



WHY *LYCOSPORA* DOMINATED MANY PENNSYLVANIAN SPORE ASSEMBLAGES

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Abstract: The microspore genus *Lycospora* in its wider sense is produced by both heterosporous cones, *Flemingites*, and homosporous cones *Lepidostrobus*. Calculations are made of the number of microspores that are produced by cones and then by individual Pennsylvanian arborescent lycophytes. The distribution of the rooting rhizophores, *Stigmara* can be extrapolated to a square kilometre of forest. A calculation of the number of spores produced in such a forest is enormous which explains why some dispersed spore floras are dominated by these spores. There are dispersed spore assemblages prepared from coal with high percentages of *Lycospora*. However, the methods of preparation and counting of the spores do not give enough information to make a meaningful calculation of their total numbers in the samples.

Key words: *Lycospora*, arborescent lycophytes, *Flemingites*, *Lepidostrobus*, coal seams, Pennsylvanian

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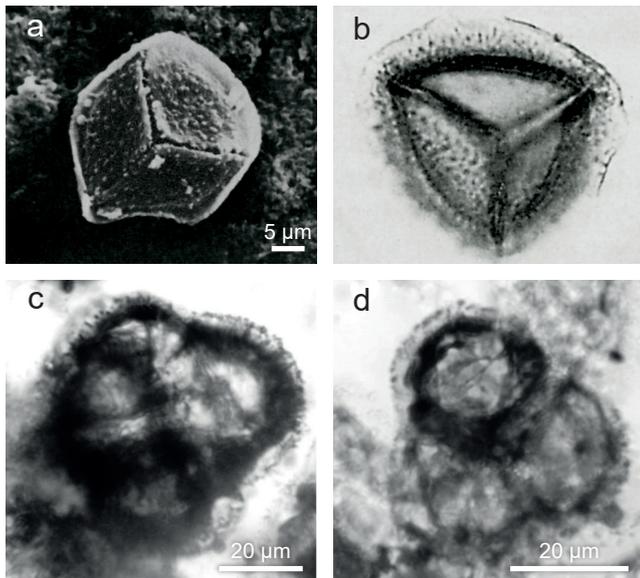
Introduction

The arborescent lycophytes *Lepidodendron* STERNB. and *Lepidophloios* STERNB. grew in the extensive Pennsylvanian swamps where they often dominated the vegetation. The discovery of clusters of their rooting organs, called *Stigmara* BRONGN., suggests that the arborescent lycophytes grew at the same time to form closed forests (McGregor and Walton 1972, Thomas and Seyfullah 2015). The fossilized remains of these lycophytes reveal a diversity of form, with some of them growing up to ca. 45 m in height, with the basal parts of their trunks up to 2 m in diameter (Thomas and Watson 1976, Thomas and Seyfullah 2015). The plants had determinate growth patterns and started life as an unbranched leafy stem that grew vertically and expanded in diameter until it finally branched in a variety of ways to produce either a crown of dichotomizing branches or a series of lateral dichotomizing branches (Thomas 1978, Bateman et al. 1992, DiMichele et al. 2013).

It is of course impossible to know the precise length of time it took arborescent lycophytes to grow and reach fertile maturity. Indeed, it is highly probable that some types of plants became fertile long before others. The autecology of the arborescent lycophytes does however suggest that they were very fast growing trees. This is supported by the economic construction of the stems that had little secondary xylem, the large number of stomata that they possessed, the persistence of the laminae, and the relatively well-illuminated conditions in which the young plants grew (Thomas and

Cleal 2018). Maturity would have been reached in much less time than it takes conifer and angiosperm trees to do so. The large “ulodendroid” scars that are borne by some stems such as *Lepidodendron veltheimii* STERNB. (e.g., Hirmer 1927), *Lepidodendron nathorstii* KIDST. (e.g., Crookall 1966: pl. 67, fig. 1), *Bothrodendron minutifolium* BOULAY (Lindsey 1915) and *Ulodendron majus* LINDL. et HUTTON (Lindley and Hutton 1831) most probably show the positions of abscised branches that may have borne cones. Such a growth pattern would have produced cones while the plant was still growing. Others with a crown of dichotomizing branches would have almost certainly reached full size before becoming fertile with cones on their terminal branches. Ultimately, after the plants reached full size and ceased to produce cones they presumably died and started to decay, otherwise the next generation of plants would have been suppressed through over-crowding and shading.

