lepidostrobus* sp. cf. *ornatus* (Tidwell *et al.* 1992), but *in situ* spores are unknown.

It follows from the above comparisons that it is not possible to reliably assign the studied cone to any already described species from which *in situ* spores are known. It is possible that as the number of works devoted to *in situ* spores from type specimens increases, a match with some previously described *Lepidostrobus* species will appear both in the type of microspore and in morphological characteristics. This cannot be ruled out. But at the current level of knowledge, it is appropriate to name the studied specimen as a new species and so we proceeded to establish that new species as *Lepidostrobus willardii* sp. nov.

The plant association with *Lepidostrobus willardii* sp. nov.

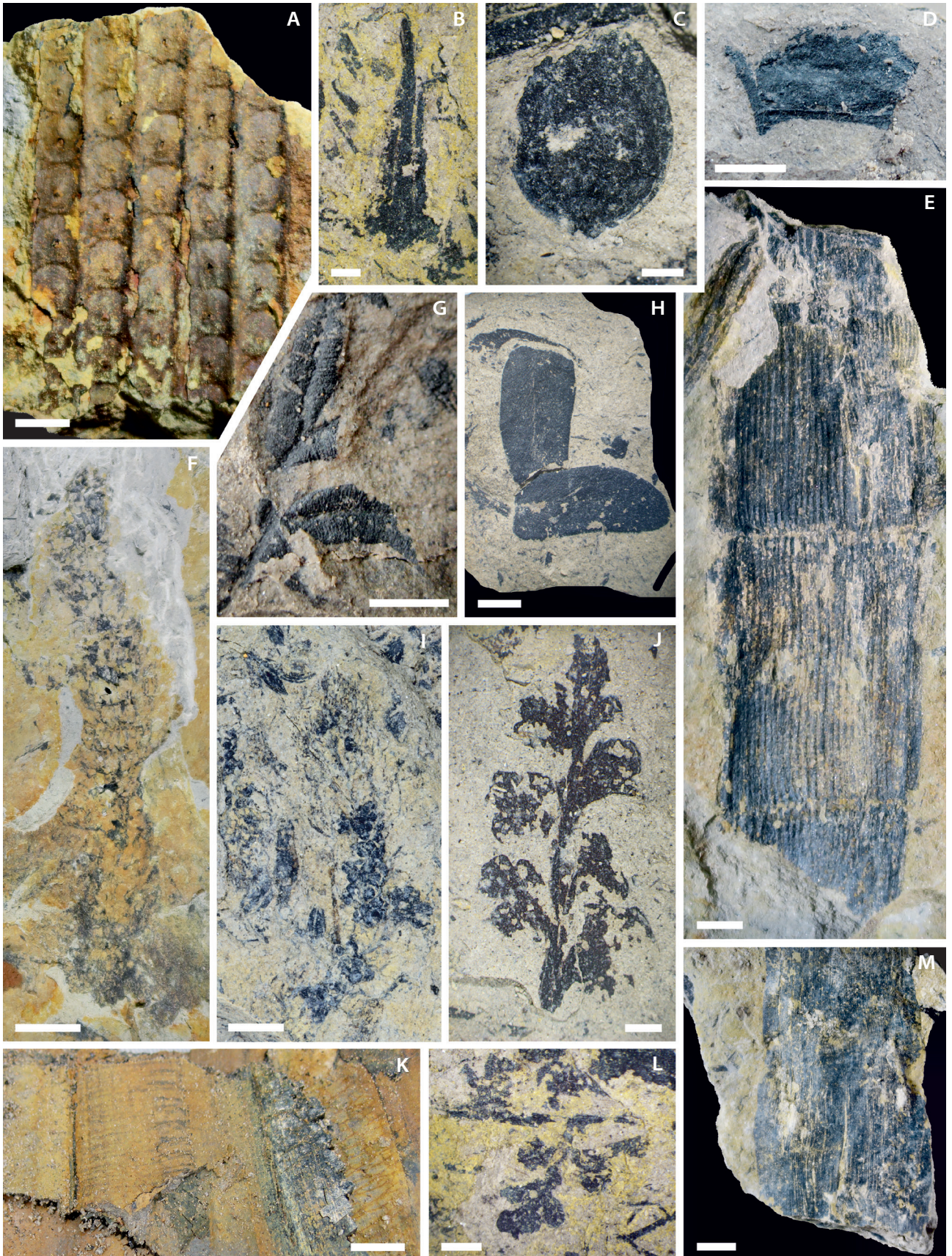
The holotype of *Lepidostrobus willardii* sp. nov. was collected during a fieldtrip (in 2009) seeking plant fossils in southern Illinois. The strata belong to the basal Tradewater Formation, under the Reynoldsburg Coal Bed. *Lepidostrobus willardii* sp. nov. is associated with *Sigillaria tessellata* Brongniart (Fig. 8A), *Sigillariostrobus* sp. (Fig. 8B), *Lepidocarpon* sp. (Fig. 8D), *Stigmaria ficoides* (Sternberg) Brongniart, *Calamites suckowi* Brongniart (Fig. 8E), *Palaeostachya* sp. (Fig. 8F), *Bowmanites* sp. (Fig. 8I), *Cordaites* sp. (Fig. 8M), *Artisia* sp.

