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A reassessment of the Pennsylvanian lycophyte cone *Triplosporite* Brown

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ABSTRACT:

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The type collection of the lycopsid cone species *Triplosporite brownii* Unger was re-examined to assess its *in situ* spores. The cones are monosporangiate with only microspores that possess both cingulum and zona. They equate to the dispersed miospore genus *Lycospora* and would be identified as *Lycospora* cf. *pseudoannulata.* Therefore, the genus *Triplosporite* Brown is shown to be a junior synonym to *Lepidostrobus* and a species emendation is given. A comparison is given with the other *Lepidostrobus* cones which yielded similar *in situ* microspores of the *Lycospora pellucida* Group.

Key words: *Lepidostrobus*; *Lycospora*; *in situ* spores; *Triplosporite*; Cones; Carboniferous.

INTRODUCTION

For over 159 years the lycophyte cone genus *Lepidostrobus* Brongniart was accepted to contain species that were wholly microsporangiate and others that were bisporangiate containing both megaspores and microspores. Thomas (1970, 1978) and Thomas and Dytko (1980) suggested that the microspores, referred to the genus *Lycospora* (Schopf, Wilson and Bentall) Potonié and Kremp, extracted from microsporangiate species of *Lepidostrobus* have both cingulum and zona, differing from those produced by bisporangiate cones.

The lectotype of *Lepidostrobus*, *L. ornatus* Brongniart, was shown to have only microspores that had a cingulum and a developed zona (both 2.5–3 μm wide, see Bek 2012) with ornamented proximal and distal surfaces (Brack-Hanes and Thomas 1983). From this evidence *Lepidostrobus* was restricted to microsporangiate cones that yielded cingulate and cingulizonate microspores of the *Lycospora*-type, whereas the genus *Flemingites* Carruthers was redefined to include those bisporangiate cones that were originally referred to *Lepidostrobus*. The *Lycospora* microspores in *Flemingites* do not have a zona and possess prominent densely microspinate distal surface. The proximal sculpture is usually laevigate, sometimes microverrucate to microgranulate (Bek 2012).

Within the systematic descriptions in Brack-Hanes and Thomas (1983) the microsporangiate *Triplosporite brownii* Unger was referred to the genus *Flemingites* on

the basis of the structure of its microspores figured by Brown (1848). By examining the drawings of the microspores in Brown's paper Brack-Hanes and Thomas (1983) came to the conclusion that the spores had only a narrow cingulum and therefore included *Triplosporites brownii* in *Flemingites* naming it *Flemingites brownii* (Unger) comb. nov. They did not see Brown's preparations.

Brown (1848) first used the name *Triplosporite* in describing the upper part of a petrified cone from an unknown locality in the Carboniferous of France. Later Brown (1851) described the cone as having bractae (sporophylls) with sporangia on their upper surfaces "filled with innumerable microscopic sporules, originally connected in threes (very rarely in fours) but ultimately separating…". It is because he thought the majority of the sporules (microspores) to be in threes that Brown called it *Triplosporite* to distinguish the cone from those genera having spores in "constant quadruple union" i.e. in tetrads. Brown gave no diagnosis for *Triplosporite* but did remark that it "approaches most nearly, among recent tribes, to *Lycopodiaceae* and *Ophioglosseae*; and among fossils, no doubt, to *Lepidostrobus*, and consequently to *Lepidodendron*." In an addendum to the paper, Brown accepted Joseph Hooker's observation (Hooker 1843) that some microspores in a specimen of *Lepidostrobus* appeared to be in threes and also noted the general acceptance of Brongniart's (1828–1838) view of *Lepidostrobus* being the fructification of *Lepidodendron* Sternberg. Nevertheless, Brown hesitated from referring *Triplosporite* to *Lepidostrobus* on the grounds that he believed the structure of the latter to be imperfectly known.

Although Brown gave no diagnosis for *Triplosporite* we regard it as being validly published. A few years later, Unger (1850) gave a Latin diagnosis of what he now called *Triplosporites* Rob. Brown in his *Genera et Species* (p. 270) and a single sentence diagnosis for his solitary species *Triplosporites brownii*. The generic diagnosis included Unger´s details of the sporophylls and sporangia and that the spores were in threes and occasionally fours. The species diagnosis was based on the structure of the sporangia "Capsules lenticulares compressae, obcordatae, v. reniformes, acuminatae." The species was later referred to *Lepidostrobus brownii* by Schimper (1870).