Descriptions of in situ spores recovered from the fructifications of arborescent lycophytes have been published many times (e.g., Thomas 1970, Thomas and Dytko 1980, Thomas et al. 2009, Drábková et al. 2004, Bek and Opluštil 2006, Bek et al. 2008, 2009a, b, Opluštil and Bek 2009, Bek 2012, 2013, 2017, Thomas and Bek 2014). Some arborescent lycophytes, such as *Lepidodendron* STERNB. produced bisporangiate cones, called *Flemingites* CARRUTH. (emended by Brack-Hanes and Thomas 1983), that contained *Microspinosporites* BEK microspores and *Lagenicula* (BENNIE et KIDST.) R.POTONIE et KREMP / *Lagenosporites* R.POTONIE et KREMP megaspores. Others,



Text-fig. 1. *Lycospora*. **a:** Microspore from the bisporangiate cone *Flemingites gracilis* CARRUTH. (from Brack-Hanes and Thomas 1983). This type of microspore should be referred to *Microspinosporites* BEK. **b:** Flanged microspore from the microsporangiate cone *Lepidostrobus binneyanus* A.ARBUR (from Thomas 1970), same magnification as in (a). **c, d:** Microspores from the microsporangiate cone *Lepidostrobus brownii* (UNGER) SCHIMP. (from Thomas and Bek 2014).

such as *Lepidophloios* STERNB. produced monosporangiate cones with *Cappasporites* L.L.URB. microspores and *Cystosporites diabolicus* (H.V.SCOTT) A.R.HEMSL. seed-like megaspores in *Achlamydocarpon* SCHUM.-LAMBR. The third type produced monosporangiate cones called *Lepidostrobus* BRONGN. (emended by Brack-Hanes and Thomas 1983) that contained *Lycospora* J.M.SCHOPF, L.R.WILSON et BENTALL (emended by Potonié and Kremp 1954) microspores (Text-fig. 1) and *Cystosporites giganteus* (ZERNDT) J.M.SCHOPF (sensu Dijkstra 1946) seed-like megaspores in *Lepidocarpon* D.H.SCOTT. The sigillarian lycophytes cones called *Sigillariostrobus* (SCHIMP.) FEISTM. were monosporangiate with either had *Crassispora* D.C.BHARDWAJ microspores or *Laevigatisporites* R.POTONIÉ et GELLETICH / *Tuberculatisporites* A.C.IBRAHIM megaspores. The bisporangiate cone *Thomasostrobus* OPLUŠTIL, BEK et DRÁBKOVÁ contained *Cadispera* KOSANKE microspores and *Sublagenicula* PIÉRART megaspores. The major problem is that there has been no distinction between *Lycospora* and *Microspinosporites* in the literature so for the purposes of this paper all comments and calculation refer to *Lycospora*.

Schopf et al. (1944), Potonié and Kremp (1954) and Somers et al. (1972) mentioned a great number of *Lycospora* species including holotypes. Microspores, known to have come from arborescent lycophytes, can be prepared both from coal seams, where they can be related to the coal petrology (Smith 1962, 1964, 1968, Kosanke 1988), and from sediments associated with the coals (e.g., Alpern 1963, Peppers 1964, 1997, Dimitrova et al. 2005, 2010).

The knowledge of the affinities of these fructifications makes it possible to suggest palaeoecological interpretations from the microspore assemblages (Thomas and Dimitrova 2017).

Calculations of in situ *Lycospora* produced by forests of arborescent lycophytes

Even though there are many accounts of arborescent cones and their spores, as yet there has been no attempt to estimate the number of spores that were released from these plants. In studying museum collection specimens and published figures of branching, the dichotomies on average appear to reduce the diameters of the stems to approximately 55 % of the original size. Accepting that the vertical stem tapered upwards, the diameter of the terminal part of the main trunk would have been approximately one meter in diameter. It would take 10 dichotomies to reduce the diameter to about 2.5 mm, which is the approximate size of the terminal shoots (Text-fig. 2). This calculation involving reductions in diameter would result in approximately 1,000 terminal branches on a mature tree. Studies of the plant assemblages at Brymbo, North Wales (Thomas et al. 2020) revealed that the number of small leafy shoots bearing terminal cones (Text-fig. 3) is less than the number of similar sized shoots not bearing terminal cones. This suggests that either cones had been dehisced from the terminal shoots or not all the shoots produced cones. If it is the latter, it is possible that only the outermost shoots produced cones. So, assuming a low number of shoots with terminal cones to be approximately 45 % of the total, it would mean that a plant produced approximately 450 cones.



