A reassessment of the Pennsylvanian lycophyte cone

*Triplosporite* Brown

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ABSTRACT:


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 lycopsid cone genus *Lepidostrobus* Brongniart was accepted to contain species that were wholly microsporangiate and others that were bisporangiate containing both megsapores 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 cingu-lizone 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 Lepidodostrobus appeared to be in threes and also noted the general acceptance of Brongniart’s (1828–1838) view of Lepidodostrobus 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 microspinose 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.
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.
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. 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 of 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 brownii* (Unger, 1850). A – Transverse section of the cone (No. V.10980c), 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
gulum. Proximal surface laevigate, distal surface microspinulate 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 microspores 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 *Azaniophyllum 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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