This produced a taxonomic problem that was missed at the time by Brack-Hanes and Thomas (1983), because, if the two genera were synonyms as they suggested, *Triplosporite* Brown (1845, 1850) predated *Flemingites* Carruthers (erected in 1865) it has priority. To resolve this problem, the slides of *Triplosporite brownii*, which are in the Natural History Museum, London (numbers V10980, V10980a-b, V1326, V1326 a-s), were examined.

The sporangia were full of microspores [Text-fig. 1a, 2] approximately 28–36 μm in diameter. However, the slide sections were thick enough to make focusing on the spores difficult and the preservation of many spores was not perfect showing very indistinct outlines and ornamentation. Many were still in tetrads that in some views could be mistaken for clusters of three as Brown had assumed [Text-figs 1c, d]. Other spores were better preserved and clearly showed equatorial structures 3–5 μm wide, consisting of a cingulum and probably a perforated zona [Text-figs 2d]. It was difficult to be certain about the ornamentation of the exine, but the distal surface is microspinate to microgranulate and proximal sculpture seems to be laevigate. The structure of these spores shows that *Triplosporite* is part of a microsporangiate cone and not bisporangiate as in *Flemingites*. Therefore, *Triplosporite* is a junior synonym of *Lepidostrobus*.

MATERIAL AND METHODS

There is no hand specimen of the cone because it has been completely cut into sections. Most sections were transverse although the more apical part of the cone was cut longitudinally. Measurements of the sporangia, sporophyll pedicels and laminae were made by combining information from transverse and longitudinal sections. The spores had to be examined in the slides because there was no opportunity to extract them for closer study. Specimen is stored in the Natural History Museum, London, UK (No. V.10980c).

The spores are classified according to the system of dispersed spores suggested by Potonié and Kremp (1954, 1955) and improved by Dettmann (1963) and Smith and Butterworth (1967). The terms used for the description of the morphology, including the sculptural elements follows the Punt *et al*. (2007) classification. The species determination is based only on these original diagnoses, and not on the interpretations of subsequent authors. Measurements of the holotypes of dispersed species of this group, *in situ* microspores of this type and their parent cones are given in Table 1.

In situ spores are generally accepted to be as an integral part of the diagnoses of any fructification and as part of this the spores are compared with known dispersed species of spores; preferably with the types of the dispersed spore species (Thomas 1987). The details of the *in situ* spores in *Triplosporite brownii* must, therefore, be included in the emended diagnosis for the cone.

Dispersed spores (holotypes)					
Dispersed species	Diameter (μm)	Width of cingulum (μm)	Width of zona (μm)	Stratigraphic level of holotype	Reference
Lycospora pellucida	39 × 46	2	2-4	Bolsovian	Somers *et al.* 1972
Lycospora pseudoannulata	32 × 35	2	3-4	Langsettian	Somers *et al.* 1972
Lycospora intermedia	47 × 49	2	3-4	Bolsovian	Somers *et al.* 1972
Lycospora loganii	32 × 34	2	2	Duckmantian	Somers *et al.* 1972

In situ spores					
Parent plant	Diameter (μm)	Width of cingulum (μm)	Width of zona (μm)	Stratigraphic level	Reference
Lepidostrobus fayettevillense	42-50	Not measured	Not measured	Pendleian	Taylor and Eggert, 1968
Lepidostrobus barnsleyensis	20-35	1.5-2.5	2-4.5	Duckmantian	Thomas, 1965
Lepidostrobus spinosus	21-39	1.5	5	Duckmantian	Thomas, 1965
Lepidostrobus binneyanus	20-35	2.5	4	Duckmantian	Thomas, 1970
Azaniadendron fertile	21-36	Not measured	Not measured	Early Permian	Rayner, 1986
Lepidostrobus oldhamius (associated with *Lepidophloios harcourtii*)	29-41.6	2-3	4-11	Langsettian-Duckmantian	Willard, 1989
Lepidostrobus sp. C	33-37	2	3-5	Duckmantian	Hagemann, 1966
Lepidostrobus brownii	28-36	2-3.3	2.5-4	Mississippian	Herein

Table 1. Measurements and stratigraphic ranges of holotypes of dispersed and *in situ* spores of the *Lycospora pellucida* Group (from Bek 2012) and their parent cones

SYSTEMATIC PALAEONTOLOGY

Class Lycopsida Scott, 1909
Order Lepidocarpaceae Thomas and Brack-Hanes, 1984
Genus *Lepidostrobus* Brongniart, 1828