Text-fig. 2. Dichotomising terminal shoots of *Lepidodendron ophiurus* BRONGN. from Brymbo (bed C4). No 2013.43G.147 (National Museum of Wales) (from Thomas et al. 2019).



Text-fig. 3. Terminal cone attached to *Lepidodendron ophiurus* BRONGN., leafy shoot. No. 2013.43G.120 (National Museum of Wales).

Cones vary considerably in size, but an average length of a bisporangiate cone, referable to *Flemingites* CARRUTH., is about 130 mm long in which the lower 1/3 is megasporangiate and the upper 2/3 microsporangiate. With 13 fertile sporophylls per whorl (see Thomas and Bek 2014) this would suggest approximately 150 microsporangia in an average sized cone. In microsporangiate cones, referable to *Lepidostrobus* BRONGN., the number would be higher and of the order of 190.

Calculating the number of microspores in a microsporangium is difficult. Microspores develop in tetrads through meiosis and they are often seen in tetrads in cones preserved as petrifications. *Lepidostrobus brownii* SCHIMP. is such a cone and measuring the diameter of tetrads in sections as ca. 50 μm , gives means of determining the number of spores in a single sporangium (fig. 4 from Thomas and Bek 2014). The sporangia are 13 mm long, 7 mm tall and 3 mm wide in the central part but they become smaller distally. Estimating the average internal width and height to be 2/3 of the maximum size gives a volume of $12 \times 4.7 \times 2 = 122 \text{ mm}^3$. Taking the volume of tetrads to be ca. 50 μm^3 and accepting there will be some space between them the estimate of the number of tetrads is 650, which would result in there being 2,600 microspores per sporangium. Taking these numbers it would result in a bisporangiate cone with 150 microsporangia producing about 390,000 microspores, whereas a microsporangiate cone with 190 sporangia would produce about 494,000 microspores. Taking the calculated figure of 450 cones per mature plant, the number of microspores produced by single mature plants would be of the order of 175 million and 222 million respectively.

Some cones of the *Lepidostrobus crassus/sternbergii* type are known to be almost one meter long so the number of *Lycospora* in such a long cone would have been enormous compared to the average size of 10–15 cm and probably being of the order of 5 million. Following the assumptions above, a mature plant with such cones would produce 2,220 million spores.

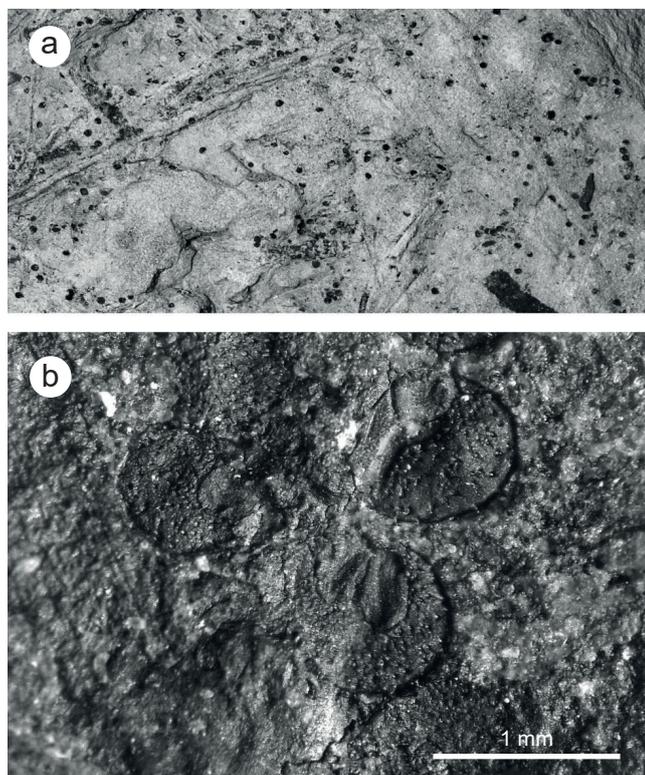
Stands of *Stigmaria* permit an estimation to be made of the abundance of arborescent lycophytes. For example, an extrapolation from the 11 *Stigmaria* in the Glasgow Fossil Grove (see Thomas and Seyfullah 2015) gives an estimate of about 4,500 trees per square kilometre (Gastaldo 1986), thus suggesting a very dense coverage of arborescent lycophytes. Dominance of *Lepidodendron* cannot be assumed over the total area so supposing it to be over two-thirds of the area, the number of microspores from such extensive forests would, therefore, be somewhere in the region of 500,000 million per km^2 (or 5,000,000 million if using the meter-long cones).