(Fig. 8K), *Alethopteris* cf. *decurrens* (Artis) Frech (Fig. 8G), *Paripteris gigantea* (Sternberg) Gothan (Fig. 8H), *Eusphenopteris* cf. *obtusiloba* (Brongniart) Novik (Fig. 8J), *Sphenopteris* sp. (Fig. 8L) and *Cardiocarpus* sp. (Fig. 8C).

We interpret the paratchonous flora (*sensu* Bateman 1991) to represent plants that grew on a landscape that became increasingly wet as rainfall increased on the formerly better drained paleosol, which probably developed on low, swampy spots on the landscape. Eventually peat began to form as the wettest phase of a glacial cycle began (oral communication with W.A. DiMichele, Smithsonian Institution). As typical elements of Carboniferous peat environments, lycopsid trees preferred waterlogged soils (Phillips & DiMichele 1992, Bashforth *et al.* 2011). The lycopsid species *Lepidostrobus willardii* sp. nov., *Sigillaria tessellata*, *Sigillariostrobus* sp., *Lepidocarpon* sp. and *Stigmaria ficoides* are representatives from the plant association that inhabited such an environment. On the other hand, *Cordaites* sp. occupied wet freshwater environments (but even as a salt-tolerant plant – Raymond *et al.* 2010), but they were also able to grow in drier places around swamps with relatively wet and stable substrate (Bashforth *et al.* 2011).

A numerically significant group of plants in the assemblage from the studied locality are pteridosperms. Thanks to their reproductive strategy and overall architectural complexity as seed plants, these plants preferred undisturbed habitats in the domain of better-drained, stable substrates (Bashforth *et al.* 2011). Of the stratigraphically important pteridosperm species, isolated leaves of *Paripteris gigantea* were found abundantly at the site. *Paripteris gigantea* is a common element of Euramerican as well as Cathaysian floras from Chorkierian (in the Cathaysian realm) to Bolsovian or rarely Asturian (in the American basins) (Laveine 1967; Šimůnek 2009, 2010). Laveine *et al.* (1993, 2003) attempted to trace the migration of *Paripteris* from Asia through Europe to North America. *Paripteris gigantea* is accompanied by the species *Alethopteris* cf. *decurrens* according to vein density ~35 veins per cm of pinnule margin. However, the specimen is very fragmentary so identification cannot be accurate. According to Crookall (1955) and Šimůnek (1996) *Alethopteris decurrens* (Artis) Frech ranges from Namurian C to Langsetian and occurs rarely in the Bolsovian. Significant for the stratigraphy is the discovery of the arborescent lycophyte *Sigillaria*

Figure 8. Fossil plants collected from the I-24 roadcut together with *Lepidostrobus willardii* sp. nov. cone. • A – *Sigillaria tessellata* Brongniart, specimen F24018A. • B – *Sigillariostrobus* sp., specimen F24015. • C – *Cardiocarpus* sp., specimen F24025. • D – *Lepidocarpon* sp., specimen (photo by W.A. DiMichele). • E – *Calamites suckowi* Brongniart, specimen F24020. F – *Palaeostachya* sp., specimen F24027. • G – *Alethopteris* cf. *decurrens* (Artis) Frech, specimen (photo by W.A. DiMichele). • H – *Paripteris gigantea* (Sternberg) Gothan, specimen F24009. • I – *Bowmanites* sp., specimen F24011. • J – *Eusphenopteris* cf. *obtusiloba* (Brongniart) Novik, specimen F24010. • K – *Artisia* sp., specimen (photo DiMichele, W.A.). • L – *Sphenopteris* sp., specimen F24012. • M – *Cordaites* sp., specimen F24014. Scale bars: 2 mm (B, C, J, L), 4 mm (D, G), 5 mm (H, I), 8 mm (K), 10 mm (A, E, F, M).



tessellata. According to Crookall (1966) the species *S. tessellata* occurs in Europe from Langsettian to Bolsovian.

The common occurrence of these three stratigraphically significant species at the collection locality indicates an affiliation to the upper Bashkirian (lowermost Pennsylvanian) in agreement with Peppers' (1996) correlation.

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