TYPE SPECIES: *Lepidostrobus ornatus* Brongniart, 1828

Lepidostrobus brownii (Unger, 1850) Schimper 1870
(Text-figs 1–2)

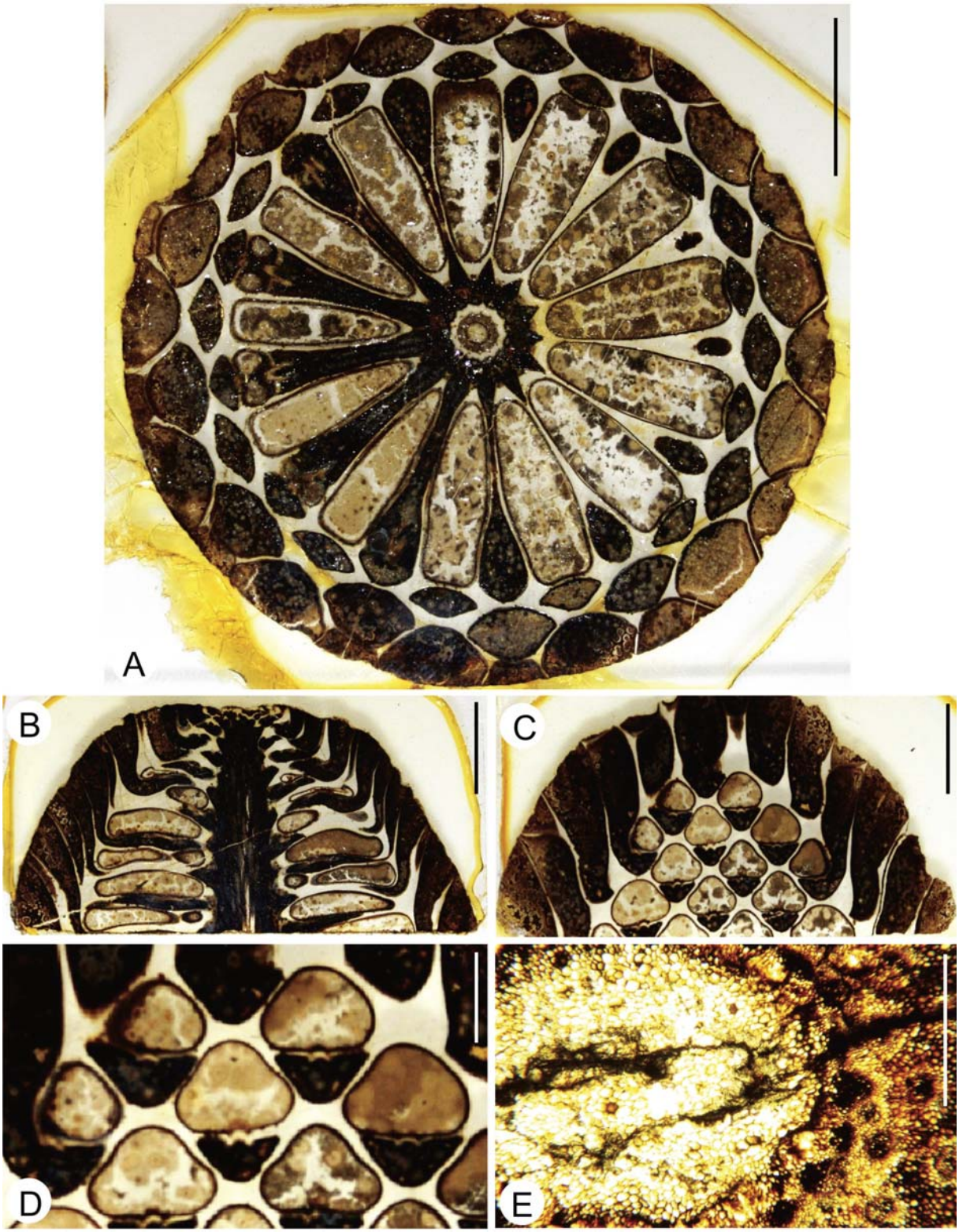
1848. *Triplosporite* sp.; Brown 1848, p. 344.
1850. *Triplosporite brownii* Unger; Unger, p. 270.
1851. *Triplosporite* sp.; Brown, pls 23, 24.
1870. *Lepidostrobus brownii* Unger; Schimper, pl. 62: figs 13,14, 16–19, 21–22, (V13236), 15 (V1098c), 17 (V13236a), 19 and 20 (V10980a), 23–26.
1894 *Lepidostrobus brownii* Unger; Bower, pl. 47, p. 103.