Discussion

Given such huge numbers of microspores being produced by the lycophyte forests it is not surprising that some spore assemblages, from coals of Pennsylvanian (especially Westphalian) age, described in the literature are dominated by *Lycospora*. Kremp (1952) suggested an alternation of forest and open moor associations and showed changes in spore content corresponding to changes in coal lithology. He also demonstrated the microscopical evidence of wood in his “forest produced coal” agreeing with the work of Hickling and Marshall (1933), who had described arborescent lycopod bark as only occurring in Carboniferous coals of a similar petrographical kind. Teichmüller (1952) and Teichmüller and Teichmüller (1968) also proposed a relationship between coal lithology and plant assemblages. Smith (1957, 1962, 1964, 1968) refined this spore work to suggest that there were four basic plant communities, which were likely to have been controlled by an interplay of water table and climatic conditions of humidity, rainfall and temperature. His work, supported by that of Habib and Groth (1967), showed that the lycophyte forests, characterised by abundant *Lycospora*, were the first to actively produce peat. This is, of course, consistent with the occurrence of *Stigmaria* in the seat earths below the coal seams. Such forests, which were probably formed in standing water, usually gave way to the more open communities that were richer in species and had many calamites and ferns. It either reverted to lycophyte forest, or less frequently to an open moor type of vegetation dominated by smaller, sub-arborescent lycophytes. This gradual change to the open moor is thought to have been produced by a combination of climatic change and a drying of the peat surface, either by growth above the water table or by a withdrawal of surface water. Any subsequent flooding of the peat surface would have produced a reversion to the lycophyte forest. Smith’s interpretation of plant communities can perhaps be taken a little further. Smith’s transition zone suggests a mixed assemblage, reflecting an open community growing in wet peat rather than open water. Fern spores and *Crassispora* (the microspore of *Sigillaria* BRONGN.) were present, but

there was also *Lycospora* (*Microspiosporites*) *granulate* KOSANKE showing that bisporangiate lepidodendroids (i.e., *Lepidodendron* producing *Flemingites*) were present. Butterworth (1964) illustrated lateral differences in spore floras showing that the lycopod forests were more common and lasted longer in the central areas of the coal measure basins, while the more open moor communities occurred mostly towards the edges of the basins.

There have been a number of published accounts showing that *Lycospora* numbers were very high in many samples. For example, Thomas and Dimitrova (2015) recorded *Lycospora* as 58 % of the total spores and 96.5 % of the lycophyte spores in the roofing shales above the Asturian No. 2 Llantwit Seam in the South Wales Coalfield and 45 % of the total spores and 85 % of the lycophyte spores in the Asturian Brazilly Seam in the Forest of Dean Coalfield. A preliminary study of the North American Coalfields also shows similar occasions when spore assemblages were dominated by *Lycospora*. For example, in the Gilbert Coal (Lower and Upper Benches) of the West Virginia coalfield described by Kosanke (1988) *Lycospora* was 77 % and 85 % of the total spore contents of the Benches. However, Peppers (1964), who used the Kosanke (1950) technique of preparing microspores, explained that only a small portion of the filtered spore residue from each sample was taken for examination. So when Kosanke (1988) counted 200 spores from his 50 g sample of coal it was only a very small percentage of the spores prepared from the samples. If the whole microspore residue had been examined and all the spores counted the number would have been very much larger. It would also have provided a means of comparing the numbers of *Lycospora* produced from the plants to that in the coal.



Text-fig. 4. Dispersed megaspores on the surface of 1,000 mm² of shale at Brymbo (a) with an enlargement showing *Lagenicula horrida* ZERNDT (b).

Conclusion

It is generally accepted that arborescent lepidodendroids dominated much of the Euramerican coal swamps in the early Pennsylvanian and that the number of plants in these forests was huge. From the calculations of the number of cones on mature arborescent lepidodendroids and the number of spores that these cones produced the swamp surface must have been densely covered by *Lycospora*. Under such circumstances it is not surprising that *Lycospora* dominates the spore counts in so many coals. It is however impossible to calculate the total number of *Lycospora* in the coal because of the very limited sizes of the counts. It is also certain that the plants must have produced very large numbers of megaspores and occasionally they are visible on the surface of sediments (Text-fig. 4). Unfortunately, yet there have been no attempts to quantify the numbers of the different genera and species in either coals or sediments.

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