HOLOTYPE: Brown, 1848, pl. 23, fig. A.

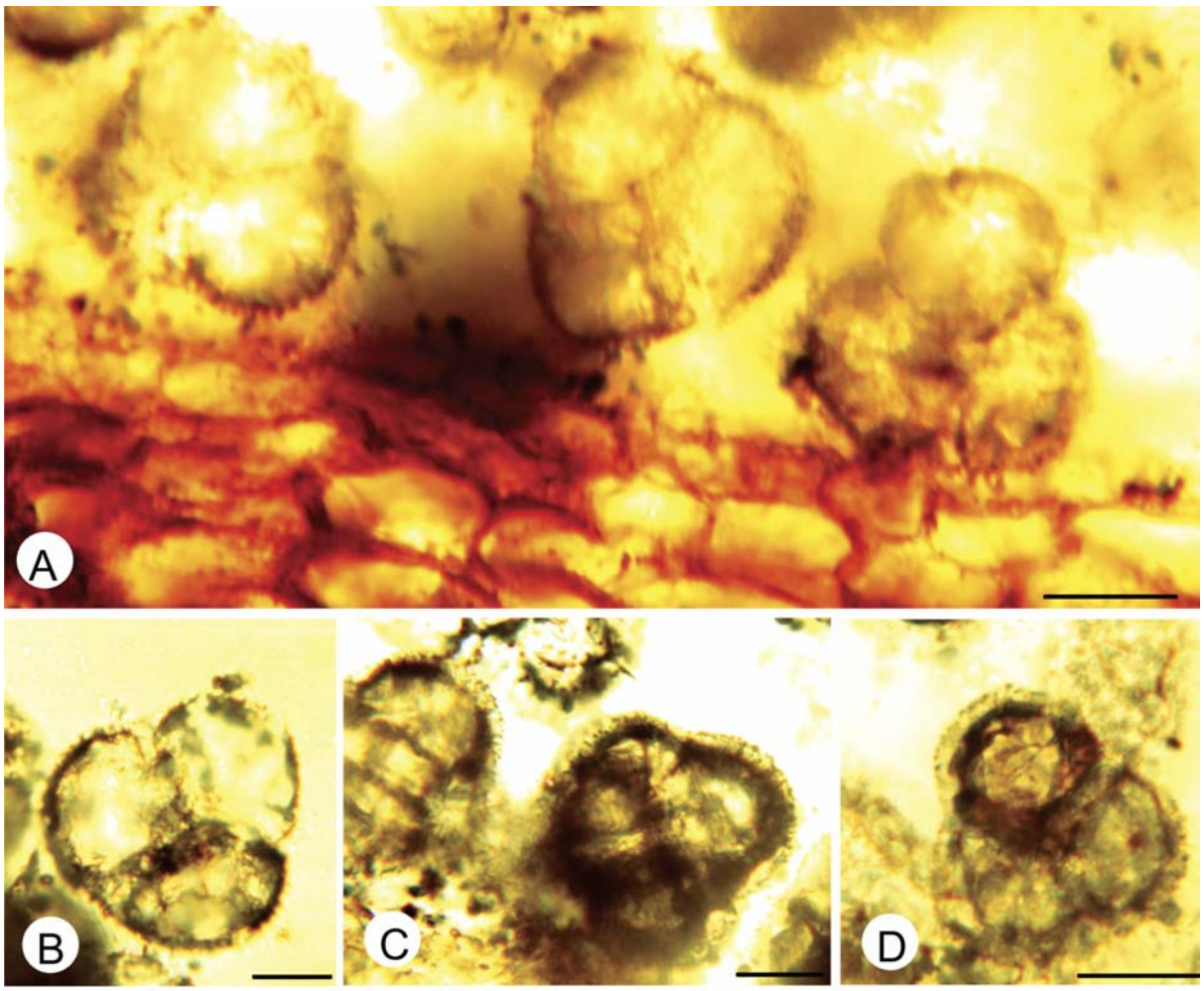
TYPE LOCALITY: Unknown locality in France.

STRATIGRAPHY: Mississippian (see Brown 1848).

EMENDED DIAGNOSIS: Microsporangiate cone, c. 54 mm in diameter, central cone axis 3.1 mm in diameter with vascular traces 80 μm across. Sporangia 12–14 in each whorl. Sporangia 13 mm long and 7 mm broad and 3 mm high at the distal end. Sporangial wall c. 11 μm thick. Sporophyll pedicel 900 μm thick, dipping slightly at end of sporangium with lamina slightly divergent from the vertical. Lamina c. 7 mm broad, c. 5 mm thick, with a single vascular bundle c. 60 μm in diameter. Trilete circular to subcircular microspores, 28–36 μm in diameter. Cingulum 2 (2.6) 3 μm wide, developed as a dark ring on the outer margin of the central body. Zona is 2.5 (3.2) 4 μm in width in form of lighter ring on the outer margin of cin-



Text-fig. 1. Sections of *Triplosporite browni* (Unger, 1850). A – Transverse section of the cone (No. V.10980e), scale bar 10 mm; B – Tangential longitudinal section of the apical part of the cone (No. V.10980k), scale bar 10 mm; C – Close to a radial longitudinal section of the apical part of the cone (No. V.10980r), scale bar 10 mm; D – Enlargement of b showing sporangia and sporophylls in transverse section, scale bar 5 mm; E – Central stele of the cone (No. V.10980e), scale bar 3 mm



Text-fig. 2. A – Section of sporangial wall and microspore tetrads. B, C – Microspore tetrads; D – Spore showing dark cingulum and outer zona. Scale bars 20 µm

gulum. Proximal surface laevigate, distal surface microspinate to microgranulate. Zona pitted or perforated. Rays of trilete mark extend to the inner margin of cingulum.

COMPARISON

Zeiller (1911) gave a detailed account of a specimen in the Paris Natural History Museum, France that he named *Lepidostrobus brownii* (Unger) Schimper and suggested that it might even have been a part of the same cone described by Brown. However the specimen described by Zeiller is bisporangiate with microsporangia in the upper part and megasporangia in the lower part. The microspores (his pl. 11, figs 15, 17, 18) show no sign of a zona, therefore being of the type found in the genus *Flemingites*. For these reasons we cannot accept that Zeiller's specimen belongs to *Lepidostrobus brownii* as we have redefined it here. At this stage we do not give Zeiller's specimen a new name other than to suggest that it does not equate to any described species of *Flemingites*. Chaloner (1967) included several other species as synonyms of *L. brownii* to: *L. dabadianus* Schimper, *L. rouville* Renault and Saporta and *L. laurentia* Zeiller (1907). On the available evidence we cannot accept these as synonyms because nothing is known about their in situ spores.

In comparing the *in situ* spores of *Lepidostrobus brownii* with dispersed and other known *in situ* microspores of the genus *Lycospora* we determine that the microspores are of the cingulizonate type and belong to the *Lycospora pellucida* Group (Bek 2012). These miospores are typified by having a relatively broad cingulum and zona that can be pitted or perforated. Measurements of holotypes of dispersed species of this group, *in situ* microspores of this type and their parent cones are in Table 1. The microspores can be

equated to the dispersed spore *Lycospora* cf. *pseudoannulata* Kosanke. They differ from the original diagnosis (Kosanke 1950, p. 45) in having a wider and more prominent cingulum.

Microspores macerated from *Lepidostrobus binneyanus* Arber by Thomas (1970) are similar in dimensions and morphology to those described here, but the sculpture of their surfaces is different, i.e. distal surfaces of *L. binneyanus* microspores are laevigate and not microgranulate. *In situ* microspores isolated from *Lepidostrobus fayettevillense* Taylor and Eggert by Taylor and Eggert (1968) and those macerated from *Lepidostrobus barnsleyensis* Thomas by Thomas (1965) differ in prominent perforations of the zona and larger diameter. Microspores described by Hagemann (1966) from *Lepidostrobus* sp. C do not possess pitted or perforated zona. Willard (1989) macerated microspores of this type from cones identified as *Lepidostrobus oldhamius* Williamson (associated with *Lepidophloios harcourtii* Witham), which differ in having a much wider cingulum and zona (10 μm on average). *In situ* microspores from *Lepidostrobus spinosus* Kidston described by Thomas (1965) possess different sculpture, narrow cingulum and wider zona. Microspores from the Permian cone *Azaniodendron fertile* Rayner possesses different sculpture, lack perforations of the zona and were isolated not from mono- but a bisporangiate cone (Rayner 1986).

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